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Coastal and interior Douglas-fir provenances differ in growth performance and response to drought episodes at adult age

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Abstract

• *Context* Since the 2003 drought and heat wave, Douglas-fir dieback has been reported in France in trees older than 30 years. Consequently, it is questioned whether selected Douglas-fir provenances are suited to the frequent and severe drought events which are forecast due to climate change.
• *Aims* Our objective was to contribute to the screening of variability in productivity and growth response to soil-water deficit of mature trees from provenances not currently used for plantation in France.
• *Methods* We sampled 22 provenances, including coastal and interior Douglas-fir, covering a wide part of its natural distribution, from Oregon to California for coastal provenances and from British Columbia to New Mexico for interior provenances. These provenances were planted at the mid 1970s in two provenance trials located in the south-west area of France. Variability of productivity, of wood density, and of radial growth in response to drought episodes among provenances was quantified and related to soil-water deficit computed by daily water balance calculations.
• *Results* Whatever the provenance, annual radial growth is highly dependent on local soil-water deficit (Felines $R^2 = 0.57$, Le Treps $R^2 = 0.49$). Radial growth and wood properties exhibit large differences between provenances at 30 years old. Variability between provenances for all wood characteristics studied is mainly structured geographically. Coastal provenances perform best for productivity at 30 years old (619 cm^2±59), and exhibit a small growth reduction in 2004, the second successive year of drought (−10.7 %±3.8). Surprisingly, the southern interior provenances from the driest environments in the natural range show a large growth reduction in 2004 (−30.5 %±5.2).
• *Conclusions* The provenances tested exhibited significant differences in growth performance and growth reduction induced by the soil-water deficit. The approach coupling retrospective analysis of radial growth on mature trees and water balance modelling is relevant for evaluating provenance adaptation to more frequent or severe drought episodes.

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1 Introduction

Douglas-fir was first introduced in France in 1850, and has been widely planted since 1960. Today, it is one of the most frequently planted conifer species in France. The interest of forest owners in this fast-growing species is explained by its appreciated high-quality wood properties. In the last decade, mortality and dieback have been reported in several Douglas-fir production areas in France. These losses mainly occurred

after the drought of 2003 (Sergent et al. 2014), which affected a large part of Europe and was particularly long-lasting and intense (Bréda et al. 2006; Rebetez et al. 2006). Douglas-fir mortality represented 35 % of the mortalities reported in 2003 for all forest tree species in France. Declines on mature trees were observed for several years after 2003. Sergent et al. (2014) demonstrated, by coupling dendrochronological approaches and water balance modelling, that declines were induced by extreme or recurrent drought events. The frequency and the severity of drought events, such as that in 2003, are expected to increase with ongoing climatic change (Meehl Gerald and Tebaldi 2004; Schär et al. 2004). The production capacity of Douglas-fir in France is therefore questioned, in the context of the forecasted scenario of more frequent and severe drought events.

The natural distribution of Douglas-fir is one of the widest among tree species, and covers an extensive geographical and climatic gradient (see Fig. 1a). Douglas-fir is divided into two major varieties, the coastal variety *Pseudotsuga menziensii* var. *menziensii* (or "green Douglas-fir") and the interior variety *P. menziensii* var. *glauca* (or "Rocky Mountain Douglas-fir"). In Europe, and more specifically in France, all Douglas-fir plantation material has originated from a limited part of the natural area of the coastal variety *menziesii*. A vast majority of the stands close to rotation age, including the declining stands, as well as the breeding population and the seed orchards of the French Douglas-fir breeding programme, comprise the fast-growing coastal provenances of Washington and Oregon States. As a result, all or nearly all Douglas-fir seedlings planted today in France are descendants of the coastal Washington–Oregon seed orchards.

Few provenance studies have been conducted in response to drought in Europe and in the natural range. Most of them were carried out on very young trees or seedlings, on a very limited number of provenances and in controlled conditions (Pharis and Ferrell 1966; White 1987; Aussenac et al. 1989; Joly et al. 1989). More recently, studies were conducted on older trees, and have shown a genetic variation for productivity (Krakowski and Stoehr 2009) and for drought response (Chen et al. 2010; Eilmann et al. 2013), but never calculated soil-water deficit, the only way to properly quantify the water shortage for the trees.

