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

Thibaud Chauvin, Cochard, Vincent Segura, Philippe Rozenberg

▶ **To cite this version:**

Thibaud Chauvin, Cochard, Vincent Segura, Philippe Rozenberg. Native-source climate determines the Douglas-fir potential of adaptation to drought. Forest Ecology and Management, 2019, 444, pp.9 - 20. 10.1016/j.foreco.2019.03.054 . hal-02620286

HAL Id: hal-02620286
https://hal.inrae.fr/hal-02620286

Submitted on 22 Oct 2021

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

2

3   **Authors**

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

5   **Affiliations**

6   [1] UMR 0588 BIOFORA, INRA ONF, Orléans, France, F-45075 Cedex 2,

7   thibaud.chauvin@hotmail.fr

8   [2] UMR 0547 PIAF, INRA Université Clermont-Auvergne, Clermont-Ferrand, France, F-63100,

9   herve.cochard@inra.fr

10   [1] UMR 0588 BIOFORA, INRA ONF, Orléans, France, F-45075 Cedex 2,

11   vincent.segura@inra.fr,

12   [1] UMR 0588 BIOFORA, INRA ONF, Orléans, France, F-45075 Cedex 2,

13   philippe.rozenberg@inra.fr

14   **Corresponding author**

15   Philippe Rozenberg

16   **Summary**

17   *Context:* Douglas-fir, a fast growing conifer from western North America, recently suffered

18   diebacks following drought in France. We investigated the link between native-source climate

19   and provenance drought resistance in a common garden in France. We compared the adaptive

20   potential of provenances from different parts of the natural area.

21 *Methods:* We collected branches from a 25-year-old provenance trial replicated in two test sites

22 in southern France. We estimated provenance variation of cavitation resistance traits, survival

23 and circumference. We compared Washington-Oregon provenances to coastal and interior

24 Californian provenances.

25 *Results:* In the common gardens, the hydraulic traits were significantly variable between

26 provenances, with a strong site × provenance interaction, and significantly related to the climate

27 of the natural area and survival. The relationships were different between variables and test-sites.

28 The two test-sites and their particular climatic selective pressure revealed different geographical

29 adaptive structures in the natural area.

30 *Conclusions:* Douglas-fir evolutionary adaptation to drought results from natural selection to

31 summer climate and shapes populations for cavitation resistance. In the dryer site only, the

32 Interior California provenances seem more drought resistant. The strong within-provenance

33 variations suggest that there is also a certain within-provenance adaptation potential to drought at

34 the cost of variable mortality rates.

35

36 **Key words:** cavitation resistance; climate change; common garden; evolutionary adaptation;

37 hydraulic traits; phenotypic plasticity; provenance variation; *Pseudotsuga menziesii* (Mirb.)

38 Franco

39

40

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).

64   Provenance studies are one of the three main approaches that can be used to investigate

65   the genetic basis of drought tolerance (Moran *et al.*, 2017). In this article, we investigated the

66   variation of drought resistance of provenances originating from California, a part of the Douglas-

67   fir natural area warmer and dryer than Washington-Oregon (Fig. **1** and Table 1). We compared

68   their resistance to drought to that of Washington and Oregon provenances. We worked on

69   replicated Douglas-fir common garden experiments, two provenance trials planted in the south of

70   France (Pineta in Corsica and L'Homol in Gard, insert Fig. **1**, Table 2). Both sites are located in

71   regions with a warmer and dryer climate and a smaller probability of Douglas-fir presence

72   (Boiffin *et al.*, 2017) than in the Douglas-fir introduction area in France. To some extent, these

73   test sites simulate the future climate of the introduction area. Thanks to this experimental trial,

74   we are able to anticipate the behaviour of Oregon and Washington provenances and of putatively

75   more drought resistant Californian provenances in warmer and dryer conditions than those of the

76   current French Douglas-fir introduction area.

77   The physiological mechanisms underlying a tree's resistance to drought are multiple. For

78   example, foliar nitrogen and carbon metabolism has been shown to be affected by soil water

79   availability but to vary little between interior and coastal Douglas-fir provenances with assumed

80   different drought tolerance (Du *et al.*, 2016, 2018). In a controlled drought experiment, Kleiber

81   et al. (2017) found a clear difference in the terpenoid content of needles between interior and

82   coastal Douglas-fir provenances. However, based also on two coastal and interior provenances,

83   Hess *et al.* (2016) concluded that transcriptome responses to water availability were only weakly

84   affected by local adaptation. Other drought-resistance traits, such as transpiration, water deficit

85   and specific leaf area, show significant provenance variation, with populations originating from

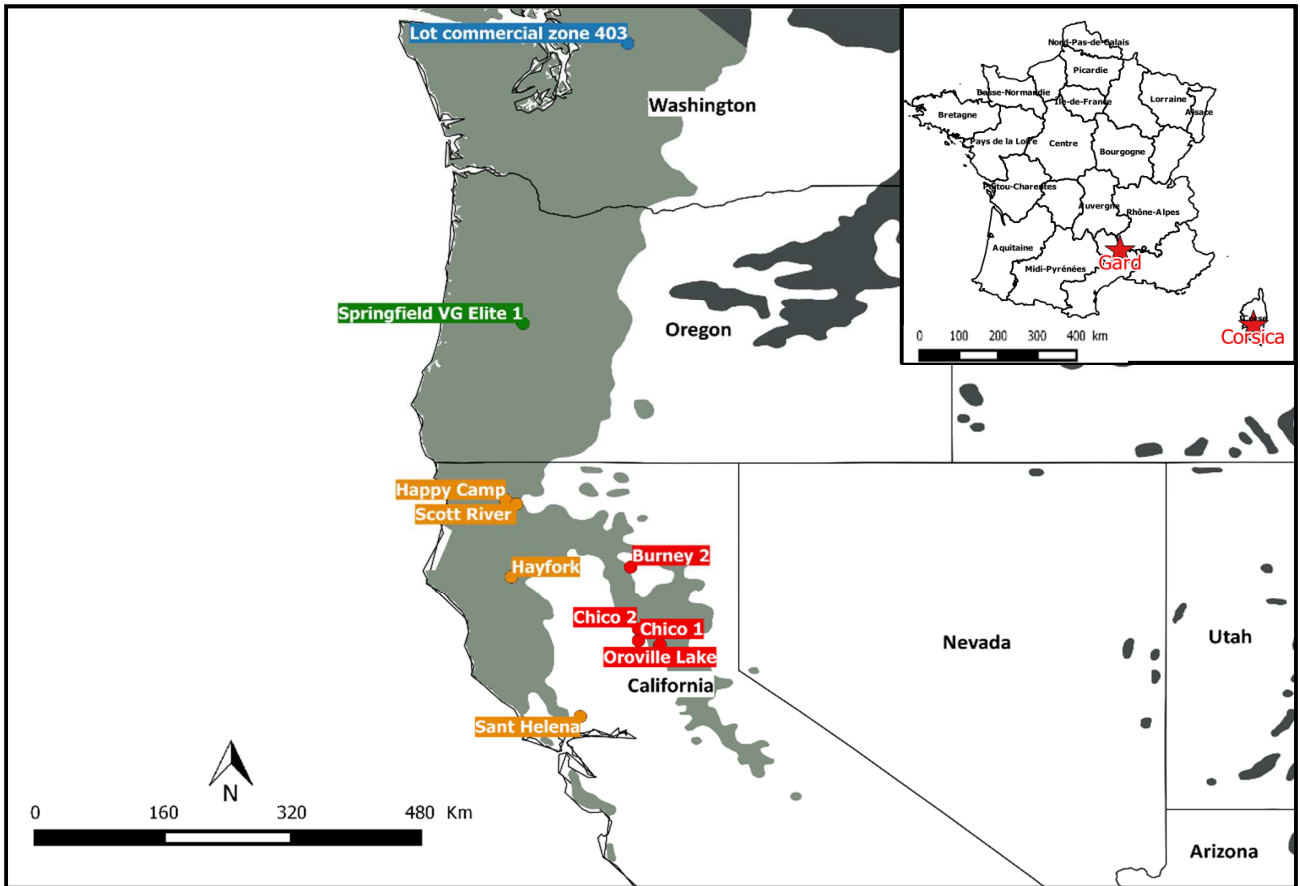86   dryer climates having greater drought-resistance (Bansal *et al.*, 2015).

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.

