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Native-source climate determines the Douglas-fir potential of adaptation to drought

Authors

Thibaud Chauvin[1][2], Hervé Cochard[2], Vincent Segura[1], Philippe Rozenberg[1]

Affiliations

[1] UMR 0588 BIOFORA, INRA ONF, Orléans, France, F-45075 Cedex 2,
thibaud.chauvin@hotmail.fr

[2] UMR 0547 PIAF, INRA Université Clermont-Auvergne, Clermont-Ferrand, France, F-63100,
herve.cochard@inra.fr

[1] UMR 0588 BIOFORA, INRA ONF, Orléans, France, F-45075 Cedex 2,
vincent.segura@inra.fr,

[1] UMR 0588 BIOFORA, INRA ONF, Orléans, France, F-45075 Cedex 2,
philippe.rozenberg@inra.fr

Corresponding author

Philippe Rozenberg

Summary

Context: Douglas-fir, a fast growing conifer from western North America, recently suffered diebacks following drought in France. We investigated the link between native-source climate and provenance drought resistance in a common garden in France. We compared the adaptive potential of provenances from different parts of the natural area.

Methods: We collected branches from a 25-year-old provenance trial replicated in two test sites in southern France. We estimated provenance variation of cavitation resistance traits, survival and circumference. We compared Washington-Oregon provenances to coastal and interior Californian provenances.

Results: In the common gardens, the hydraulic traits were significantly variable between provenances, with a strong site × provenance interaction, and significantly related to the climate of the natural area and survival. The relationships were different between variables and test-sites. The two test-sites and their particular climatic selective pressure revealed different geographical adaptive structures in the natural area.

Conclusions: Douglas-fir evolutionary adaptation to drought results from natural selection to summer climate and shapes populations for cavitation resistance. In the dryer site only, the Interior California provenances seem more drought resistant. The strong within-provenance variations suggest that there is also a certain within-provenance adaptation potential to drought at the cost of variable mortality rates.

Key words: cavitation resistance; climate change; common garden; evolutionary adaptation; hydraulic traits; phenotypic plasticity; provenance variation; *Pseudotsuga menziesii* (Mirb.) Franco

Introduction

Current and predicted global warming questions the adaptation potential of forest tree species to drought (Allen *et al.*, 2015; Hartmann *et al.*, 2015). Some, such as Douglas-fir, have already suffered declines and diebacks (Sergent *et al.*, 2012). Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco) is a fast growing conifer originating from the western side of the North American continent (Fig. **1**) and has been successfully introduced in France, where it has become the second species planted for reforestation (national inventories carried out by the Ministry of Agriculture and Food). Apparent climatic similarities encouraged breeders to introduce Douglas-fir originating from coastal Washington and Oregon. However, between the 1990s and the 2000s, Douglas-fir diebacks appeared in France due to outstanding summer drought (Sergent *et al.*, 2014). Yet, Douglas-fir faces a very large climatic variation in its vast natural area, ranging from British Columbia to Mexico (Chen *et al.*, 2010). Species covering such a large climatic variation have most probably highly differentiated populations regarding stress resistance (Campbell & Sorensen, 1973). A tree-ring width study revealed a clear north to south latitudinal trend of increasing tolerance to drought with a set of provenances ranging from British Columbia, Canada, to Oregon, USA (Eilmann *et al.*, 2013). In a provenance test covering a large part of the natural area, including both subspecies (the coastal one: *var menziesii* and the interior one: *var glauca*), Sergent *et al.* (2014) observed that *glauca* provenances exhibited a smaller growth reduction to drought than southern menziesii provenances. Montwé *et al.* (2015) noticed that the provenances most resilient to a drought event came from dryer parts of the natural area. Warmer and dryer climates may have shaped Douglas-fir provenances more resistant to drought and hence more adapted to future climatic conditions (Bansal *et al.*, 2015). However, the genetics of drought tolerance have not been studied much yet in Douglas-fir (Moran *et al.*, 2017).

Provenance studies are one of the three main approaches that can be used to investigate the genetic basis of drought tolerance (Moran *et al.*, 2017). In this article, we investigated the variation of drought resistance of provenances originating from California, a part of the Douglas-fir natural area warmer and dryer than Washington-Oregon (Fig. **1** and Table 1). We compared their resistance to drought to that of Washington and Oregon provenances. We worked on replicated Douglas-fir common garden experiments, two provenance trials planted in the south of France (Pineta in Corsica and L'Homol in Gard, insert Fig. **1**, Table 2). Both sites are located in regions with a warmer and dryer climate and a smaller probability of Douglas-fir presence (Boiffin *et al.*, 2017) than in the Douglas-fir introduction area in France. To some extent, these test sites simulate the future climate of the introduction area. Thanks to this experimental trial, we are able to anticipate the behaviour of Oregon and Washington provenances and of putatively more drought resistant Californian provenances in warmer and dryer conditions than those of the current French Douglas-fir introduction area.

The physiological mechanisms underlying a tree's resistance to drought are multiple. For example, foliar nitrogen and carbon metabolism has been shown to be affected by soil water availability but to vary little between interior and coastal Douglas-fir provenances with assumed different drought tolerance (Du *et al.*, 2016, 2018). In a controlled drought experiment, Kleiber et al. (2017) found a clear difference in the terpenoid content of needles between interior and coastal Douglas-fir provenances. However, based also on two coastal and interior provenances, Hess *et al.* (2016) concluded that transcriptome responses to water availability were only weakly affected by local adaptation. Other drought-resistance traits, such as transpiration, water deficit and specific leaf area, show significant provenance variation, with populations originating from dryer climates having greater drought-resistance (Bansal *et al.*, 2015).