Interestingly, some of the oldest French collections included not only coastal Oregon and Washington provenances, but also coastal Californian and interior provenances. These provenances are currently neither planted in the French Douglas-fir production regions nor used in the French breeding programme. It is therefore of interest to assess the growth of these Californian and interior provenances, as well as the degree to which they respond to drought.

We studied two provenance trials including coastal Californian and interior provenances planted in the 1970s, Félines and Le Treps. They are located outside of the French Douglas-fir production area, in the south of France, where they sometimes face severe soil-water deficit. While these trials do not include any fast-growing provenance from the Coastal-Oregon and Washington zone, the collection includes 22 provenances from a vast and climatically-contrasting part of the natural range: in the USA, from the Southern-Oregon and Californian coastal areas to the southern interior states of Arizona, New Mexico and Colorado and up to the interior of British Columbia in Canada. The site–provenance combination used in our study is very unusual and especially interesting to address the issue of the diversity of soil-water deficit response near harvesting age with an annual temporal resolution.

We decided to address the following specific questions:

–   In these two trials, is soil-water deficit a limiting factor of annual radial growth?
–   Is there variability between provenances for productivity near harvesting age, for wood microdensity variables, and for growth response to drought episodes?

The productivity of the provenances for these three traits with regard to drought response will be discussed with regard to their geographical origins.

2 Materials and methods

2.1 Trials description

Two provenance trials planted by the French National Institute of Agronomic Research (see Fig. 1b) were selected for this study. The history of these trials started with the collection of seeds in the natural range through the IUFRO (International Union of Forest Research Organizations) programme between 1966 and 1969. These seeds were then germinated and grown in a nursery. The two sites were clear-cut prior to planting. Vegetation was mechanically controlled 4 times during the first 12 years. During the first 20 years, trees were assessed periodically for growth, survival, and form.

Félines n°709.3 is a provenance trial planted in 1973 in the Forêt Domaniale du Minervois (Aude 11, France). Sub-soiling was performed prior to planting, which consisted of 2+0 seedlings at 2.5 m × 2 m spacing. The provenances were separated by varieties. For each variety, trees were planted in 60 randomized complete blocks of one tree plot per provenance. Thirteen years after planting, survival was low (44.9 %) and dead trees were not replaced. The site was thinned several times between 2002 and 2004.