87   There is increasing evidence that hydraulic traits play an important role in physiological

88   response to drought (Hartmann *et al.*, 2015; Choat *et al.*, 2018). Sap flowing from the roots to the

89   leaves is exposed to a negative pressure. During a strong drought, under a critical pressure

90   threshold, air bubbles enter the xylem conduits, spread, and disrupt the water columns. This

91   phenomenon, called cavitation, directly decreases the hydraulic conductivity of the sapwood

92   (Tyree & Sperry, 1989). The consequence of such a dysfunction ranges from a simple growth

93   diminution to death. The capacity to maintain conductivity during a drought is called cavitation

94   resistance (CR). CR is a complex trait depicting the dynamics of the conductivity loss. In the

95   relevant range of drought intensity, CR is related to survival—the link between CR and survival

96   to drought was found to be statistically significant at the species level for *Fagus sylvatica*,

97   *Populus* sp. and *Quercus sp.* (Barigah *et al.*, 2013; Urli *et al.*, 2013) for angiosperms. For

98   conifers, this relationship was found significant for four *Callitris* species from Oceania (Brodribb

99   *et al.*, 2010) as well as at the population level for *Pinus canariensis* (López *et al.*, 2013).

100 Survival, together with reproductive success, is one of the two components of fitness (Crow &

101 Kimura, 1970). For some species facing drought conditions, CR is therefore an adaptive trait. CR

102 is evaluated in the laboratory by vulnerability curves depicting the percentage loss of

103 conductivity (PLC) as a function of the pressure applied to the xylem (Fig. **2**).

104 *Table 1: Studied provenances and region of origin. The table shows latitude, longitude, and elevation at the place of origin. WA*
105 *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

106

107   To model vulnerability curves from raw data, we fitted a sigmoidal parametric model

108 (Pammenter & Van der Willigen, 1998). This model has two parameters, the P_{50}, the pressure

109 applied to obtain a 50 % loss of conductivity, and the Slope of the curve at the inflexion point.

110   P_{50} is the trait most often used in CR studies, and the Slope determines the pressure range over

111   which conductivity is lost (Pammenter & Van der Willigen, 1998).

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

115

116   While large and significant between-species variation was often found for P_{50} (Delzon *et*

117   *al.*, 2010; Choat *et al.*, 2012), there is only a small number of studies on between-population

118   variation, and less evidence of significant variation. In *Fagus sylvatica*, *Pinus pinaster* and *Pinus*

119   *hartwegii*, no significant differences were found between provenances for P_{50} (Cochard *et al.*,

120   2008; Lamy *et al.*, 2011; Wortemann *et al.*, 2011; Sáenz-Romero *et al.*, 2013). In *Pinus pinaster*

121   Lamy *et al.*, (2011) wrote that "uniform selection has shaped the phenotypic variability of this

122   trait". In *Picea abies*, Chmura *et al.* (2016) found limited genetic variation between families for

123   resistance to embolism. However, other studies found significant intra-specific variation for CR.

124   In a recent *in-situ* study, González-Muñoz *et al.* (2018) found between-provenance variability for

125   P_{50} for four different species (*Betula pendula*, *Populus tremula*, *Picea abies* and *Pinus sylvestris*)

126   across their natural range. P_{50} was found to be significantly different between populations in a

127   common garden experiment for *Pinus pinaster* and *Pinus canariensis* (Corcuera *et al.*, 2011;

128   López *et al.*, 2013). In Douglas-fir, (Domec & Gartner, 2002; Dalla-Salda *et al.*, 2014) found

129   significant variation between a limited number of genetic entities (clones, families, and

130   provenances) from the Washington-Oregon coastal area. Such contradictory results could be

7

131 explained by a low genetic variation in some species or in the studied sample, or by a low

132 statistical power, unable to reveal existing variation. In this study, compared to previous ones, we

133 increased the number of samples to increase the statistical power of the analysis. We measured

134 CR on two branches per tree on 20 trees per provenance for ten provenances in each site,

135 resulting in, to our knowledge, the largest CR dataset for Douglas-fir so far.

136   The relationship with survival provides information about the adaptive value of the traits.

137 A significant between-provenance variation is interpreted as the result of past evolutionary

138 adaptation in the Douglas-fir natural range, leading to local adaptation (Kawecki & Ebert, 2004;

139 Savolainen *et al.*, 2007). CR resistance is known to be related to wood density in Douglas-fir

140 (Dalla-Salda *et al.*, 2011), and Nabais *et al.* (2018) have shown that Douglas-fir was among 10

141 forest tree species for which wood density variation in provenance trials was affected by native-

142 source climate. Recent inter-specific studies found a link between hydraulic features and the

143 species native-source climate (Bourne *et al.*, 2017; Li *et al.*, 2018). In this article, we investigate

144 this link at the intra-specific level in Douglas-fir.

145   Together with genetic adaptation, phenotypic plasticity is an important response

146 mechanism to new environmental conditions (Aitken *et al.*, 2008). Trees are sessile long-lived

147 organisms, while global warming is fast. Phenotypic plasticity precedes evolutionary adaptation

148 and thus has a particular significance in the climate change context. Vulnerability curves

149 represent a phenotypic variable (PLC) as a function of an environmental variable reflecting

150 drought intensity, the xylem applied pressure. Thus, by definition (DeWitt & Scheiner, 2004),

151 the vulnerability curves are *de facto* reaction norms estimating the phenotypic plasticity of

152 conductivity loss in function of a proxy of drought intensity. Hence, while studying CR, we

153 study not only this trait genetic variation but also the genetic variation of the phenotypic

154 plasticity of the conductivity loss.

155   In this article, we investigate the ability of Douglas-fir to adapt to a new climatic

156 condition in the general context of evolutionary adaptation and phenotypic plasticity through

157 three main hypotheses. First, we hypothesize that there is a relationship between the climatic

158 variation in the natural area and the variation of CR in the provenance trials. Second, we

159 hypothesize that CR traits are adaptive traits related to the survival component of fitness, and are

160 variable between provenances. Third, we hypothesize that the Californian provenances are more

161 adapted to the climate of Gard and Corsica than the Washington and Oregon provenances.

162

163 **Materials and methods**

164

165 *Plant material, experimental design and sampling strategy*

166   The study is buttressed by a provenance trials established 25 years ago (1992) and

167 replicated at two test sites in the south of France, one in the Gard (44°18'N, 3°59'E) and the other

168 in Corsica (41°57N, 9°00'E) (insert Fig. **1**, Table 1). Twenty-eight Douglas-fir provenances (only

169 the *var menziesii*) from three US states (Washington, Oregon and California) were planted.

170 California provenances come from two regions: coastal California (COCA) and internal

171 California (INCA). The trial is a randomized single-block design with 68 and 60 blocks in Gard

172 and Corsica, respectively, which means that the 28 provenances are represented in each block.

173 The 2014 inventory of these well-maintained trial gave us an estimate of the survival rate (SR).

174 In 2016, we measured the circumference at breast height of all the trees (Ci_{16}).

175   We measured CR on a subsample of ten provenances (one from Washington, one from

176   Oregon and eight from California) (Fig. **1**, Table 2).

177   The Californian provenances were selected to be representative of the native-source

178   climate of all the Californian provenances available in the trial. We used the online interactive

179   platform ClimateNA_MAP (Wang *et al.*, 2016) to obtain monthly climatic data of the natural

180   area of the provenances: mean temperature, sum of precipitation and mean relative humidity. We

181   selected the random subsample of eight Californian provenances that minimize the difference

182   between the subsample and the entire provenance set (variance and mean).

183   We sampled the trials during late spring and early summer 2016 to obtain a new-formed-

184   ring without native embolism (from May 23 to 27 in Corsica and from June 27 to July 1st in

185   Gard). We sampled south-exposed branches from a given whorl. We took the sample in the 2014

186   growth-unit to measure CR on the same rings (2014 to 2016) throughout all samples. The sample

187   length was at least 30 cm, with a maximum diameter of one centimetre. We collected two

188   branches per tree and 20 trees per provenance out of the 10 selected provenances on each site for

189   a total of 800 branches. We immediately wrapped the collected branches into soaked cloth and

190   then put them into a black and opaque plastic bag to prevent dehydration. We rapidly transported

191   and stored the samples at 3-4°C, and we measured CR within three weeks of collection.