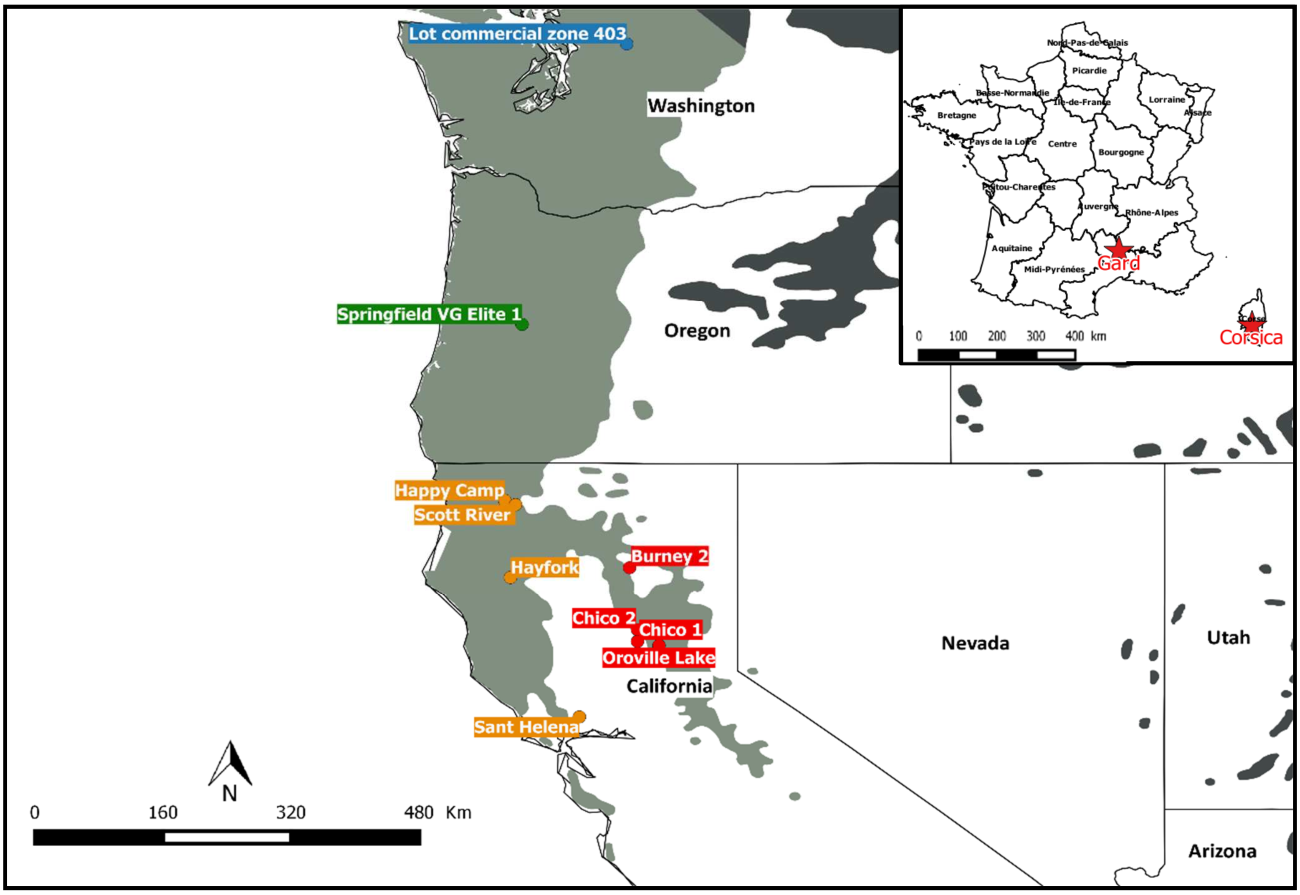

Figure 1: Map of the western coast of USA showing part of the natural range of Douglas-fir (var glauca in dark grey and var menziensii in light grey) and the location of the 10 provenances studied here (white name). Insert : Map showing the location of the two provenance trials in France.

There is increasing evidence that hydraulic traits play an important role in physiological response to drought (Hartmann *et al.*, 2015; Choat *et al.*, 2018). Sap flowing from the roots to the leaves is exposed to a negative pressure. During a strong drought, under a critical pressure threshold, air bubbles enter the xylem conduits, spread, and disrupt the water columns. This phenomenon, called cavitation, directly decreases the hydraulic conductivity of the sapwood (Tyree & Sperry, 1989). The consequence of such a dysfunction ranges from a simple growth diminution to death. The capacity to maintain conductivity during a drought is called cavitation resistance (CR). CR is a complex trait depicting the dynamics of the conductivity loss. In the relevant range of drought intensity, CR is related to survival—the link between CR and survival to drought was found to be statistically significant at the species level for *Fagus sylvatica*, *Populus* sp. and *Quercus sp.* (Barigah *et al.*, 2013; Urli *et al.*, 2013) for angiosperms. For conifers, this relationship was found significant for four *Callitris* species from Oceania (Brodribb *et al.*, 2010) as well as at the population level for *Pinus canariensis* (López *et al.*, 2013). Survival, together with reproductive success, is one of the two components of fitness (Crow & Kimura, 1970). For some species facing drought conditions, CR is therefore an adaptive trait. CR is evaluated in the laboratory by vulnerability curves depicting the percentage loss of conductivity (PLC) as a function of the pressure applied to the xylem (Fig. **2**).

Table 1: Studied provenances and region of origin. The table shows latitude, longitude, and elevation at the place of origin. WA is for Washington, OR for Oregon, COCA for COastal CAlifornia and INCA for INterior California.

Code	**Names**	**State or Region**	**Latitude (°N)**	**Longitude (°W)**	**Elevation (m)**
HAC	Happy Camp	COCA	41.46	-123.24	800
HAY	Hayfork	COCA	40.35	-123.16	1000
SCR	Scott River	COCA	41.40	-123.09	1000
STH	Sant Helena	COCA	38.33	-122.2	570
BUR	Burney 2	INCA	40.49	-121.5	1000
CH1	Chico 1	INCA	39.42	-121.39	900
CH2	Chico 2	INCA	39.59	-121.39	1200
ORL	Oroville Lake	INCA	39.36	-121.09	1100
SV1	Springfield VG Elite 1	OR	44.00	-123	170
403	Commercial lot zone 403	WA	48.06	-121.54	170

To model vulnerability curves from raw data, we fitted a sigmoidal parametric model (Pammenter & Van der Willigen, 1998). This model has two parameters, the P_{50}, the pressure applied to obtain a 50 % loss of conductivity, and the Slope of the curve at the inflexion point.

P_{50} is the trait most often used in CR studies, and the Slope determines the pressure range over which conductivity is lost (Pammenter & Van der Willigen, 1998).

Table 2: Characteristics of experimental plots. Climatic data come from the closest Météo-France weather stations to the trials and are for the 1992 to 2015 period. Summer Rainfall is the sum of rainfall from June to August. MAT is for Mean Annual Temperature, PPT means annual rainfall and PPT_ sm is for the summer rainfall.

Site	Elevation (m)	Exposure	T°min (°C)	T°max (°C)	MAT (°C)	PPT (mm)	PPT_sm (mm)
Corsica	700	NNO	-5.6	31.2	13.0	1263	121
Gard	600 - 680	ONO	-5.8	31.8	12.8	1640	187

While large and significant between-species variation was often found for P_{50} (Delzon *et al.*, 2010; Choat *et al.*, 2012), there is only a small number of studies on between-population variation, and less evidence of significant variation. In *Fagus sylvatica*, *Pinus pinaster* and *Pinus hartwegii*, no significant differences were found between provenances for P_{50} (Cochard *et al.*, 2008; Lamy *et al.*, 2011; Wortemann *et al.*, 2011; Sáenz-Romero *et al.*, 2013). In *Pinus pinaster* Lamy *et al.*, (2011) wrote that "uniform selection has shaped the phenotypic variability of this trait". In *Picea abies*, Chmura *et al.* (2016) found limited genetic variation between families for resistance to embolism. However, other studies found significant intra-specific variation for CR. In a recent *in-situ* study, González-Muñoz *et al.* (2018) found between-provenance variability for P_{50} for four different species (*Betula pendula*, *Populus tremula*, *Picea abies* and *Pinus sylvestris*) across their natural range. P_{50} was found to be significantly different between populations in a common garden experiment for *Pinus pinaster* and *Pinus canariensis* (Corcuera *et al.*, 2011; López *et al.*, 2013). In Douglas-fir, (Domec & Gartner, 2002; Dalla-Salda *et al.*, 2014) found significant variation between a limited number of genetic entities (clones, families, and provenances) from the Washington-Oregon coastal area. Such contradictory results could be explained by a low genetic variation in some species or in the studied sample, or by a low statistical power, unable to reveal existing variation. In this study, compared to previous ones, we increased the number of samples to increase the statistical power of the analysis. We measured CR on two branches per tree on 20 trees per provenance for ten provenances in each site, resulting in, to our knowledge, the largest CR dataset for Douglas-fir so far.

The relationship with survival provides information about the adaptive value of the traits. A significant between-provenance variation is interpreted as the result of past evolutionary adaptation in the Douglas-fir natural range, leading to local adaptation (Kawecki & Ebert, 2004; Savolainen *et al.*, 2007). CR resistance is known to be related to wood density in Douglas-fir (Dalla-Salda *et al.*, 2011), and Nabais *et al.* (2018) have shown that Douglas-fir was among 10 forest tree species for which wood density variation in provenance trials was affected by native-source climate. Recent inter-specific studies found a link between hydraulic features and the species native-source climate (Bourne *et al.*, 2017; Li *et al.*, 2018). In this article, we investigate this link at the intra-specific level in Douglas-fir.

Together with genetic adaptation, phenotypic plasticity is an important response mechanism to new environmental conditions (Aitken *et al.*, 2008). Trees are sessile long-lived organisms, while global warming is fast. Phenotypic plasticity precedes evolutionary adaptation and thus has a particular significance in the climate change context. Vulnerability curves represent a phenotypic variable (PLC) as a function of an environmental variable reflecting drought intensity, the xylem applied pressure. Thus, by definition (DeWitt & Scheiner, 2004), the vulnerability curves are *de facto* reaction norms estimating the phenotypic plasticity of conductivity loss in function of a proxy of drought intensity. Hence, while studying CR, we study not only this trait genetic variation but also the genetic variation of the phenotypic plasticity of the conductivity loss.