Le Treps n°714 1–2 is a provenance trial test planted in 1976, in the Forêt Domaniale des Maures (Var 83, France). The site was clear-cut prior to planting, consisting of 1+1 seedlings at 3 m × 1.33 m spacing. The provenances were laid out in 3 x 2 tree plots in an incomplete block design with five
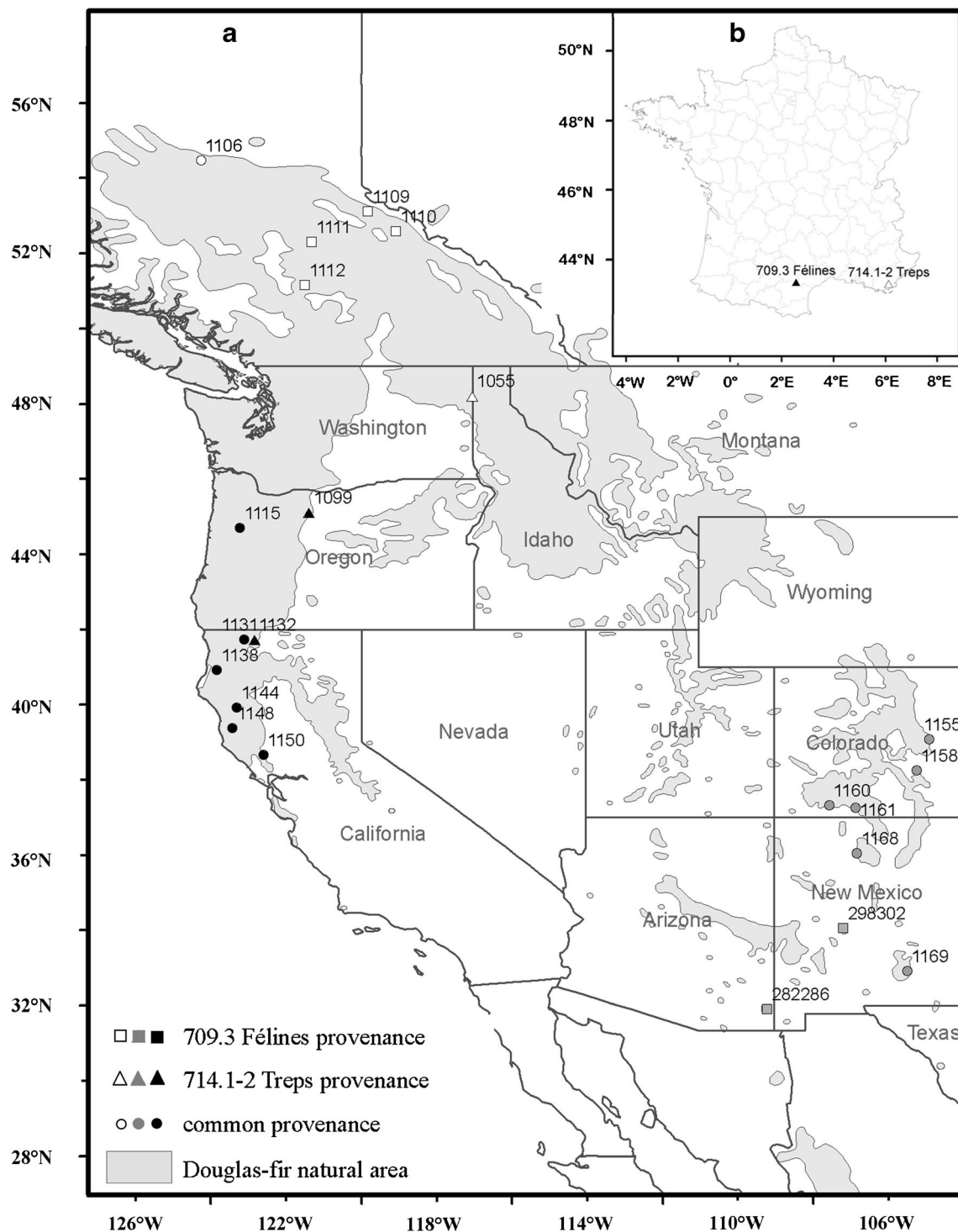
Fig. 1 Location of the provenances in the Douglas-fir natural area (**a**) and location of the trials in France (**b**). Colours indicate different geographical origins: *black* for Californian and Oregon coastal provenances, *grey* for south interior provenances, *white* for northern provenances from British Columbia

replications. Eleven years after planting, survival was high (81 %). The site was thinned once in 1993.

The identities, localisation and climatic characteristics in the natural area of the sampled provenances are summarised in Table 1. The ecological characteristics of the two trials are summarized in Table 2.

2.2 Data collection

For each site, six to 21 trees per provenance (Table 1) were cored at breast height up to the pith by using a mechanical Pressler borer of 5 mm in diameter to measure annual radial growth. Whenever the number of available trees per

Table 1 Identities, localisation, and climatic characteristics in the natural area of the sampled provenances ranging from Oregon (OR) and California (CA) for coastal provenances and from British Columbia (BC), Washington (WA) Colorado (CO), New Mexico (NM) and Arizona (AR) for interior provenances

Provenance				Local characteristics			Number of trees sampled	
State	Code IUFRO	Names	Elevation (m)	MAT (°C)	MAP (mm)	AHM	709.3 Félines	714.1–2 Le Treps
OR	1099	Pine Grove	732	9.6	542	36.2	–	20
	1115	Corvallis	76	11.2	1221	17.4	9	19
CA	1131	Scott Bar	1006	10.4	989	20.6	10	20
	1132	Fort Jones	1158	9.2	773	24.8	–	19
	1138	Arcata I	488	11.8	1701	12.8	12	14
	1144	Covelo I	914	12.6	1514	14.9	8	20
	1148	Willits	548	12.7	1351	16.8	10	21
	1150	St. Helena Mountain	716	13.6	1328	17.8	10	17
BC	1106	Fort St. James	853	2.1	487	24.8	20	6
	1109	Dunster	818	2.7	665	19.1	20	–
	1110	Clemia	879	3.0	970	13.4	19	–
	1111	Horsefly	818	3.8	571	24.2	20	–
	1112	Clinton	1030	3.6	337	40.4	19	–
WA	1055	New Port	727	7.1	692	24.7	–	16
CO	1155	Monument Nursery	2212	7.1	502	34.1	11	6
	1158	Welmore Newlin	2697	6.0	528	30.3	10	12
	1160	Pine River Bayfield	2255	7.0	708	24	13	12
	1161	Pagosa Springs	2438	5.4	623	24.7	14	18
NM	1168	Clear Creek	NA	2.9	1018	12.7	12	11
	1169	New of St James Canyon	2438	8.8	510	36.9	19	13
	282286	Chirachua Mountain	1875	12.3	756	29.5	15	–
AR	298302	Magdalina Mountain Hop Canyon	2485	9.0	446	42.6	10	–