192

193   *Cavitation resistance measurements*

194   We built xylem vulnerability curves (VCs) using the centrifugation-induced method or

195   Cavitron technique (Cochard, 2002; Cochard *et al.*, 2005). The aim here is to use centrifugal

196   force to induced a negative pressure in the xylem to simulate drought.

197   All samples were re-cut under water to a standard length of 28 cm, bark was removed,

198   and both ends were trimmed with a fresh razor blade to obtain perfectly smooth surfaces. A

199   solution of ultrapure and degassed water including 10 mM KCl and 1 mM $CaCl_2$ was used as the

200   reference solution for hydraulic measurements. After measuring maximum hydraulic

201   conductance (Kmax) under high xylem pressure (i.e., -0.5 MPa), centrifuge rotation speed was

202   gradually increased to determine the percentage loss of hydraulic conductance (PLC in %).

203   CAVI_SOFT software (version 5.0, University of Bordeaux) was used to measure conductance

204   and compute the vulnerability curves. According to Pammenter and Van der Willigen (1998), a

205   sigmoid function was fitted on the VCs using the following equation:

206

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

207

208

209   where P_i (MPa) is the xylem pressure at speed i, P_{50} (MPa) is the xylem pressure at which there

210   is 50 % loss of conductivity, and Sl (% MPa^{-1}) is the Slope of the tangential line at the P_{50}

211   (indicator for the pressure range over which maximum embolism development occurs in the

212   branch). Sl is a dynamic character enabling the evaluation of the phenotypic plasticity of

213   conductivity loss.

214   We used the VC sigmoid models to extract two more variables from the vulnerability

215   curves: P_{12} and P_{88}; they characterize the beginning (P_{12}, pressure corresponding to early, low

216   conductivity loss under moderate hydric stress) and the end (P_{88}, pressure corresponding to late

217   and high conductivity loss under severe hydric stress) of the vulnerability curves (Fig. 2). In

218   addition, we calculated the xylem specific hydraulic conductivity, Ks ($kg.s^{-1}.m^{-2}.MPa^{-1}$), using

219   the equation hereafter:

220

221 $$Ks = \frac{Kmax}{S} \times L, \hspace{4cm} (2)$$

222

223 where Kmax is the maximum hydraulic conductance (kg.s^{-1}.MPa^{-1}), S is the basal area of the

224 measured branch, and L is its length (standardized by the length of the rotor: 28 cm).
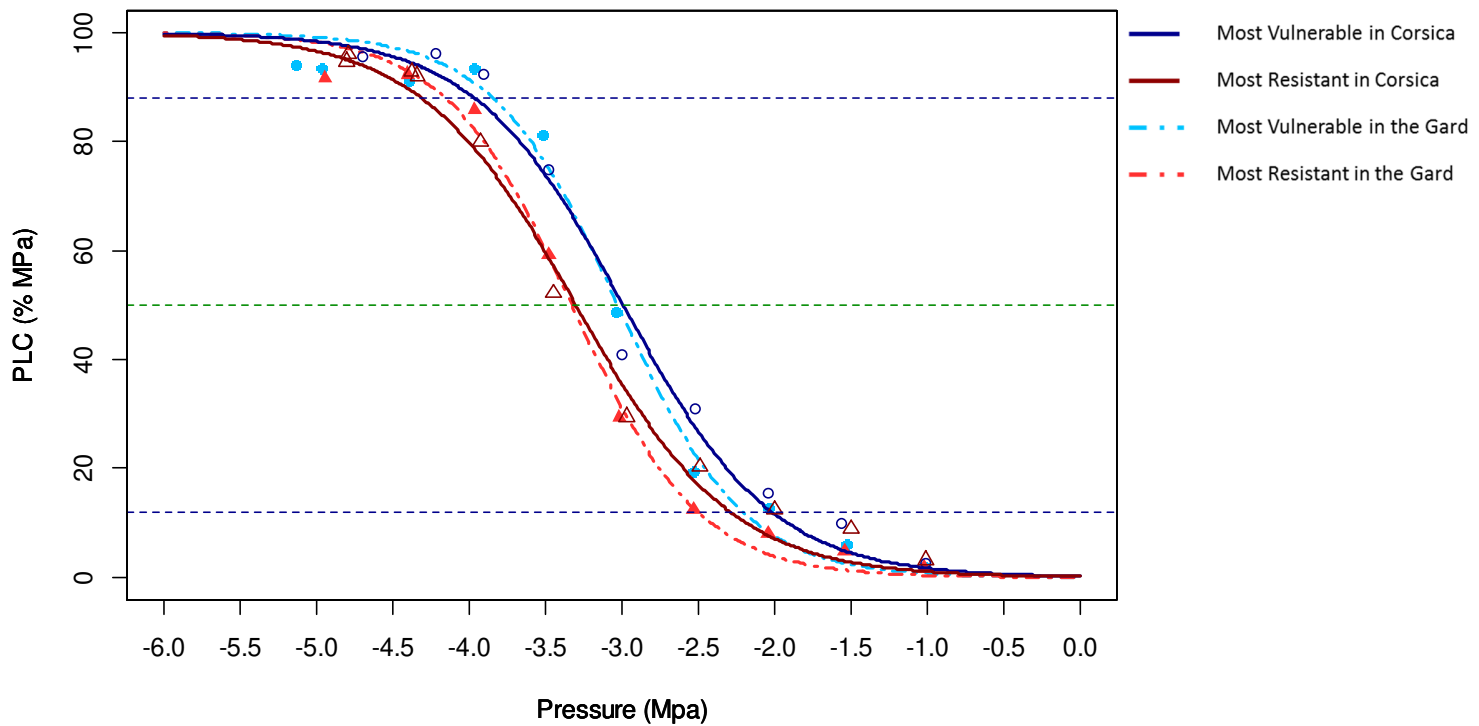
225

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.

226 ***Statistical analyses***

227   All statistical analyses were performed at the provenance level using R software (R

228 Development Core Team, 2013, version 3.4.1).

229   We analysed the data with two successive PCAs, PCA_Geo/clim and PCA_Pheno. We

230   used the "FactoMineR" package (Lê *et al.*, 2008). The first PCA, PCA_Geo/clim, explains the

231   provenance variation with the climatic and geographic variables (elevation, latitude, longitude,

232   summer rainfall (PPT_sm), annual mean temperature (MAT) and annual mean relative humidity

233   (RH)) in the natural range of the provenances. The second PCA, PCA_Pheno, explains

234   provenance variation using the phenotypic variables (SR, Ks, Slope, P12, P50, P88, and Ci16)

235   measured in the two trials of the common garden experiment. We compared separated PCAs for

236   each trial with a grouped PCA and found this one graphically more efficient. We further used the

237   first principal components of PCA_Geo/clim as quantitative continuous covariables to be

238   associated to the discrete provenance factor in the analysis of

239   variance: $PC1_{Geo/clim}, PC2_{Geo/clim}, PC3_{Geo/clim}$ and $Prov$.

240   PCA_Pheno depicts the network of relationships between provenance phenotypic

241   variation in the common garden trials. Both PCAs provide information about the links between

242   the hydraulic properties and the climatic features of the provenances in the natural area.

243   There was no significant intra-tree difference between branches for any hydraulic trait,

244   thus we averaged the two branch values. Intra-specific variation for each cavitation trait was

245   determined with a linear mixed model using the residual maximum likelihood option (REML)

246   included in the "lme4" package (Bates et al., 2015.). A first global model including both trials

247   was setup as

248

249    $y = \mu + Bloc : Site + Site + Prov \times Site + PC1_{Geo/clim} + PC2_{Geo/clim} + PC3_{Geo/clim} +$

250    $Prov + \varepsilon,$ (2)

251

13

252 where y is the phenotypic value at the individual level; μ is the overall mean; $Bloc : Site$ is a

253 fixed bloc effect nested in $Site$. $Site$ is a fixed trial effect; $Prov \times Site$ is the interaction

254 between the trial and provenances effects. $PC1_{Geo/clim}$, $PC2_{Geo/clim}$ and $PC3_{Geo/clim}$ are

255 random effects of the 3 first principal components of PCA_Geo/Clim; and $Prov$ is a random

256 effect of provenance to account for the climate and geographic effects that are not accounted for

257 by the principal components of PCA_Geo/clim. We selected the best model using the Akaike

258 Information Criterion (AIC).

259   As the interaction between *Prov* and *Site* was significant for most of the variables, we

260 split up the model at the site level:

261

262 $$y = μ + Bloc + PC1_{Geo/clim} + PC2_{Geo/clim} + PC3_{Geo/clim} + Prov + ε. \hspace{2cm} (3)$$

263

264   We assessed the significance of the pairwise differences between the provenances and the

265 sites via the TukeyHSD (Honest Significant Differences) test for phenotypic values except for

266 SR. To assess the between-provenance differences for survival rate (SR), we compared

267 generalized linear model (GLM) at the tree level based on a logit function with likelihood ratio

268 test in each site.