In this article, we investigate the ability of Douglas-fir to adapt to a new climatic condition in the general context of evolutionary adaptation and phenotypic plasticity through three main hypotheses. First, we hypothesize that there is a relationship between the climatic variation in the natural area and the variation of CR in the provenance trials. Second, we hypothesize that CR traits are adaptive traits related to the survival component of fitness, and are variable between provenances. Third, we hypothesize that the Californian provenances are more adapted to the climate of Gard and Corsica than the Washington and Oregon provenances.

Materials and methods

Plant material, experimental design and sampling strategy

The study is buttressed by a provenance trials established 25 years ago (1992) and replicated at two test sites in the south of France, one in the Gard (44°18'N, 3°59'E) and the other in Corsica (41°57N, 9°00'E) (insert Fig. **1**, Table 1). Twenty-eight Douglas-fir provenances (only the *var menziesii*) from three US states (Washington, Oregon and California) were planted. California provenances come from two regions: coastal California (COCA) and internal California (INCA). The trial is a randomized single-block design with 68 and 60 blocks in Gard and Corsica, respectively, which means that the 28 provenances are represented in each block. The 2014 inventory of these well-maintained trial gave us an estimate of the survival rate (SR). In 2016, we measured the circumference at breast height of all the trees (Ci_{16}).

We measured CR on a subsample of ten provenances (one from Washington, one from Oregon and eight from California) (Fig. **1**, Table 2).

The Californian provenances were selected to be representative of the native-source climate of all the Californian provenances available in the trial. We used the online interactive platform ClimateNA_MAP (Wang *et al.*, 2016) to obtain monthly climatic data of the natural area of the provenances: mean temperature, sum of precipitation and mean relative humidity. We selected the random subsample of eight Californian provenances that minimize the difference between the subsample and the entire provenance set (variance and mean).

We sampled the trials during late spring and early summer 2016 to obtain a new-formed-ring without native embolism (from May 23 to 27 in Corsica and from June 27 to July 1st in Gard). We sampled south-exposed branches from a given whorl. We took the sample in the 2014 growth-unit to measure CR on the same rings (2014 to 2016) throughout all samples. The sample length was at least 30 cm, with a maximum diameter of one centimetre. We collected two branches per tree and 20 trees per provenance out of the 10 selected provenances on each site for a total of 800 branches. We immediately wrapped the collected branches into soaked cloth and then put them into a black and opaque plastic bag to prevent dehydration. We rapidly transported and stored the samples at 3-4°C, and we measured CR within three weeks of collection.

Cavitation resistance measurements

We built xylem vulnerability curves (VCs) using the centrifugation-induced method or Cavitron technique (Cochard, 2002; Cochard *et al.*, 2005). The aim here is to use centrifugal force to induced a negative pressure in the xylem to simulate drought.

All samples were re-cut under water to a standard length of 28 cm, bark was removed, and both ends were trimmed with a fresh razor blade to obtain perfectly smooth surfaces. A solution of ultrapure and degassed water including 10 mM KCl and 1 mM $CaCl_2$ was used as the reference solution for hydraulic measurements. After measuring maximum hydraulic conductance (Kmax) under high xylem pressure (i.e., -0.5 MPa), centrifuge rotation speed was gradually increased to determine the percentage loss of hydraulic conductance (PLC in %). CAVI_SOFT software (version 5.0, University of Bordeaux) was used to measure conductance and compute the vulnerability curves. According to Pammenter and Van der Willigen (1998), a sigmoid function was fitted on the VCs using the following equation:

$$PLC = \frac{1}{(1+exp(\frac{Sl}{25} \times (Pi - P50))}, \qquad (1)$$

where P_i (MPa) is the xylem pressure at speed *i*, P_{50} (MPa) is the xylem pressure at which there is 50 % loss of conductivity, and Sl (% MPa^{-1}) is the Slope of the tangential line at the P_{50} (indicator for the pressure range over which maximum embolism development occurs in the branch). Sl is a dynamic character enabling the evaluation of the phenotypic plasticity of conductivity loss.

We used the VC sigmoid models to extract two more variables from the vulnerability curves: P_{12} and P_{88}; they characterize the beginning (P_{12}, pressure corresponding to early, low conductivity loss under moderate hydric stress) and the end (P_{88}, pressure corresponding to late and high conductivity loss under severe hydric stress) of the vulnerability curves (Fig. 2). In addition, we calculated the xylem specific hydraulic conductivity, Ks ($kg.s^{-1}.m^{-2}.MPa^{-1}$), using the equation hereafter:

$$Ks = \frac{Kmax}{S} \times L, \qquad (2)$$

where Kmax is the maximum hydraulic conductance ($kg.s^{-1}.MPa^{-1}$), S is the basal area of the measured branch, and L is its length (standardized by the length of the rotor: 28 cm).

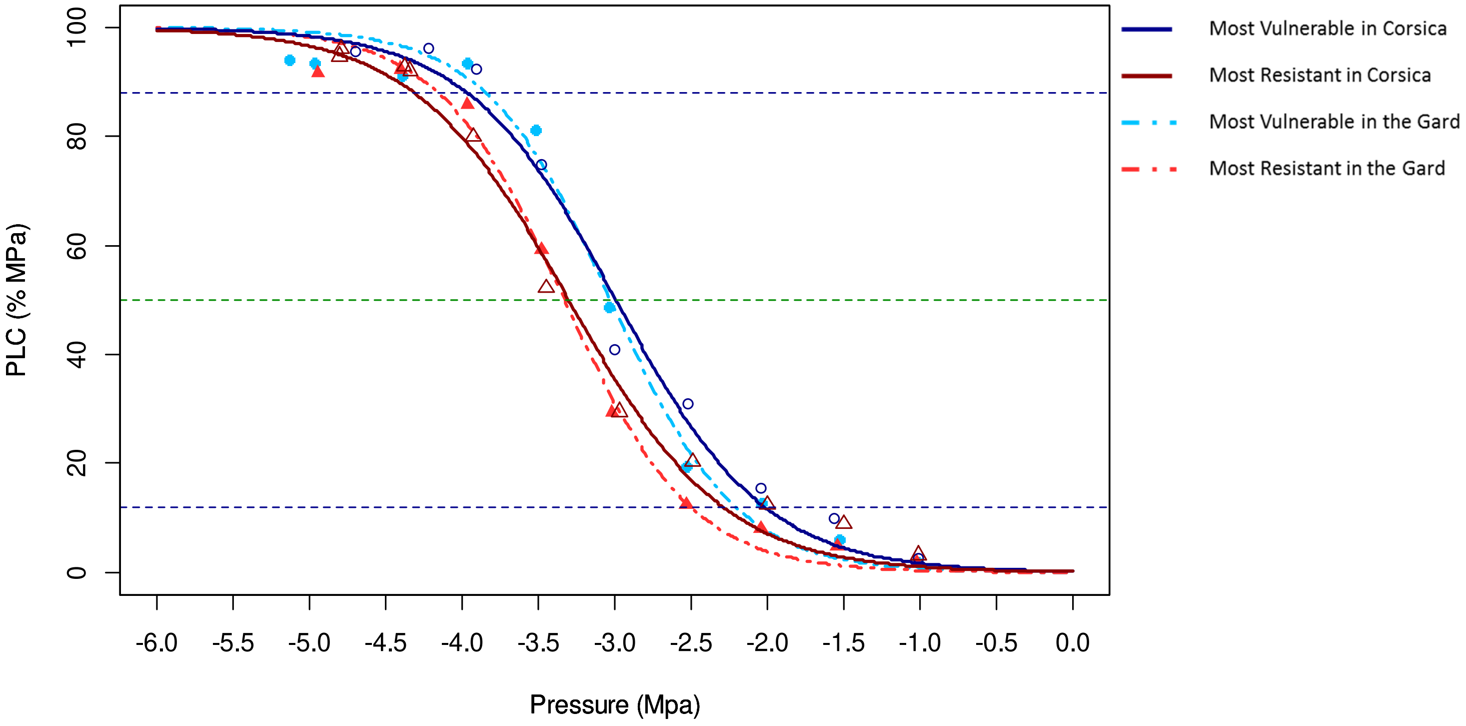

Figure 2: Vulnerability curves of the most resistant and the most vulnerable provenance in each site. Open circles and triangles are the measured data for Corsica and full circles and triangles are for Gard. The lines (solid lines and dotted for Corsica and Gard respectively) represent the fitted models.