MAT (mean annual temperature), MAP (Mean annual precipitation) and AHM (annual heat-moisture index) extracted from the application ClimateWNA_v4.62 (Wang et al. 2012) for the period 1961–1990

provenance was over 20, the trees to be cored were randomly selected from the pool of available trees. A total of 505 tree cores were then collected for analysis. According to the methodology described by Polge and Nicholls (1972), each increment core was air-dried, and sawn into 2-mm constant thickness longitudinal strips (Perrin and Ferrand 1984), at right angles to the fibre direction They were exposed 15 min into X-ray radiation together with a 12-density-steps calibration wedge, the source being 1.57 m from the samples, using Kodak Industrex M100 film and standard electrical conditions (accelerating tension=9 kV; flux intensity=10 mA). The resulting radiographs of the samples were digitized at 1,000 dpi resolution using a scanner (Epson 1680 Pro). The images were analysed using specific image analysis software (Windendro) (Guay et al. 1992). Ring width was measured. Density value was computed along the profile at a resolution of 25.4 μm. In each ring, the limit between earlywood and latewood was defined as the density point, with the density value being equal to the mean between the maximum and the minimum density. The following ring variables were calculated: mean ring density (MRD), minimum ring density (MID), maximum ring density (MAD), earlywood (EWD) and latewood (LWD) mean density, latewood proportion (LWP), and within-ring standard deviation (STD), as a measure of the intra-ring density dispersion. Earlywood (or latewood) mean density was computed as the average ring density of all values

Table 2 Ecological features of the experimental sites in France

Sites	Elevation (m)	Aspect	Extractable water (mm)	Geology	Leaf area index	Mean annual precipitation (mm)	Mean annual temperature (°C)
708.3 Félines	650	South-east	78	Schist	5	1609	14.3
714.1–2 Le Treps	620	East	84	Gneiss	8	1241	13.8

lower (or higher) than the earlywood–latewood limit. Minimum (or maximum) ring density was computed as the average of the lowest (or highest) 5 % of density values. Finally, an average at tree level between 1993 and 2007 was computed for each density variable. This period of 14 years corresponds to the combination of available climatic data, and retrospectively measured annual growth and density data excluding ring closer to the pith, as they correspond to juvenile wood.

2.3 Basal area and radial growth index calculation

Ring widths were measured along the core from the pith to the bark. Ring width time-series were cross-dated using Interdat software (Dupouey J.L., unpublished). Basal area increment (BAI) was computed from ring width, assuming circularity of the rings and taking into account the distance to the pith. The basal area (BA) in cm^2 of each tree was calculated, as cumulated BAI from the pith to the ring corresponding to the age of 30 years old (year 2006 in Le Treps and 2003 in Felines). This method allowed quantification of the productivity at the same age in both sites. BAI were used to characterize climatic variation in tree radial growth. All BAI series were standardized to allow comparison of the growth response to soil-water deficit events of provenances. Trends in the radial growth time series that were likely to be related to age and long-term growth dynamic were removed from each individual series using a cubic smoothing spline allowing the analysis of the high frequency signal related to annual climatic variations. The cubic smoothing spline with a 50 % frequency response cut-off of 15 years (Cook and Perters, 1981) was fitted along all the ring series (all rings from pith to the bark). A dimensionless growth index (GI_{year}) was calculated for each tree and year, as the ratio of the measured radial growth to the predicted growth at each ring age. GI_{year} is expressed in percentage, with 100 % corresponding to the expected growth relative to the age. Hereafter, all references to growth response refer to radial growth estimation using the growth index previously described, and all references to productivity refer to basal area at 30 years old.