269   To compare the observed variation for the different variables in both provenance trials,

270 we calculated and compared two statistics: i) the coefficient of variation (CV), and ii) the

271 coefficient of quartile variation (CQV) (Zwillinger & Kokoska, 2000) using equation (4):

272

273 $$CQV(x) = \frac{|(Q3(x) - Q1(x))|}{|(Q3(x) + Q1(x))|} \times 100, \hspace{2cm} (4)$$

274

275   where Q1 and Q3 are the first and third quartiles of the trait considered (x). CQV is a more

276   robust index than CV for datasets involving log-transformed data or isotopic measurements

277   (Brendel, 2014; Canchola *et al.*, 2017). There are concerns about the validity of the coefficient of

278   variation for variables estimated using non-linear models (Brendel, 2014; Canchola *et al.*, 2017).

279   The CQV is another way to quantify and compare the variability of traits with a non-linear

280   model, such as P_{50} and Slope. Finally, we found very similar trends between CV and CQV, and

281   we decided to present only the results obtained with CQV.

282

283   **Results**

284

285   *Relationships between the climatic variation in the natural area and the phenotypic variation*

286   *in the provenance trials*

287   The relationships between the provenance geographic distribution and the climate in the

288   Douglas-fir natural area is described by the geographic and climatic principal component

289   analysis (PCA_Geo/Clim, Fig. **3**). The first three principal components of PCA_Geo/Clim

290   explain 95.4 % of the total variance (PC1 = 60.4 %, PC2 = 21.4 %, PC3 = 13.6 %; Fig. **3**). PC1

291   is mainly positively associated with latitude, summer rainfall (PPT_sm) and relative humidity

292   (RH) and negatively associated with elevation and temperature (MAT) (Table 3). PC2 is chiefly

293   associated with longitude (47 %) and then with MAT and RH (17.9 and 20.9 %, Supporting

294   Information, Table S1). PC3 is associated with Longitude, MAT and RH (Supporting

295   Information, Table S1). PC1 principally separates the Californian provenances from the Oregon

296   and Washington ones. According to PC1, the northern low elevation Washington provenance is

297   located in the coldest and wettest region, while the Southern high elevation Californian

298 provenances are in the warmest and driest part of the sampled area (Fig. **3**). The Oregon

299 provenance is intermediate. PC2 separates WA (Washington) from OR (Oregon), and INCA

300 (Internal California) from COCA (Coastal California). The Eastern WA and INCA provenances

301 are from relatively colder regions with a higher RH than the further west OR and COCA

302 provenances. The Easternmost INCA provenance BUR appears to be in an even colder zone with

303 lower relative humidity. Fig. **3(b)** confirms that BUR comes from a particularly cold and dry

304 zone, while the COCA provenance STH originates from an especially warm and humid area.

305 Table 3 presents the correlation coefficients calculated between the climatic variables in

306 the natural area and the phenotypic variables in the two experimental sites in France. The

307 relationships are different according to the test sites. In Corsica, the strongest relationship is

308 between Ks and PPT_sm and is negative ($r = -0.73$, $P < 0.05$; Table 3), while in Gard, the

309 strongest relationship is between Slope and PPT_sm and is positive ($r = 0.95$, $P < 0.001$; Table

310 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

314

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

316   SR is significantly different between sites, and between provenances only in Corsica. We

317   found the lowest SR in Corsica (average values 63 % ± 0.4 in Corsica vs 78 % ± 0.3 in Gard,

318   minimum values 48 % for WA and OR provenances in Corsica, Table 4).

319   Table 3 shows the relationships between SR and the hydraulic traits within each site. In

320   Corsica, there is one significant positive correlation between SR and maximum specific

321   conductivity (Ks, r = 0.82) (Fig. **4a**). In Gard, SR is significantly and negatively related to P_{50}

322   and P_{88} (r = -0.75 and -0.71, respectively) (Table 5 and Fig. **4b**).

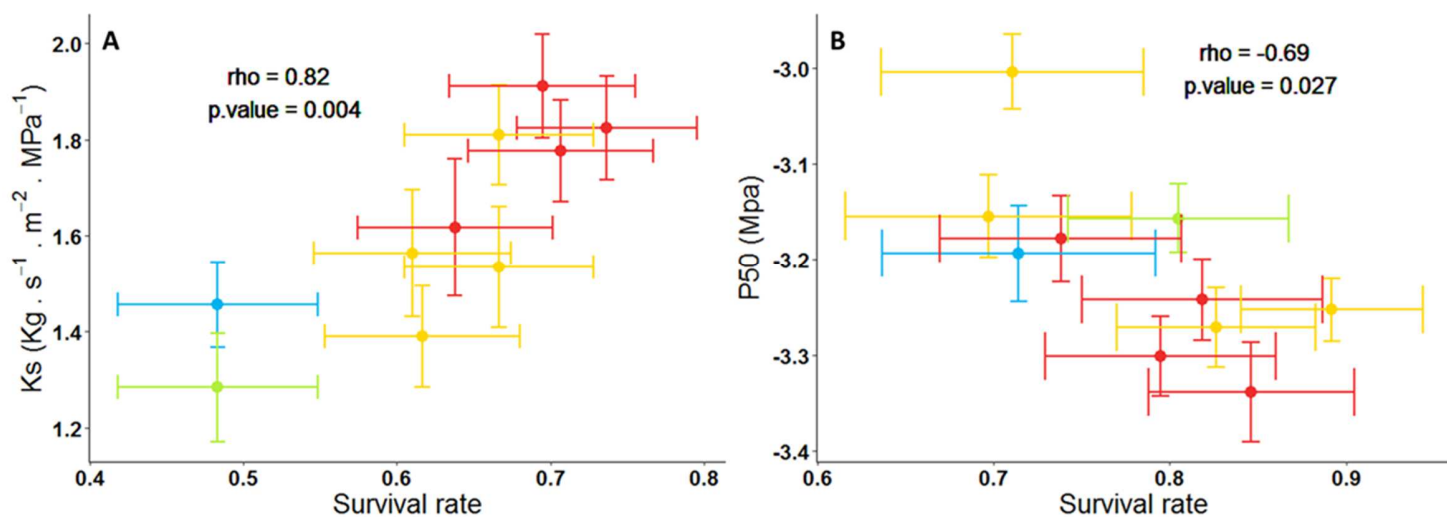*Figure 3: Graph showing the relationship between survival and (A) Xylem specific hydraulic conductivity (Ks) in Corsica and (B) pressure causing 50% loss of conductance (P50) in Gard. Error bars are standard error.*

323

324   The results presented in Table 5 show the relationships between the first, second and

325   third principal components of PCA_Geo/clim and the provenance factor, as well as the

326   phenotypic variables measured in the common garden experiments.

327   The results show that the combinations of significant and non-significant effects are

328   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

342   *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

343

344

Phenotypic variation

346   Table 6 presents the coefficients of variation of the phenotypic variables (Ks, SR, Ci_{16},

347   P_{12}, P_{50} and P_{88} and Slope). The highest value is for Ks (CQV_{Ks} = 80.9 % and 72.3 % in Corsica

348   and Gard, respectively; Table 6), whereas the lowest value is for P_{88} and P_{50} in Corsica and Gard,

349   respectively (Table 6). In Corsica, the variability is greater for all the variables except P_{88}.