Statistical analyses

All statistical analyses were performed at the provenance level using R software (R Development Core Team, 2013, version 3.4.1).

We analysed the data with two successive PCAs, PCA_Geo/clim and PCA_Pheno. We used the "FactoMineR" package (Lê *et al.*, 2008). The first PCA, PCA_Geo/clim, explains the provenance variation with the climatic and geographic variables (elevation, latitude, longitude, summer rainfall (PPT_sm), annual mean temperature (MAT) and annual mean relative humidity (RH)) in the natural range of the provenances. The second PCA, PCA_Pheno, explains provenance variation using the phenotypic variables (SR, Ks, Slope, P12, P50, P88, and Ci16) measured in the two trials of the common garden experiment. We compared separated PCAs for each trial with a grouped PCA and found this one graphically more efficient. We further used the first principal components of PCA_Geo/clim as quantitative continuous covariables to be associated to the discrete provenance factor in the analysis of variance: $PC1_{Geo/clim}, PC2_{Geo/clim}, PC3_{Geo/clim}$ and $Prov$.

PCA_Pheno depicts the network of relationships between provenance phenotypic variation in the common garden trials. Both PCAs provide information about the links between the hydraulic properties and the climatic features of the provenances in the natural area.

There was no significant intra-tree difference between branches for any hydraulic trait, thus we averaged the two branch values. Intra-specific variation for each cavitation trait was determined with a linear mixed model using the residual maximum likelihood option (REML) included in the "lme4" package (Bates et al., 2015.). A first global model including both trials was setup as

$$y = \mu + Bloc : Site + Site + Prov \times Site + PC1_{Geo/clim} + PC2_{Geo/clim} + PC3_{Geo/clim} + Prov + \varepsilon, \qquad (2)$$

where y is the phenotypic value at the individual level; μ is the overall mean; $Bloc : Site$ is a fixed bloc effect nested in $Site$. $Site$ is a fixed trial effect; $Prov \times Site$ is the interaction between the trial and provenances effects. $PC1_{Geo/clim}$, $PC2_{Geo/clim}$ and $PC3_{Geo/clim}$ are random effects of the 3 first principal components of PCA_Geo/Clim; and $Prov$ is a random effect of provenance to account for the climate and geographic effects that are not accounted for by the principal components of PCA_Geo/clim. We selected the best model using the Akaike Information Criterion (AIC).

As the interaction between *Prov* and *Site* was significant for most of the variables, we split up the model at the site level:

$$y = \mu + Bloc + PC1_{Geo/clim} + PC2_{Geo/clim} + PC3_{Geo/clim} + Prov + \varepsilon. \qquad (3)$$

We assessed the significance of the pairwise differences between the provenances and the sites via the TukeyHSD (Honest Significant Differences) test for phenotypic values except for SR. To assess the between-provenance differences for survival rate (SR), we compared generalized linear model (GLM) at the tree level based on a logit function with likelihood ratio test in each site.

To compare the observed variation for the different variables in both provenance trials, we calculated and compared two statistics: i) the coefficient of variation (CV), and ii) the coefficient of quartile variation (CQV) (Zwillinger & Kokoska, 2000) using equation (4):

$$CQV(x) = \frac{|(Q3(x) - Q1(x))|}{|(Q3(x) + Q1(x))|} \times 100, \qquad (4)$$

where Q1 and Q3 are the first and third quartiles of the trait considered (x). CQV is a more robust index than CV for datasets involving log-transformed data or isotopic measurements (Brendel, 2014; Canchola *et al.*, 2017). There are concerns about the validity of the coefficient of variation for variables estimated using non-linear models (Brendel, 2014; Canchola *et al.*, 2017). The CQV is another way to quantify and compare the variability of traits with a non-linear model, such as P_{50} and Slope. Finally, we found very similar trends between CV and CQV, and we decided to present only the results obtained with CQV.

Results

Relationships between the climatic variation in the natural area and the phenotypic variation in the provenance trials

The relationships between the provenance geographic distribution and the climate in the Douglas-fir natural area is described by the geographic and climatic principal component analysis (PCA_Geo/Clim, Fig. **3**). The first three principal components of PCA_Geo/Clim explain 95.4 % of the total variance (PC1 = 60.4 %, PC2 = 21.4 %, PC3 = 13.6 %; Fig. **3**). PC1 is mainly positively associated with latitude, summer rainfall (PPT_sm) and relative humidity (RH) and negatively associated with elevation and temperature (MAT) (Table 3). PC2 is chiefly associated with longitude (47 %) and then with MAT and RH (17.9 and 20.9 %, Supporting Information, Table S1). PC3 is associated with Longitude, MAT and RH (Supporting Information, Table S1). PC1 principally separates the Californian provenances from the Oregon and Washington ones. According to PC1, the northern low elevation Washington provenance is located in the coldest and wettest region, while the Southern high elevation Californian provenances are in the warmest and driest part of the sampled area (Fig. **3**). The Oregon provenance is intermediate. PC2 separates WA (Washington) from OR (Oregon), and INCA (Internal California) from COCA (Coastal California). The Eastern WA and INCA provenances are from relatively colder regions with a higher RH than the further west OR and COCA provenances. The Easternmost INCA provenance BUR appears to be in an even colder zone with lower relative humidity. Fig. **3(b)** confirms that BUR comes from a particularly cold and dry zone, while the COCA provenance STH originates from an especially warm and humid area.

Table 3 presents the correlation coefficients calculated between the climatic variables in the natural area and the phenotypic variables in the two experimental sites in France. The relationships are different according to the test sites. In Corsica, the strongest relationship is between Ks and PPT_sm and is negative ($r = -0.73$, $P < 0.05$; Table 3), while in Gard, the strongest relationship is between Slope and PPT_sm and is positive ($r = 0.95$, $P < 0.001$; Table 3).

Table 3: Spearman's rank correlation coefficient at the provenance level between studied variables and significant values ($p < 0.05$; ** $p < 0.01$; *** $p < 0.001$). The upper diagonal of the table is for the Gard trial while the lower diagonal corresponds to the Corsica trial.*

	Ks	**P12**	**P50**	**P88**	**MAT**	**RH**	**PPT_sm**	**Slope**	**Survival**	**Ci16**
Ks	X	-0.09	-0.07	-0.22	0.39	-0.22	-0.21	-0.35	-0.24	-0.33
P12	-0.15	X	**0.81** **	0.59	0.01	0.38	-0.04	0.13	-0.53	0.25
P50	-0.10	**0.83** **	X	**0.93** ***	-0.45	0.37	0.49	**0.64** *	**-0.75** *	-0.04
P88	-0.20	0.33	**0.72** *	X	**-0.64** *	0.46	**0.68** *	**0.84** **	**-0.71** *	-0.13
MAT	0.61	0.43	0.19	-0.22	X	-0.15	**-0.89** ***	**-0.88** ***	0.16	0.09
RH	-0.35	-0.03	-0.06	0.35	-0.15	X	0.29	0.36	-0.35	0.38
PPT_sm	**-0.73** *	-0.31	-0.10	0.28	**-0.89** ***	0.29	X	**0.95** ***	-0.37	-0.05
Slope	-0.21	-0.47	-0.05	0.60	**-0.65** *	0.53	**0.64** *	X	-0.48	-0.12
Survival	**0.82** **	-0.09	0.07	-0.20	0.46	-0.59	-0.56	-0.26	X	0.41
Ci16	0.24	0.31	-0.04	-0.22	0.52	-0.02	-0.54	-0.49	-0.22	X

Table 4: Mean and confidence interval values of the studied traits for the ten provenances (mean ± confidence interval). Corresponding graphics are available in the supplementary data.