2.4 Climatic data and soil water balance

Daily climatic data for precipitation, temperature, air humidity, wind speed, and global radiation were collected from the nearest Météo-France weather station to each site, in order to quantify local drought episodes. A daily forest water balance model, Biljou© (Granier et al. 1999) was used to compute elementary water fluxes (stand transpiration, rainfall interception, drainage, etc.) and the resulting daily soil-water content. This ecophysiological-based process model includes stand transpiration reduction through stomatal regulation as a function of soil-water deficit. According to Black (1979), Douglas-fir (and most other tree species) transpiration is affected when

soil-water content drops below 40 % of extractable water. The Biljou© model computes annual soil-water deficit index (dimensionless) taking into account the duration and intensity of the episodes of soil-water deficit reported to the extractable soil water.

Soil parameters (extractable water, bulk density, water content at permanent wilting point for each soil layer, fine root distribution) were determined for each trial by soil description based on a pedological survey. For water balance calculation, the leaf area index of the stand was fixed to an average value per trial of five for Félines and eight for Le Treps, according to stand densities. The combination of available climatic data and annual growth data allowed us to study 14 successive years of growth.

Climatic data within the natural range was obtained for each provenance using the application ClimateWNA_v4.62 (Wang et al. 2012). Mean annual precipitation (MAP), mean annual temperature (MAT) and annual heat-moisture index (AHM) [corresponding to (MAT+10)/(MAP/1 000)] were extracted from 1961–1990 monthly normal data, and were based on latitude, longitude, and elevation of seed harvesting records in the natural range.

2.5 Statistical analysis

The relationship between mean annual intensity of soil-water deficit and mean annual growth index was examined at the regional trial level using a linear regression for the period 1993–2007. In each trial, regression was also calculated excluding outlying points (2002 and 2007 in Le Treps and 1996 in Féline) corresponding to years with exceptional climatic characteristics.
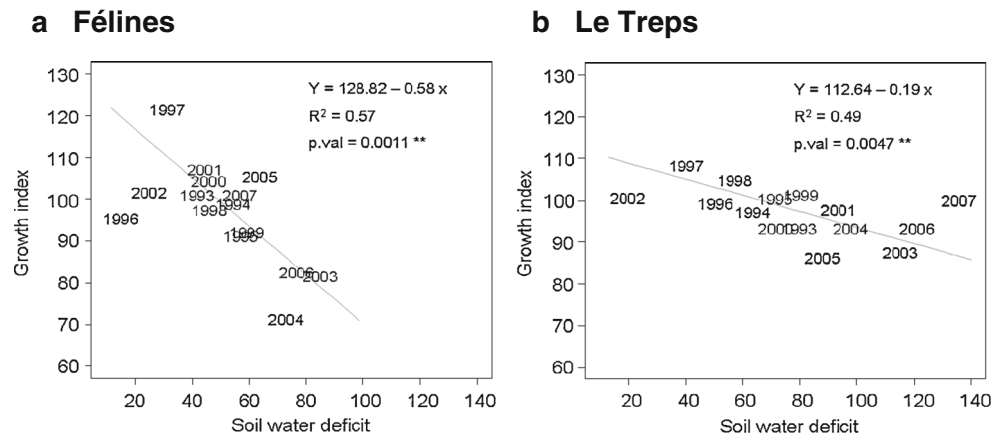
Provenance and site effects on basal area, density, and growth index response variables were analysed using a generalized linear model (GLM) approach. An ANOVA with Type III sum of squares was performed, using the following model:

$$Yij = \mu + Si + Rj + Si \times Rj + \varepsilon ij$$

with Y being the response variable, μ the general mean, S_i the effect of site i, R_j the effect of the provenance, $S_i \times R_j$ the interaction between site and provenance and ε the error term. The Shapiro–Wilk W and Levene tests were used to test for normality and homogeneity of variances respectively. Classic transformation variables were used whenever necessary and in order to meet the assumptions of normality and homoscedasticity required for analysis of the model. Provenances were compared by a multiple comparison procedure with Duncan's new multiple range test (MRT). Correlations between variables at site level were performed using a Pearson correlation. An ascendant hierarchical classification (AHC) coupled with

Fig. 2 Relationship between growth index (%) and soil water deficit (dimensionless) at site level averaged for all provenances: **a** in the Félines trial, and **b** in the Le Treps trial. Year 1996 of the Félines trial and years 2002 and 2007 of the Le Treps trial were not taken into account in the regression fit (see section 3.1)