350   The phenotypic principal component analysis (PCA_Pheno, Fig. **5**) describes the

351   relationships between the provenances and the phenotypic variables measured in both

352   experimental trials. The first three principal components of PCA_Pheno explain 88.7 % of the

353   total variance (PC1 = 45.4 %, PC2 = 30 %, PC3 = 13.3 %; Fig. **5**). PC1 is mainly positively

354   related with Circumference (Ci_{16}), Slope and SR and negatively associated to P_{12} (Supporting

355   Information, Table S2). PC2 is mainly positively linked to P_{88} and P_{50} and marginally with Ks

356   (Supporting Information, Table S2). PC3 is built principally around Ks, then SR and P_{50}. PC1

357   best explains the differences between the two experimental sites (Fig. **5**). In Gard, the

358   provenances have a bigger circumference, survive better and are more resistant to the initiation

359   of cavitation with a steeper Slope than in Corsica (Fig. **2** and Table 4). PC2 highlights the intra-

360   site between-provenance variation, especially in Corsica. In Corsica, PC2 separates the INCA

361   provenances with high P_{50} and P_{88} from the COCA, while OR and WA coincide with the COCA

362   provenances (Fig. **5**, Top). Still in Corsica, WA and BUR from INCA are isolated from the other

363   provenances and less distant from Gard provenances along PC1 (Fig. **5**). In Gard, the

364   provenances are more grouped than in Corsica, except for one provenance from COCA, SCR,
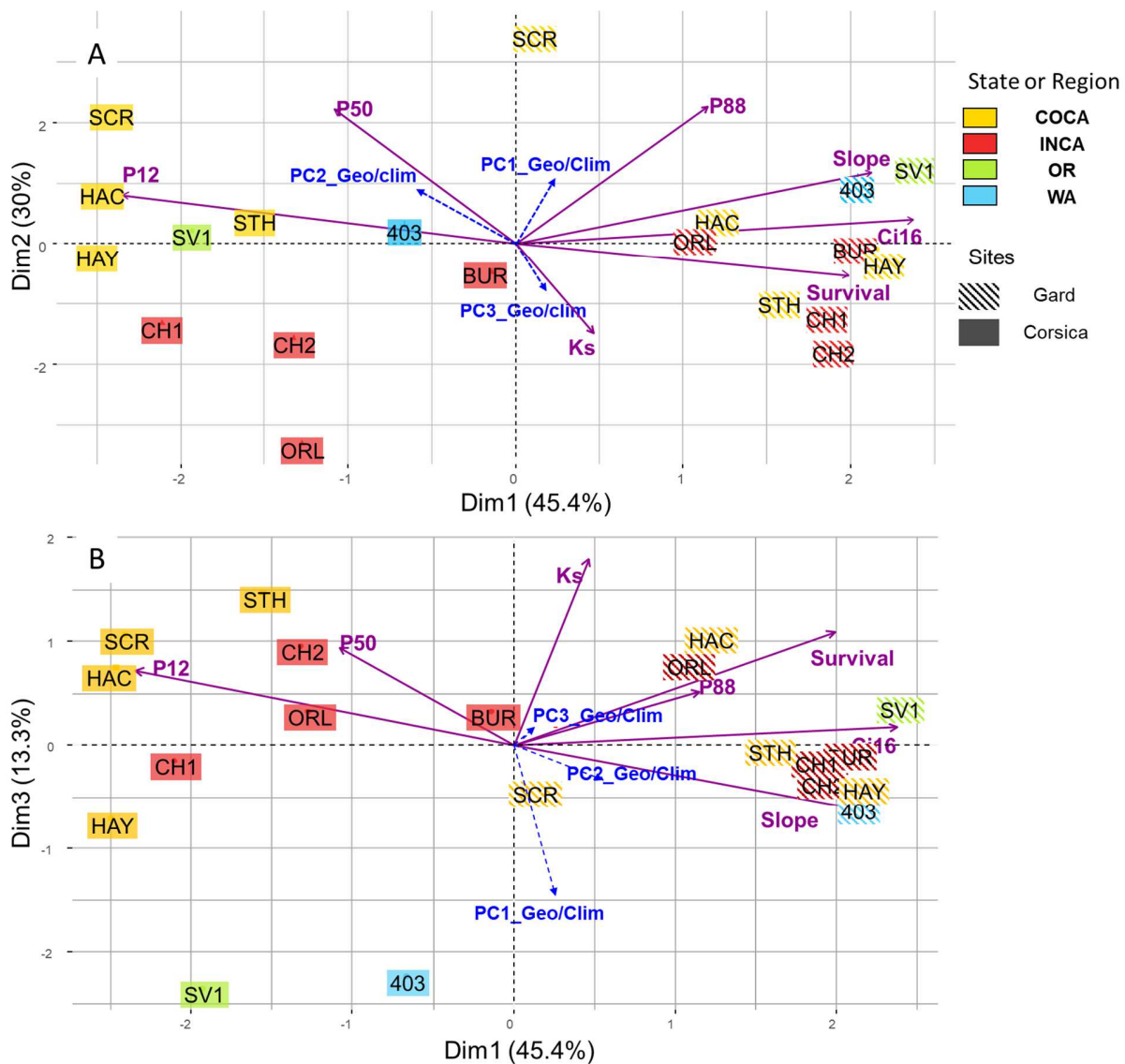
Figure 3: A: First two axes of the PCA_Geo/clim. PC1 represents 60.4 % and PC2 21.4 % of the total variation. B: Second and third axes of the PCA_Geo_Clim. PC3 represent 13.6 % of the total variation. The purple arrows represent the contribution of the explanatory variables.

365 which is completely separated with high P_{12}, P_{50} and P_{88} values (Fig. **5**). In Corsica, the same

366 SCR provenance also has the highest P_{50} and P_{88} values and among the highest P_{12} values.

367

368 **Discussion**

369

370 *Adaptation and natural selection in the natural area*

371   The PCA_Geo/Clim synthesized the provenance geographic and climatic information. As

372 expected, they show that the Washington and Oregon provenances are the wettest and coldest

373 origins of the study and that annual mean temperature, to some extent, and relative humidity

374 overall, discriminate the interior and the coastal parts of California. They also show that there is

375 substantial climatic variation within these two regions. More importantly, they reduce the

376 number of environmental variables to a lower number of independent principal components

377 (PCs) quantitatively depicting a part of the provenance environmental variation.

378   The phenotypes we observe in the common gardens result from the evolutionary history

379 of Douglas-fir in its natural range. In temperate climates, summer is the warmest and driest

380 period of the year and the most stressful time for trees' hydraulic functioning. Annual mean

381 temperature and rainfall from June to August in the natural area significantly explain the

382 variation of several of the provenance hydraulic traits in the common gardens. The lower

383 survival rate in Corsica (63 % vs 78 % in Gard) shows that overall growing conditions are more

384 favourable in Gard than in Corsica, especially for the Washington-Oregon provenances (Table

385 4). Annual average temperature is very similar (12.8°C and 13.0°C in Gard and Corsica,

386 respectively), while annual precipitation is 1640 mm in Gard and 1263 mm in Corsica. The even

387 greater rainfall difference in summer, 187 and 121 mm in Gard and Corsica, respectively, and the

388   corresponding difference in the mortality rate suggest that summer precipitation is a key

389   selective pressure in the test sites. Similar impact of precipitation has already been noted on

390   *Pinus edulis* (Grossiord *et al.*, 2017). This is consistent with the significant correlation found

391   between native-source summer precipitation and Ks in Corsica, P88 in Gard and Slope in both

392   test-sites. These correlations show that populations coming from warmer and/or more arid

393   regions tend to have a higher resistance to drought. Similar combined influence of climatic

394   conditions in the test sites and of long-term genetic differentiation on drought-resistance was also

395   observed on Douglas-fir by Bansal *et al.* (2015) with other drought-resistance traits. The

396   relationships found in Gard between P88 and mean annual temperature and summer precipitation

397   (Table 3) are in accordance with results reported by López *et al.* (2013) for *Pinus canariensis*

398   populations coming from an aridity gradient.

399   Survival is, with reproductive success, one of the two components of fitness. A trait

400   significantly related to fitness is adaptive. We found significant relationships with survival for

401   three traits (Table 3): maximum specific conductivity (Ks) in Corsica and P_{50} and P_{88} in Gard.

402   The relationship with P_{88} is consistent with the results found by López *et al.* (2013) on *Pinus*

403   *canariensis*. The results suggest that different types of hydric stressors activate different

404   adaptation mechanisms to drought involving distinct hydraulic traits. Still, the differences

405   between the sites for the relationships cannot be easily explained with the available data. More

406   information on xylem structure and wood anatomy would be necessary to understand the distinct

407   and complementary roles of the different hydraulic traits. It is also necessary to consider multiple

408   drought response traits and climate variables to efficiently cope with the effect of global

409   warming on widespread species like Douglas-fir (Bansal *et al.*, 2016). We found significant

410   provenance variation for all the hydraulic traits in at least one test site (Table 5). This is in

6

411   agreement with genetic variation found in several conifer species for different types of hydraulic

412   traits and genetic entities (Domec & Gartner, 2002; Dalla-Salda *et al.*, 2011; Corcuera *et al.*,

413   2012; Klein *et al.*, 2013; López *et al.*, 2013).