Code	State or Region	Ks		P12		P50		P88		Slope	
		Corsica	Gard	Corsica	Gard	Corsica	Gard	Corsica	Gard	Corsica	Gard
HAC	COCA	0.30 ± 0.025	0.37 ± 0.032	-2.20 ± 0.22	-2.52 ± 0.13	-3.06 ± 0.12	-3.15 ± 0.09	-3.92 ± 0.1	-3.79 ± 0.11	67.66 ± 8.85	91.81 ± 12.30
HAY	COCA	0.28 ± 0.021	0.29 ± 0.019	-2.29 ± 0.21	-2.62 ± 0.10	-3.17 ± 0.10	-3.25 ± 0.07	-4.04 ± 0.11	-3.88 ± 0.11	64.57 ± 8.38	91.31 ± 12.13
SCR	COCA	0.30 ± 0.026	0.23 ± 0.020	-2.16 ± 0.17	-2.31 ± 0.17	-2.97 ± 0.08	-3.00 ± 0.08	-3.79 ± 0.11	-3.69 ± 0.13	74.86 ± 13.63	93.76 ± 14.87
STH	COCA	0.36 ± 0.022	0.30 ± 0.019	-2.30 ± 0.16	-2.57 ± 0.11	-3.08 ± 0.09	-3.27 ± 0.08	-3.86 ± 0.09	-3.97 ± 0.12	73.98 ± 10.67	80.23 ± 10.27
BUR	INCA	0.36 ± 0.023	0.30 ± 0.018	-2.54 ± 0.11	-2.64 ± 0.12	-3.21 ± 0.07	-3.24 ± 0.09	-3.88 ± 0.09	-3.84 ± 0.10	84.04 ± 10.90	93.37 ± 11.11
CH1	INCA	0.31 ± 0.030	0.35 ± 0.027	-2.32 ± 0.18	-2.66 ± 0.14	-3.22 ± 0.11	-3.30 ± 0.08	-4.12 ± 0.16	-3.94 ± 0.10	63.96 ± 8.92	88.44 ± 10.48
CH2	INCA	0.35 ± 0.022	0.34 ± 0.022	-2.38 ± 0.18	-2.66 ± 0.15	-3.22 ± 0.09	-3.34 ± 0.11	-4.05 ± 0.08	-4.02 ± 0.16	67.87 ± 8.24	85.05 ± 10.19
ORL	INCA	0.37 ± 0.026	0.34 ± 0.018	-2.45 ± 0.14	-2.52 ± 0.13	-3.34 ± 0.08	-3.18 ± 0.09	-4.23 ± 0.14	-3.84 ± 0.12	65.36 ± 9.18	87.70 ± 13.02
SV1	OR	0.26 ± 0.028	0.33 ± 0.019	-2.44 ± 0.22	-2.61 ± 0.11	-3.22 ± 0.11	-3.16 ± 0.07	-4.01 ± 0.12	-3.70 ± 0.09	78.69 ± 13.35	102.64 ± 12.14
403	WA	0.28 ± 0.018	0.33 ± 0.043	-2.55 ± 0.18	-2.63 ± 0.14	-3.24 ± 0.07	-3.19 ± 0.10	-3.94 ± 0.11	-3.76 ± 0.13	96.39 ± 19.49	104.29 ± 15.48

Code	State or Region	Survival		Ci16	
		Corsica	Gard	Corsica	Gard
HAC	COCA	0.67 ± 0.12	0.70 ± 0.17	432.79 ± 42.91	836.02 ± 36.34
HAY	COCA	0.62 ± 0.13	0.89 ± 0.10	438.50 ± 59.01	839.89 ± 39.03
SCR	COCA	0.61 ± 0.13	0.71 ± 0.15	462.14 ± 49.83	822.92 ± 39.82
STH	COCA	0.67 ± 0.12	0.83 ± 0.11	455.57 ± 42.82	957.23 ± 37.39
BUR	INCA	0.71 ± 0.12	0.82 ± 0.14	405.06 ± 41.25	811.29 ± 46.49
CH1	INCA	0.64 ± 0.13	0.79 ± 0.13	483.64 ± 59.95	809.56 ± 41.05
CH2	INCA	0.74 ± 0.12	0.85 ± 0.12	435.69 ± 48.02	829.70 ± 47.26
ORL	INCA	0.69 ± 0.12	0.74 ± 0.14	460.91 ± 45.00	803.47 ± 40.30
SV1	OR	0.48 ± 0.13	0.80 ± 0.13	433.52 ± 30.56	839.57 ± 37.76
403	WA	0.48 ± 0.13	0.71 ± 0.16	437.03 ± 38.15	812.19 ± 37.85

Relationships with SR (survival) and provenance variation

SR is significantly different between sites, and between provenances only in Corsica. We found the lowest SR in Corsica (average values 63 % ± 0.4 in Corsica vs 78 % ± 0.3 in Gard, minimum values 48 % for WA and OR provenances in Corsica, Table 4).

Table 3 shows the relationships between SR and the hydraulic traits within each site. In Corsica, there is one significant positive correlation between SR and maximum specific conductivity (Ks, r = 0.82) (Fig. **4a**). In Gard, SR is significantly and negatively related to P_{50} and P_{88} (r = -0.75 and -0.71, respectively) (Table 5 and Fig. **4b**).

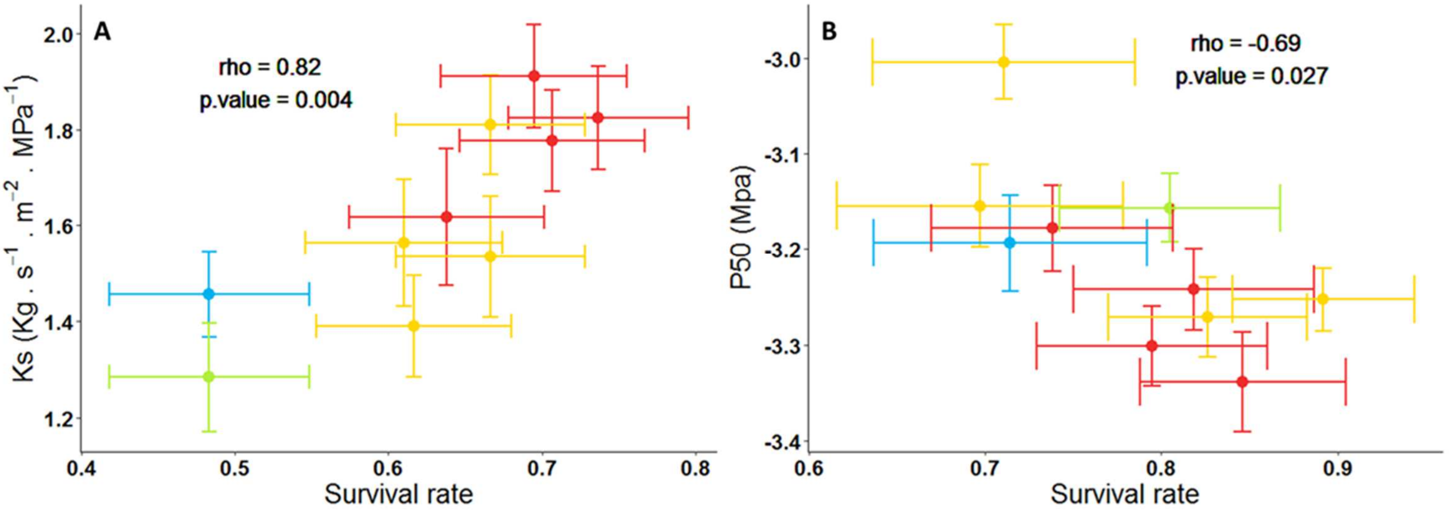

Figure 3: Graph showing the relationship between survival and (A) Xylem specific hydraulic conductivity (Ks) in Corsica and (B) pressure causing 50% loss of conductance (P50) in Gard. Error bars are standard error.