414   The changing structure of provenance variation between test sites and traits is well

415   revealed by the quantitative decomposition of the provenance effect using the Geo/Clim PCA

416   principal components: the principal components quantitatively outline the components of origin-

417   source geographic and climatic variation that explains the part of provenance variation that is

418   driven by evolutionary adaptation. Different combinations of the three principal components and

419   of the remaining provenance effect explain the phenotypic trait variation in both test sites. The

420   second and third components and the remaining discrete provenance effect explain more

421   generally P_{12}, P_{50} and P_{88}, while the first principal component alone explains Slope. The three

422   principal components of PCA_Geo/Clim explain Ks in Corsica, while the discrete Provenance

423   effect alone explains Ks in Gard. These results suggest that provenance variation for Slope is

424   more driven by selective pressure related with latitude, elevation and precipitation, while

425   provenance variation for P_{12}, P_{50} and P_{88} is more constrained by selective pressure related with

426   longitude and temperature. The significant remaining provenance effect for P_{12}, P_{50} in Corsica,

427   and P_{50}, P_{88}, Ks, circumference and survival in Gard suggests that some environmental selective

428   pressure in the natural area are not accounted by the geographical and climatic variables of the

429   study. Other non-selective evolutionary mechanisms accounted by this provenance effect may

430   also have contributed to the provenance variation.

431   The lower survival rate in Corsica did not reduce the phenotypic variation (Table 6). On

432   the contrary, trait variation is generally higher in Corsica than in Gard. The most variable traits in

433   both test sites are Ks and Slope, and the less variable ones are P_{50} and P_{88}. The low provenance

434 variation found for P_{50} and P_{88} has often been observed and could explain why in *Fagus*

435 *sylvatica*, *Pinus pinaster* and *Pinus hartwegii*, no significant between-provenance variation was

436 found for these hydraulic variables (Cochard *et al.*, 2008; Lamy *et al.*, 2011; Wortemann *et al.*,

437 2011; Sáenz-Romero *et al.*, 2013). A high statistical power is necessary to reveal, when it exists,

438 the low provenance variation for these traits.

439

440 ***Washington-Oregon and Californian provenances***

441   In the introduction, we hypothesized that the Californian provenances were more adapted

442 to the climate of Gard and Corsica than the Washington and Oregon ones. Our results show that

443 the situation is more complex. In the dryer Corsica site, the INCA provenances are the most

444 cavitation resistant (Fig. **5**), while the WA and OR provenances are as resistant as the COCA

445 ones. WA and one INCA provenance (BUR) have a higher Slope. The lowest survival rate is 48

446 % for both WA and OR (Table 4). These provenances are also more cavitation resistant in

447 Corsica than in Gard, where their survival rate is higher (P_{50} and P_{88}, Table 4). Hence, it may

448 well be that the highest selective pressure in Corsica eliminated the less cavitation resistant

449 individuals of WA and OR and increased their average cavitation resistance. The most

450 vulnerable provenance in both trials is SCR (Table 4, Fig. **5**), with a survival rate of 61 % in

451 Corsica. The PCA_Geo/Clim does not provide any obvious geographic or climatic explanation

452 for the high vulnerability of this COCA provenance.

453   In Gard, the distinction between the slightly more cavitation resistant INCA provenances

454 and the COCA provenances is less clear. Except for the special position of SCR, the less drought

455 resistant provenances are WA and OR, with a low cavitation resistance and a high Slope. Most

456 Douglas-fir drought resistance studies in common gardens used different provenance groups,

457   with different types of drought resistance traits. Our results confirm the consistent trend of

458   increasing drought resistance from the coastal to the interior and south interior part of the

459   Douglas-fir natural range found by Bo Larsen (1978), Eilmann *et al.* (2013), Sergent *et al.*

460   (2014), Bansal *et al.* (2015), Montwé *et al.* (2015), Du *et al.* (2016), Hess *et al.* (2016), Kleiber

461   *et al.* (2017), and Du *et al.* (2018) with a large variety of traits, experimental conditions,

462   provenance sets and numbers. Furthermore, our study is the first one showing this consistent

463   trend using cavitation resistance, the most recognized method for assessing resistance to drought.

464   The climate of the Douglas-fir introduction area in France is colder and wetter than that

465   of the trial sites. For example, in the Orne, Normandy, a region where Washington-Oregon

466   origins are planted widely, the summer precipitation is 190 mm, and the annual mean

467   temperature is 10.1°C, while they are 121, 187 mm, 13.0, and 12.8°C in Corsica and Gard,

468   respectively. Gard has a 2°C warmer climate with no change in precipitation, while Corsica's

469   climate is not only 2°C warmer but also dryer. The high mortality rate of the Washington-

470   Oregon provenances in the Corsica site suggests that it takes not only a 2°C temperature increase

471   but also a 70 mm summer precipitation decrease to exceed the adaptation potential of these

472   provenances.

473

474   *Phenotypic plasticity of conductivity loss*

475   The phenotypic plasticity of hydraulic traits allows species to deal with fast climate

476   change (Choat *et al.*, 2018). According to Choat *et al.* (2018), "adaptive plasticity of hydraulic

477   traits may enable the acclimatization of entire populations within the necessary timescales".

478   Rigorous quantification of phenotypic plasticity involves the construction of norms of reaction,

479   which are not often easy to fit (Feinard-Duranceau *et al.*, 2018). Vulnerability curves are by

480   definition reaction norms that display how a given genotype dynamically behaves during a

481   change in drought intensity. This quantitative information is mainly contained in the variation of

482   one parameter of the sigmoidal model of the vulnerability curves (Pammenter & Van der

483   Willigen, 1998): Slope. This dynamic trait describes the speed of conductivity loss (as cavitation

484   spread) along an environmental gradient, xylem pressure (as simulated drought intensity). As the

485   other variables extracted from the vulnerability curves, it is a component of drought-resistance.

486   Phenotypic plasticity of conductivity loss (PPCL) is time-related plasticity, as opposed to space-

487   related plasticity (Feinard-Duranceau *et al.*, 2018). Therefore, we found significant site variation

488   and provenance variation in both test-sites for PPCL. According to PPCL, Gard is the less

489   drought-resistant site, while WA and OR are the less drought-resistant provenances. Slope is also

490   one of the most variable hydraulic traits of our study and thus submitted to selection, whether

491   natural or artificial. The genetic determinism of PPCL or Slope is simpler than that of the other

492   hydraulic traits, since its significant provenance variation is explained by only one principal

493   component of PCA_Geo/Clim, PC1_Geo/Clim, i.e., principally by latitude, elevation and

494   summer precipitation (Table 5 and Supporting Information, Table S1). So far, to our knowledge,

495   only space-related phenotypic plasticity of hydraulic traits has been studied and was generally

496   found to be low (Corcuera *et al.*, 2011; Lamy *et al.*, 2014; Aranda *et al.*, 2017; González-Muñoz

497   *et al.*, 2018; Jinagool *et al.*, 2018). Our results suggest that not only P50 is a key-trait for

498   studying the complex determinism of resistance to drought but also the other parameters of the

499   vulnerability curves (P12 and P88), Ks and Slope, as well as, maybe, other traits not available in

500   this study. Slope appears to be an especially interesting, highly variable, potential selection trait,

501   depicting the phenotypic plasticity of the conductivity loss, with significant site and provenance

502   variation and a relatively simple provenance determinism.

503

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

11

525 phenotypic variables with a great statistical power, remains an essential source of knowledge for

526 predicting the future behaviour of the forests submitted to the climate change.

527

528 **Acknowledgements**

538

539 **Author contributions**

540 T.C. is the PhD student in charge of the study. P.R. and H.C. are the PhD thesis directors and co-

541 supervisors of T.C. P.R is the coordinator of the EMPIR and TOPWOOD projects. The PhD and

542 study experiments were designed by P.R. and H.C. and conducted by T.C. under the supervision

543 of P.R. and H.C. T.C. analysed the data under the supervision of P.R. and H.C., with significant

544 contributions and supervision by V.S. The manuscript was written by T.C. under the supervision

545 of P.R. and H.C. and was corrected and validated by all of the authors.