The results presented in Table 5 show the relationships between the first, second and third principal components of PCA_Geo/clim and the provenance factor, as well as the phenotypic variables measured in the common garden experiments.

The results show that the combinations of significant and non-significant effects are globally different between variables and sites. Only one variable shows no significant effect in one site only: circumference in Corsica. Circumference is the only trait that is independent from all the other traits in both sites (Table 3). Two variables have the same significant effects in Corsica and Gard: Slope and P_{50}. Slope has one significant effect in both sites, PC1, while P_{50} has three: PC2, PC3 and Provenance. Different combinations of the explanatory covariables and factors, according to the variable and the site, significantly affect all other variables. One of the PC1, PC2 and Provenance factor significantly explains Slope in both sites, P12 and P88 in Corsica and Ks in Gard.

Table 5: Significance of the effect of the PCA_Geo/Clim axes and the provenance factor on the variance of the phenotypic variables (likelihood ratio test of linear mixed model (3)).

Variables	Site	PC1_Geo/Clim	PC2_Geo/clim	PC3_Geo/clim	Provenance	R^2
P12	Corsica	*NS*	0.0013	*NS*	*NS*	0.031
P50		*NS*	3.41E-05	0.011	0.0028	0.096
P88		*NS*	*NS*	0.006	2.13E-05	0.10
Ks		0.0009	0.0225	*0.0228*	*NS*	0.052
Slope		3.13E-05	*NS*	*NS*	*NS*	0.052
Ci16		*NS*	*NS*	*NS*	*NS*	0
Survival		0.00351	*NS*	*NS*	*NS*	0.031
P12	Gard	*NS*	0.0340	*NS*	0.0070	0.042
P50		*NS*	0.0200	0.0099	1.29E-05	0.094
P88		0.0011	*NS*	0.0113	0.0072	0.061
Ks		*NS*	*NS*	*NS*	0.0002	0.056
Slope		0.0036	*NS*	*NS*	*NS*	0.008
Ci16		*NS*	0.0001	0.0339	0.0001	0.095
Survival		*NS*	*NS*	*NS*	0.0191	0.022

Table 6: Intra-specific coefficient of variation. N =200 and 193 in Corsica and Gard, respectively.

	CQV (%)	
	Corsica	Gard
SR	20.8	12.3
Ks	80.9	72.3
Ci16	47.5	28.3
P12	48.3	33.8
P50	18.9	16.2
P88	17	17.7
Slope	68.5	62.8

Phenotypic variation

Table 6 presents the coefficients of variation of the phenotypic variables (Ks, SR, Ci_{16}, P_{12}, P_{50} and P_{88} and Slope). The highest value is for Ks (CQV_{Ks} = 80.9 % and 72.3 % in Corsica and Gard, respectively; Table 6), whereas the lowest value is for P_{88} and P_{50} in Corsica and Gard, respectively (Table 6). In Corsica, the variability is greater for all the variables except P_{88}.

The phenotypic principal component analysis (PCA_Pheno, Fig. **5**) describes the relationships between the provenances and the phenotypic variables measured in both experimental trials. The first three principal components of PCA_Pheno explain 88.7 % of the total variance (PC1 = 45.4 %, PC2 = 30 %, PC3 = 13.3 %; Fig. **5**). PC1 is mainly positively related with Circumference (Ci_{16}), Slope and SR and negatively associated to P_{12} (Supporting Information, Table S2). PC2 is mainly positively linked to P_{88} and P_{50} and marginally with Ks (Supporting Information, Table S2). PC3 is built principally around Ks, then SR and P_{50}. PC1 best explains the differences between the two experimental sites (Fig. **5**). In Gard, the provenances have a bigger circumference, survive better and are more resistant to the initiation of cavitation with a steeper Slope than in Corsica (Fig. **2** and Table 4). PC2 highlights the intra-site between-provenance variation, especially in Corsica. In Corsica, PC2 separates the INCA provenances with high P_{50} and P_{88} from the COCA, while OR and WA coincide with the COCA provenances (Fig. **5**, Top). Still in Corsica, WA and BUR from INCA are isolated from the other provenances and less distant from Gard provenances along PC1 (Fig. **5**). In Gard, the provenances are more grouped than in Corsica, except for one provenance from COCA, SCR,

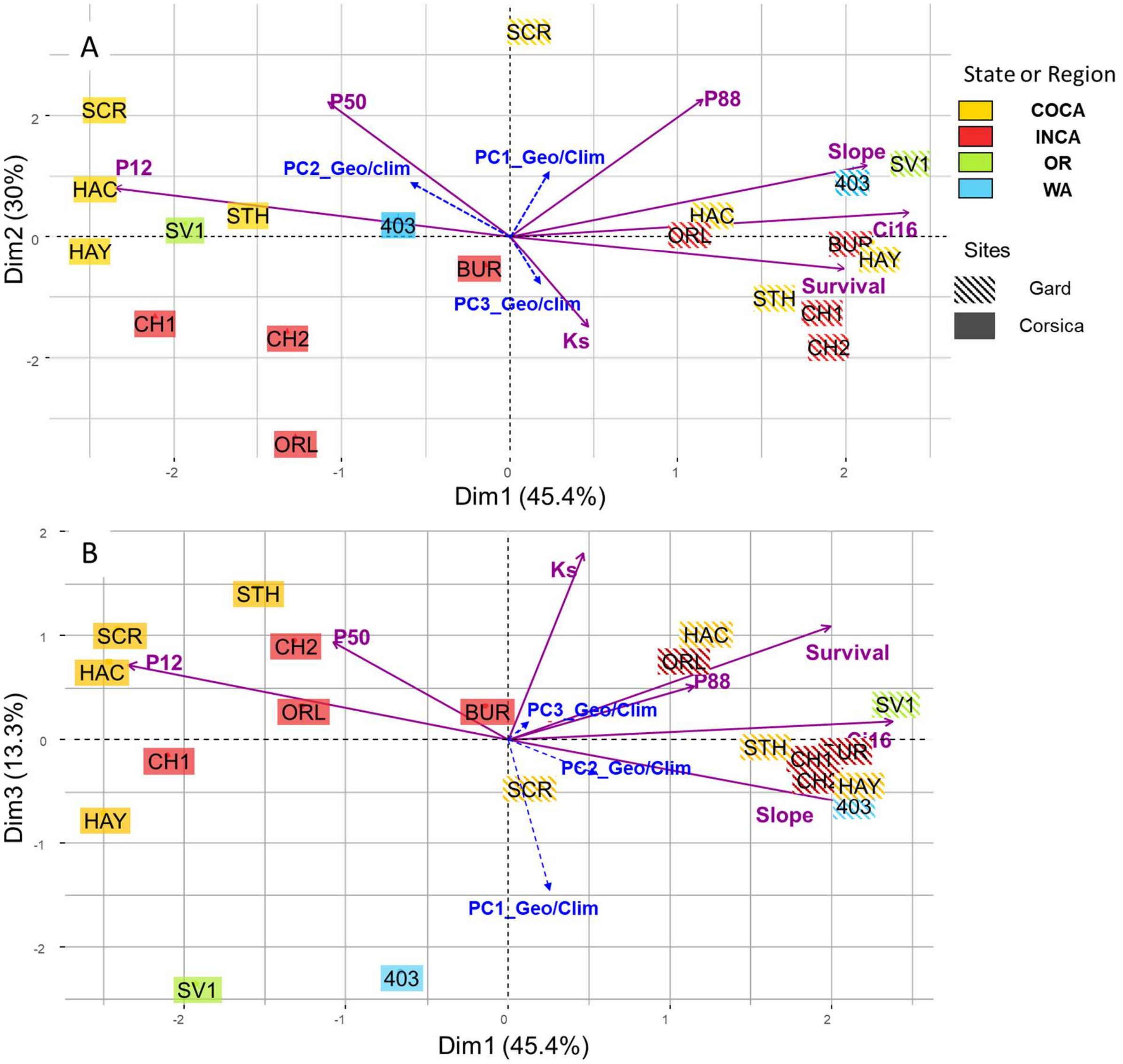

Figure 3: A: First two axes of the PCA_Geo/clim. PC1 represents 60.4 % and PC2 21.4 % of the total variation. B: Second and third axes of the PCA_Geo_Clim. PC3 represent 13.6 % of the total variation. The purple arrows represent the contribution of the explanatory variables.

which is completely separated with high P_{12}, P_{50} and P_{88} values (Fig. **5**). In Corsica, the same SCR provenance also has the highest P_{50} and P_{88} values and among the highest P_{12} values.

Discussion

Adaptation and natural selection in the natural area

The PCA_Geo/Clim synthesized the provenance geographic and climatic information. As expected, they show that the Washington and Oregon provenances are the wettest and coldest origins of the study and that annual mean temperature, to some extent, and relative humidity overall, discriminate the interior and the coastal parts of California. They also show that there is substantial climatic variation within these two regions. More importantly, they reduce the number of environmental variables to a lower number of independent principal components (PCs) quantitatively depicting a part of the provenance environmental variation.

The phenotypes we observe in the common gardens result from the evolutionary history of Douglas-fir in its natural range. In temperate climates, summer is the warmest and driest period of the year and the most stressful time for trees' hydraulic functioning. Annual mean temperature and rainfall from June to August in the natural area significantly explain the variation of several of the provenance hydraulic traits in the common gardens. The lower survival rate in Corsica (63 % vs 78 % in Gard) shows that overall growing conditions are more favourable in Gard than in Corsica, especially for the Washington-Oregon provenances (Table 4). Annual average temperature is very similar (12.8°C and 13.0°C in Gard and Corsica, respectively), while annual precipitation is 1640 mm in Gard and 1263 mm in Corsica. The even greater rainfall difference in summer, 187 and 121 mm in Gard and Corsica, respectively, and the corresponding difference in the mortality rate suggest that summer precipitation is a key selective pressure in the test sites. Similar impact of precipitation has already been noted on *Pinus edulis* (Grossiord *et al.*, 2017). This is consistent with the significant correlation found between native-source summer precipitation and Ks in Corsica, P88 in Gard and Slope in both test-sites. These correlations show that populations coming from warmer and/or more arid regions tend to have a higher resistance to drought. Similar combined influence of climatic conditions in the test sites and of long-term genetic differentiation on drought-resistance was also observed on Douglas-fir by Bansal *et al.* (2015) with other drought-resistance traits. The relationships found in Gard between P88 and mean annual temperature and summer precipitation (Table 3) are in accordance with results reported by López *et al.* (2013) for *Pinus canariensis* populations coming from an aridity gradient.

Survival is, with reproductive success, one of the two components of fitness. A trait significantly related to fitness is adaptive. We found significant relationships with survival for three traits (Table 3): maximum specific conductivity (Ks) in Corsica and P_{50} and P_{88} in Gard. The relationship with P_{88} is consistent with the results found by López *et al.* (2013) on *Pinus canariensis*. The results suggest that different types of hydric stressors activate different adaptation mechanisms to drought involving distinct hydraulic traits. Still, the differences between the sites for the relationships cannot be easily explained with the available data. More information on xylem structure and wood anatomy would be necessary to understand the distinct and complementary roles of the different hydraulic traits. It is also necessary to consider multiple drought response traits and climate variables to efficiently cope with the effect of global warming on widespread species like Douglas-fir (Bansal *et al.*, 2016). We found significant provenance variation for all the hydraulic traits in at least one test site (Table 5). This is in agreement with genetic variation found in several conifer species for different types of hydraulic traits and genetic entities (Domec & Gartner, 2002; Dalla-Salda *et al.*, 2011; Corcuera *et al.*, 2012; Klein *et al.*, 2013; López *et al.*, 2013).

The changing structure of provenance variation between test sites and traits is well revealed by the quantitative decomposition of the provenance effect using the Geo/Clim PCA principal components: the principal components quantitatively outline the components of origin-source geographic and climatic variation that explains the part of provenance variation that is driven by evolutionary adaptation. Different combinations of the three principal components and of the remaining provenance effect explain the phenotypic trait variation in both test sites. The second and third components and the remaining discrete provenance effect explain more generally P_{12}, P_{50} and P_{88}, while the first principal component alone explains Slope. The three principal components of PCA_Geo/Clim explain Ks in Corsica, while the discrete Provenance effect alone explains Ks in Gard. These results suggest that provenance variation for Slope is more driven by selective pressure related with latitude, elevation and precipitation, while provenance variation for P_{12}, P_{50} and P_{88} is more constrained by selective pressure related with longitude and temperature. The significant remaining provenance effect for P_{12}, P_{50} in Corsica, and P_{50}, P_{88}, Ks, circumference and survival in Gard suggests that some environmental selective pressure in the natural area are not accounted by the geographical and climatic variables of the study. Other non-selective evolutionary mechanisms accounted by this provenance effect may also have contributed to the provenance variation.

The lower survival rate in Corsica did not reduce the phenotypic variation (Table 6). On the contrary, trait variation is generally higher in Corsica than in Gard. The most variable traits in both test sites are Ks and Slope, and the less variable ones are P_{50} and P_{88}. The low provenance variation found for P_{50} and P_{88} has often been observed and could explain why in *Fagus sylvatica*, *Pinus pinaster* and *Pinus hartwegii*, no significant between-provenance variation was found for these hydraulic variables (Cochard *et al.*, 2008; Lamy *et al.*, 2011; Wortemann *et al.*, 2011; Sáenz-Romero *et al.*, 2013). A high statistical power is necessary to reveal, when it exists, the low provenance variation for these traits.

Washington-Oregon and Californian provenances

In the introduction, we hypothesized that the Californian provenances were more adapted to the climate of Gard and Corsica than the Washington and Oregon ones. Our results show that the situation is more complex. In the dryer Corsica site, the INCA provenances are the most cavitation resistant (Fig. **5**), while the WA and OR provenances are as resistant as the COCA ones. WA and one INCA provenance (BUR) have a higher Slope. The lowest survival rate is 48 % for both WA and OR (Table 4). These provenances are also more cavitation resistant in Corsica than in Gard, where their survival rate is higher (P_{50} and P_{88}, Table 4). Hence, it may well be that the highest selective pressure in Corsica eliminated the less cavitation resistant individuals of WA and OR and increased their average cavitation resistance. The most vulnerable provenance in both trials is SCR (Table 4, Fig. **5**), with a survival rate of 61 % in Corsica. The PCA_Geo/Clim does not provide any obvious geographic or climatic explanation for the high vulnerability of this COCA provenance.

In Gard, the distinction between the slightly more cavitation resistant INCA provenances and the COCA provenances is less clear. Except for the special position of SCR, the less drought resistant provenances are WA and OR, with a low cavitation resistance and a high Slope. Most Douglas-fir drought resistance studies in common gardens used different provenance groups, with different types of drought resistance traits. Our results confirm the consistent trend of increasing drought resistance from the coastal to the interior and south interior part of the Douglas-fir natural range found by Bo Larsen (1978), Eilmann *et al.* (2013), Sergent *et al.* (2014), Bansal *et al.* (2015), Montwé *et al.* (2015), Du *et al.* (2016), Hess *et al.* (2016), Kleiber *et al.* (2017), and Du *et al.* (2018) with a large variety of traits, experimental conditions, provenance sets and numbers. Furthermore, our study is the first one showing this consistent trend using cavitation resistance, the most recognized method for assessing resistance to drought.