546

547   **References**

548   **Aitken SN, Yeaman S, Holliday JA, Wang T, Curtis-McLane S. 2008.** Adaptation, migration

549   or extirpation: climate change outcomes for tree populations. *Evolutionary Applications*

550   **1**: 95–111.

551   **Allen CD, Breshears DD, McDowell NG. 2015.** On underestimation of global vulnerability to

552   tree mortality and forest die-off from hotter drought in the Anthropocene. *Ecosphere* **6**:

553   art129.

554   **Aranda I, Bahamonde HA, Sánchez-Gómez D. 2017.** Intra-population variability in the

555   drought response of a Beech (*Fagus sylvatica* L.) population in the southwest of Europe.

556   *Tree Physiology* **37**: 938–949.

557   **Bansal S, Harrington CA, Gould PJ, St.Clair JB. 2015.** Climate-related genetic variation in

558   drought-resistance of Douglas-fir (*Pseudotsuga menziesii*). *Global Change Biology* **21**:

559   947–958.

560   **Bansal S, Harrington CA, St. Clair JB. 2016.** Tolerance to multiple climate stressors: a case

561   study of Douglas-fir drought and cold hardiness. *Ecology and Evolution* **6**: 2074–2083.

562   **Barigah TS, Charrier O, Douris M, Bonhomme M, Herbette S, Améglio T, Fichot R,**

563   **Brignolas F, Cochard H. 2013.** Water stress-induced xylem hydraulic failure is a causal

564   factor of tree mortality in Beech and Poplar. *Annals of Botany* **112**: 1431–1437.

565   **Bates D, Mächler M, Bolker B, Walker S. 2015.** Fitting linear mixed-effects models using

566   lme4. *Journal of Statistical Software* **67**: 1–48.

567   **Bo Larsen J. 1978.** Untersuchungen über die winterliche trockenresistenz von 10 herkünften der

568   Douglasie (*Pseudotsuga menziesii*). *Forstwissenschaftliches Centralblatt* **97**: 32–40.

569 **Boiffin J, Badeau V, Bréda N. 2017.** Species distribution models may misdirect assisted

570 migration: insights from the introduction of Douglas-fir to Europe. *Ecological*

571 *Applications* **27**: 446–457.

572 **Bourne AE, Creek D, Peters JMR, Ellsworth DS, Choat B. 2017.** Species climate range

573 influences hydraulic and stomatal traits in Eucalyptus species. *Annals of Botany* **120**:

574 123–133.

575 **Brendel O. 2014.** Is the coefficient of variation a valid measure for variability of stable isotope

576 abundances in biological materials? *Rapid Communications in Mass Spectrometry* **28**:

577 370–376.

578 **Brodribb TJ, Bowman DJMS, Nichols S, Delzon S, Burlett R. 2010.** Xylem function and

579 growth rate interact to determine recovery rates after exposure to extreme water deficit.

580 *New Phytologist* **188**: 533–542.

581 **Campbell RK, Sorensen FC. 1973.** Cold-acclimation in seedling Douglas-Fir related to

582 phenology and provenance. *Ecology* **54**: 1148–1151.

583 **Canchola JA, Tang S, Hemyari P, Paxinos E, Marins E. 2017.** Correct use of percent

584 coefficient of variation (%CV) formula for log- transformed data. *MOJ Proteomics &*

585 *Bioinformatics* **6**: 1–3.

586 **Chen P-Y, Welsh C, Hamann A. 2010.** Geographic variation in growth response of Douglas-fir

587 to interannual climate variability and projected climate change. *Global Change Biology*

588 **16**: 3374–3385.

589 **Chmura DJ, Guzicka M, McCulloh KA, Zytkowiak R. 2016.** Limited variation found among

590 Norway spruce half-sib families in physiological response to drought and resistance to

591 embolism. *Tree Physiology* **36**: 252–266.

592   **Choat B, Brodribb TJ, Brodersen CR, Duursma RA, López R, Medlyn BE. 2018.** Triggers

593   of tree mortality under drought. *Nature* **558**: 531–539.

594   **Choat B, Jansen S, Brodribb TJ, Cochard H, Delzon S, Bhaskar R, Bucci SJ, Feild TS,**

595   **Gleason SM, Hacke UG *et al*. 2012.** Global convergence in the vulnerability of forests

596   to drought. *Nature* **491**: 752–755.

597   **Cochard H. 2002.** A technique for measuring xylem hydraulic conductance under high negative

598   pressures. *Plant, Cell and Environment* **25**: 815–819.

599   **Cochard H, Barigah ST, Kleinhentz M, Eshel A. 2008.** Is xylem cavitation resistance a

600   relevant criterion for screening drought resistance among *Prunus* species? *Journal of*

601   *Plant Physiology* **165**: 976–982.

602   **Cochard H, Damour G, Bodet C, Tharwat I, Poirier M, Améglio T. 2005.** Evaluation of a

603   new centrifuge technique for rapid generation of xylem vulnerability curves. *Physiologia*

604   *Plantarum* **124**: 410–418.

605   **Corcuera L, Cochard H, Gil-Pelegrin E, Notivol E. 2011.** Phenotypic plasticity in mesic

606   populations of *Pinus pinaster* improves resistance to xylem embolism (P50) under severe

607   drought. *Trees* **25**: 1033–1042.

608   **Corcuera L, Gil-Pelegrin E, Notivol E. 2012.** Differences in hydraulic architecture between

609   mesic and xeric *Pinus pinaster* populations at the seedling stage. *Tree Physiology* **32**:

610   1442–1457.

611   **Crow JF, Kimuar M. 1970.** An introductrion to population genetics theory. *An introduction to*

612   *population genetics theory.*

613   **Dalla-Salda G, Fernández ME, Sergent A-S, Rozenberg P, Badel E, Martinez-Meier A.**

614   **2014.** Dynamics of cavitation in a Douglas-fir tree-ring: transition-wood, the lord of the

615   ring? *Journal of Plant Hydraulics* **1**: e–0005.

616   **Dalla-Salda G, Martinez-Meier A, Cochard H, Rozenberg P. 2011.** Genetic variation of

617   xylem hydraulic properties shows that wood density is involved in adaptation to drought

618   in Douglas-fir (*Pseudotsuga menziesii* (Mirb.)). *Annals of Forest Science* **68**: 747–757.

619   **Delzon S, Douthe C, Sala A, Cochard H. 2010.** Mechanism of water-stress induced cavitation

620   in conifers: bordered pit structure and function support the hypothesis of seal capillary-

621   seeding. *Plant, Cell & Environment* **33**: 2101–2111.

622   **DeWitt TJ, Scheiner SM. 2004.** *Phenotypic plasticity: functional and conceptual approaches*.

623   Oxford, UK: Oxford University Press.

624   **Domec JC, Gartner BL. 2002.** How do water transport and water storage differ in coniferous

625   earlywood and latewood? *Journal of Experimental Botany* **53**: 2369–2379.

626   **Du B, Jansen K, Kleiber A, Eiblmeier M, Kammerer B, Ensminger I, Gessler A,**

627   **Rennenberg H, Kreuzwieser J. 2016.** A coastal and an interior Douglas-fir provenance

628   exhibit different metabolic strategies to deal with drought stress. *Tree Physiology* **36**:

629   148–163.

630   **Du B, Kreuzwieser J, Dannenmann M, Junker LV, Kleiber A, Hess M, Jansen K,**

631   **Eiblmeier M, Gessler A, Kohnle U *et al*. 2018.** Foliar nitrogen metabolism of adult

632   Douglas-fir trees is affected by soil water availability and varies little among

633   provenances. *PLoS One* **13**: e0194684.

634   **Eilmann B, de Vries SMG, den Ouden J, Mohren GMJ, Sauren P, Sass-Klaassen U. 2013.**

635   Origin matters! Difference in drought tolerance and productivity of coastal Douglas-Fir

636   (*Pseudotsuga menziesii* (Mirb.)) provenances. *Forest Ecology and Management* **302**:

637   133–143.