The climate of the Douglas-fir introduction area in France is colder and wetter than that of the trial sites. For example, in the Orne, Normandy, a region where Washington-Oregon origins are planted widely, the summer precipitation is 190 mm, and the annual mean temperature is 10.1°C, while they are 121, 187 mm, 13.0, and 12.8°C in Corsica and Gard, respectively. Gard has a 2°C warmer climate with no change in precipitation, while Corsica's climate is not only 2°C warmer but also dryer. The high mortality rate of the Washington-Oregon provenances in the Corsica site suggests that it takes not only a 2°C temperature increase but also a 70 mm summer precipitation decrease to exceed the adaptation potential of these provenances.

Phenotypic plasticity of conductivity loss

The phenotypic plasticity of hydraulic traits allows species to deal with fast climate change (Choat *et al.*, 2018). According to Choat *et al.* (2018), "adaptive plasticity of hydraulic traits may enable the acclimatization of entire populations within the necessary timescales". Rigorous quantification of phenotypic plasticity involves the construction of norms of reaction, which are not often easy to fit (Feinard-Duranceau *et al.*, 2018). Vulnerability curves are by definition reaction norms that display how a given genotype dynamically behaves during a change in drought intensity. This quantitative information is mainly contained in the variation of one parameter of the sigmoidal model of the vulnerability curves (Pammenter & Van der Willigen, 1998): Slope. This dynamic trait describes the speed of conductivity loss (as cavitation spread) along an environmental gradient, xylem pressure (as simulated drought intensity). As the other variables extracted from the vulnerability curves, it is a component of drought-resistance. Phenotypic plasticity of conductivity loss (PPCL) is time-related plasticity, as opposed to space-related plasticity (Feinard-Duranceau *et al.*, 2018). Therefore, we found significant site variation and provenance variation in both test-sites for PPCL. According to PPCL, Gard is the less drought-resistant site, while WA and OR are the less drought-resistant provenances. Slope is also one of the most variable hydraulic traits of our study and thus submitted to selection, whether natural or artificial. The genetic determinism of PPCL or Slope is simpler than that of the other hydraulic traits, since its significant provenance variation is explained by only one principal component of PCA_Geo/Clim, PC1_Geo/Clim, i.e., principally by latitude, elevation and summer precipitation (Table 5 and Supporting Information, Table S1). So far, to our knowledge, only space-related phenotypic plasticity of hydraulic traits has been studied and was generally found to be low (Corcuera *et al.*, 2011; Lamy *et al.*, 2014; Aranda *et al.*, 2017; González-Muñoz *et al.*, 2018; Jinagool *et al.*, 2018). Our results suggest that not only P50 is a key-trait for studying the complex determinism of resistance to drought but also the other parameters of the vulnerability curves (P12 and P88), Ks and Slope, as well as, maybe, other traits not available in this study. Slope appears to be an especially interesting, highly variable, potential selection trait, depicting the phenotypic plasticity of the conductivity loss, with significant site and provenance variation and a relatively simple provenance determinism.

Conclusions

We found significant relationships between climatic variation in the natural area and phenotypic variation of drought resistance traits, including phenotypic plasticity of conductivity loss, in the provenance trial. We also found significant relationships between the survival component of fitness and cavitation resistance variables. There is significant provenance variation for nearly all resistance to drought traits in both test sites. Thus, we conclude that the cavitation resistance variables and Ks are adaptive traits whose variation is driven by evolutionary adaptation.

Interior California provenances are overall more adapted to the climate of Corsica, and, to some extent, of Gard, than Coastal Californian and Washington-Oregon provenances. However, there is a great deal of variation within the zones as well as a certain adaptation potential within the Washington and Oregon provenances at the cost of a higher mortality rate. Subtle differences in the CR variables, Slope and Ks seem to explain quite large differences in survival and in resistance to drought. It means that a high statistical power is necessary to reveal such small but critical differences.

The study suggests that geographically and time variable climatic pressures have shaped provenance variation for different combinations of hydraulics traits, and a more detailed description of between-provenance environmental variation in the specie's natural area is necessary to better understand the observed behaviours. Testing wider provenance variation against larger environmental variation, with improved description of long-term environmental variation in the common gardens and in the natural area, including a large range of key phenotypic variables with a great statistical power, remains an essential source of knowledge for predicting the future behaviour of the forests submitted to the climate change.

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Author contributions

T.C. is the PhD student in charge of the study. P.R. and H.C. are the PhD thesis directors and co-supervisors of T.C. P.R is the coordinator of the EMPIR and TOPWOOD projects. The PhD and study experiments were designed by P.R. and H.C. and conducted by T.C. under the supervision of P.R. and H.C. T.C. analysed the data under the supervision of P.R. and H.C., with significant contributions and supervision by V.S. The manuscript was written by T.C. under the supervision of P.R. and H.C. and was corrected and validated by all of the authors.

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Figure legends

Figure 1: Map of the western coast of the USA showing part of the Douglas-fir natural range (var glauca in dark grey and var menziesii in light grey) and the location of the 10 provenances studied in this article (white name in black boxes). Insert: Map showing the location of the two provenance trials in France.

Figure 2: Vulnerability curves of the most resistant and the most vulnerable provenances in each site. Open circles and triangles are the measured data for Corsica and full circles and triangles are for Gard. The lines (solid lines and dotted for Corsica and Gard respectively) represent the fitted models.

Figure 3: A: First two axes of the PCA_Geo/clim. PC1 represents 60.4 % and PC2 21.4 % of the total variation. B: Second and third axes of the PCA_Geo_Clim. PC3 represent 13.6 % of the total variation. The purple arrows represent the contribution of the explanatory variables.

Figure 4: Graph showing the relationship between survival and (A) Xylem specific hydraulic conductivity (Ks) in Corsica and (B) pressure causing 50 % loss of conductance (P50) in Gard. Error bars are standard error.

Figure 5: A: First two axes of the PCA_pheno. PC1 represents 45.4 % and PC2 30 % of the total variation. B: First and third axes of the PCA_pheno. PC3 13.3 % of the total variation. The purple arrows represent the contribution of the explanatory variables and the blue ones represent

the additional variables. PC1_Geo/Clim and PC2_Geo/Clim, PC3_Geo/Clim are the principal components extracted from the PCA_Geo/Clim.

Tables

Table 1: Studied provenances features

Table 2: Trials characteristics. Climatic data come from the closest Météo-France weather stations to the trials for the 1992 to 2015 period. Summer Rainfall is the sum of rainfall from June to August. MAT is for Mean Annual Temperature, PPT means annual rainfall and PPT_ sm are for the summer rainfall.

Table 3: Spearman's rank correlation coefficient between studied variables and significant values (∗ $p < 0.05$; ∗∗ $p < 0.01$; ∗∗∗ $p < 0.001$). The upper diagonal of the table is for the Gard trial while the lower diagonal corresponds to the Corsica trial.

Table 4: Mean and confidence interval values of the studied traits for the ten provenances (mean ± confidence interval).

Table 5: Significance of the effect of the PCA_Geo/Clim axes and the provenance factor on the variance of the phenotypic variables (likelihood ratio test of linear mixed model (3)).

Table 6: Intra-specific coefficient of variation. N =200 and 193 in Corsica and Gard respectively.

Supporting Information

Table S1: Contribution of the variables to the axes and correlation coefficients between the variables and the axes for PCA_Geo/clim. Only the significant correlation are shown. *** means that the p-value of the correlation test is below 0.001.

Table S2: Contribution of the variables to the axes and correlation coefficients between the variables and the axes for PCA_Pheno. Only the significant correlation are shown. *** means that the p-value of the correlation test is below 0.001

Figure S1: Boxplot showing the between provenance variation in each site for Ks, P12 and P50. Data available in table 4 in the article.

Figure S2: Boxplot showing the between provenance variation in each site for P88, Slope and Ci16. Data available in table 4 in the article.

Figure S3: Barplot showing the between provenance variation in each site for the survival rate. Data are available in table 4 in the article.