638   **Feinard-Duranceau M, Berthier A, Vincent-Barbaroux C, Marin S, Lario F-J, Rozenberg**

639   **P. 2018.** Plastic response of four maritime pine (*Pinus pinaster* Aiton) families to

640   controlled soil water deficit. *Annals of Forest Science* **75**: 47.

641   **González-Muñoz N, Sterck F, Torres-Ruiz JM, Petit G, Cochard H, von Arx G, Lintunen**

642   **A, Caldeira MC, Capdeville G, Copini P *et al*. 2018.** Quantifying in situ phenotypic

643   variability in the hydraulic properties of four tree species across their distribution range in

644   Europe. *PLoS One* **13**: e0196075.

645   **Grossiord C, Sevanto S, Adams HD, Collins AD, Dickman LT, McBranch N, Michaletz ST,**

646   **Stockton EA, Vigil M, McDowell NG. 2017.** Precipitation, not air temperature, drives

647   functional responses of trees in semi-arid ecosystems. *Journal of Ecology* **105**: 163–175.

648   **Hartmann H, Adams HD, Anderegg WRL, Jansen S, Zeppel MJB. 2015.** Research frontiers

649   in drought-induced tree mortality: crossing scales and disciplines. *New Phytologist* **205**:

650   965–969.

651   **Hess M, Wildhagen H, Junker LV, Ensminger I. 2016.** Transcriptome responses to

652   temperature, water availability and photoperiod are conserved among mature trees of two

653   divergent Douglas-fir provenances from a coastal and an interior habitat. *BMC Genomics*

654   **17**: 682.

655   **Jinagool W, Lamacque L, Delmas M, Delzon S, Cochard H, Herbette S. 2018.** Is there

656   variability for xylem vulnerability to cavitation in Walnut tree cultivars and species

657   (*Juglans* Spp.)? *HortScience* **53**: 132–137.

658 **Kawecki TJ, Ebert D. 2004.** Conceptual issues in local adaptation. *Ecology Letters* **7**: 1225–

659   1241.

660 **Kleiber A, Duan Q, Jansen K, Junker LV, Kammerer B, Rennenberg H, Ensminger I,**

661   **Gessler A, Kreuzwieser J. 2017.** Drought effects on root and needle terpenoid content of

662   a coastal and an interior Douglas-Fir provenance. *Tree Physiology* **37**: 1648–1658.

663 **Klein T, Di Matteo G, Rotenberg E, Cohen S, Yakir D. 2013.** Differential ecophysiological

664   response of a major Mediterranean pine species across a climatic gradient. *Tree*

665   *Physiology* **33**: 26–36.

666 **Lamy J-B, Bouffier L, Burlett R, Plomion C, Cochard H, Delzon S. 2011.** Uniform selection

667   as a primary force reducing population genetic differentiation of cavitation resistance

668   across a species range. *PLoS One* **6**: e23476.

669 **Lamy J-B, Delzon S, Bouche PS, Alia R, Vendramin GG, Cochard H, Plomion C. 2014.**

670   Limited genetic variability and phenotypic plasticity detected for cavitation resistance in

671   a Mediterranean pine. *New Phytologist* **201**: 874–886.

672 **Lê, S., Josse, J. & Husson, F., 2008.** FactoMineR: An R Package for Multivariate Analysis. *J.*

673   *of Statistical Software*, 25(1), pp.1–18. Available at:

674   http://factominer.free.fr/more/article_FactoMineR.pdf [Accessed July 2, 2018].

675 **Li X, Blackman CJ, Choat B, Duursma RA, Rymer PD, Medlyn BE, Tissue DT. 2018.** Tree

676   hydraulic traits are coordinated and strongly linked to climate-of-origin across a rainfall

677   gradient. *Plant, Cell & Environment* **41**: 646–660.

678 **López R, López de Heredia U, Collada C, Cano FJ, Emerson BC, Cochard H, Gil L. 2013.**

679   Vulnerability to cavitation, hydraulic efficiency, growth and survival in an insular pine

680   (*Pinus canariensis*). *Annals of Botany* **111**: 1167–1179.

681 **Montwé D, Spiecker H, Hamann A. 2015.** Five decades of growth in a genetic field trial of

682 Douglas-Fir reveal trade-offs between productivity and drought tolerance. *Tree Genetics*

683 *& Genomes* **11**: 1–11.

684 **Moran E, Lauder J, Musser C, Stathos A, Shu M. 2017.** The genetics of drought tolerance in

685 conifers. *New Phytologist* **216**: 1034–1048.

686 **Nabais C, Hansen JK, David-Schwartz R, Klisz M, López R, Rozenberg P. 2018.** The effect

687 of climate on wood density: what provenance trials tell us? *Forest Ecology and*

688 *Management* **408**: 148–156.

689 **Pammenter NW, van der Willigen C. 1998.** A mathematical and statistical analysis of the

690 curves illustrating vulnerability of xylem to cavitation. *Tree Physiology* **18**: 589–593.

691 **R Development Core Team. 2005.** R: A language and environment for statistical computing. R

692 Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL:

693 http://www.R-project.org.

694 **Sáenz-Romero C, Lamy J-B, Loya-Rebollar E, Plaza-Aguilar A, Burlett R, Lobit P, Delzon**

695 **S. 2013.** Genetic variation of drought-induced cavitation resistance among *Pinus*

696 *hartwegii* populations from an altitudinal gradient. *Acta Physiologiae Plantarum* **35**:

697 2905–2913.

698 **Savolainen O, Pyhäjärvi T, Knürr T. 2007.** Gene flow and local adaptation in trees. *Annual*

699 *Review of Ecology, Evolution, and Systematics* **38**: 595–619.

700 **Sergent A-S, Bréda N, Sanchez L, Bastein J-C, Rozenberg P. 2012.** Coastal and interior

701 Douglas-Fir provenances differ in growth performance and response to drought episodes

702 at adult age. *Annals of Forest Science* **71**: 709–720.

703   **Sergent A-S, Rozenberg P, Bréda N. 2014.** Douglas-Fir is vulnerable to exceptional and

704   recurrent drought episodes and recovers less well on less fertile sites. *Annals of Forest*

705   *Science* **71**: 697–708.

706   **Tyree MT, Sperry JS. 1989.** Vulnerability of xylem to cavitation and embolism. *Annual Review*

707   *of Plant Biology* **40**: 19–36.

708   **Urli M, Porte AJ, Cochard H, Guengant Y, Burlett R, Delzon S. 2013.** Xylem embolism

709   threshold for catastrophic hydraulic failure in angiosperm trees. *Tree Physiology* **33**: 672–

710   683.

711   **Wang T, Hamann A, Spittlehouse D, Carroll C. 2016.** Locally downscaled and spatially

712   customizable climate data for historical and future periods for North America. *PLoS One*

713   **11**: e0156720.

714   **Wortemann R, Herbette S, Barigah TS, Fumanal B, Alia R, Ducousso A, Gomory D,**

715   **Roeckel-Drevet P, Cochard H. 2011.** Genotypic variability and phenotypic plasticity of

716   cavitation resistance in *Fagus sylvatica* L. across Europe. *Tree Physiology* **31**: 1175–

717   1182.

718   **Zwillinger D, Kokoska S. 2000.** Standard probability and statistics tables and formulae.

719   *Technometrics* **43**: 249–250.

720

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

743 the additional variables. PC1_Geo/Clim and PC2_Geo/Clim, PC3_Geo/Clim are the principal

744 components extracted from the PCA_Geo/Clim.

745

746

747 **Tables**

748 Table 1: Studied provenances features

749

750 Table 2: Trials characteristics. Climatic data come from the closest Météo-France weather

751 stations to the trials for the 1992 to 2015 period. Summer Rainfall is the sum of rainfall from

752 June to August. MAT is for Mean Annual Temperature, PPT means annual rainfall and PPT_ sm

753 are for the summer rainfall.

754

755 Table 3: Spearman's rank correlation coefficient between studied variables and significant values

756 (∗ p < 0.05; ∗∗ p < 0.01; ∗∗∗ p < 0.001). The upper diagonal of the table is for the Gard trial

757 while the lower diagonal corresponds to the Corsica trial.

758

759 Table 4: Mean and confidence interval values of the studied traits for the ten provenances

760 (mean ± confidence interval).

761

762 Table 5: Significance of the effect of the PCA_Geo/Clim axes and the provenance factor on the

763 variance of the phenotypic variables (likelihood ratio test of linear mixed model (3)).

764

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

766

767

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.