3 Results

3.1 Soil-water deficit and growth index at site level

In both trials, annual growth index (GI) was significantly correlated to soil-water deficit during the period 1993–2007 (Fig. 2). These relationships, being significantly negative (R^2=0.57, p=0.0011 for Félines; and R^2=0.49, p=0.0045 for Le Treps) showed that Douglas-fir growth is harmed by soil-water deficit. For a given soil-water deficit, growth was more reduced in the Félines trial than in the Le Treps trial, where higher density led to a lower sensitivity to the water balance. For instance, 1996 and 2002 in Félines and 2002 in Le Treps were among the wettest years of the analysed period, while the year 2007 was characterized by exceptionally high spring temperatures, inducing wide earlywood. The year 2003 was one of the driest years

a principal component analysis (PCA) was conducted on the three main variables studied (productivity, density, and growth response to drought) in order to observe possible groupings among provenances. All means of variables at geographical group level are calculated using provenance means and presented as mean±standard deviation.

for both sites, closely followed by 2004 and 2006. These two consecutive years, 2003 and 2004, offered the opportunity to study variation between provenances in their growth index response to recurrent droughts. The drought index was higher in Le Treps than in Félines, especially in more recent years.

3.2 Variation among provenances for wood density, basal area, and growth during the two successive dry years 2003 and 2004

Provenance effect was always significant in the ANOVA test, where it accounted for different proportions of variation among traits (Table 3). The highest proportion of total variance explained by provenance was found for basal area (BA) (47 %), earlywood mean density (EWD) (38 %), density standard deviation (STD) (36 %) and latewood proportion (LWP) (30 %). The effect of site was significant for all variables except for LWP. Variance explained by site effect was generally lower than for provenance, capturing up to 20 % of total variance. Variance explained by provenance-by-site interactions is low (3 % to 7 %), and was significant only for basal area (BA) and growth index in 2004. The term accounting for the highest proportion of variance was the residual error for all variables, except for BA (Table 3).

Table 3 Variance components as a percentage of total model variance; significant parameters ($P \leq 0.05$) in bold for each variable

Source of variation	LWP	MRD	EWD	LWD	STD	BA	GI$_{2003}$	GI$_{2004}$
Site	0.00	0.07	0.06	0.12	0.03	0.20	0.03	0.17
Provenance	0.30	0.09	0.38	0.08	0.36	0.47	0.09	0.13
Site × Provenance	0.04	0.03	0.03	0.04	0.03	0.04	0.05	0.07
Residuals	0.66	0.81	0.53	0.76	0.58	0.29	0.83	0.63

WP: latewood proportion, MRD: mean ring density, LWD: mean latewood density, EWD: mean earlywood density, STD standard deviation of intra-ring density, BA: basal area, GI$_{2003}$ growth index in 2003, GI$_{2004}$ growth index in 2004

3.3 Provenance ranking at each site for wood density, basal area and growth during the 2 successive dry years, 2003 and 2004

The significant site–provenance interaction for the two variables (BA, GI_{2004}; Table 3) required the sites to be studied separately. Of the density variables, only EWD was taken into account and used for provenance ranking and classification. Two reasons for this choice can be proposed; first, EWD was the variable with the highest provenance effect, and second, earlywood density has been shown to be significantly related to hydraulic properties such as specific conductivity and resistance to cavitation in Douglas-fir (Dalla-Salda et al. 2011).

In both trials, EWD was higher (0.34 g.cm^{-3} to 0.39 g.cm^{-3}) for provenances from the southern distribution of the interior variety, corresponding to Arizona, Colorado, and New Mexico states; while generally lower values (0.29 g.cm^{-3} to 0.36 g.cm^{-3}) were observed for coastal and interior provenances from the northern natural area (Fig. 3a). Some changes in the provenance ranking for EWD were observed between both sites, but generally varieties showed distinct behaviours, with little intermixing of provenance performances across sites. The relative difference between extreme provenances with the lowest and highest EWD was 32 % in Félines and 25 % in Le Treps.

Concerning BA (Fig. 3b), coastal provenances showed higher values than their interior counterparts on both sites. There was a strong site effect, with Félines showing values on average twice those observed in the Le Treps trial. The provenance effect was also large, with a relative difference between extreme provenances of 364 % in Félines and 333 % in Le Treps.

During dry years, all provenances showed a growth index under the expected value of 100 %, as soil-water deficit led in general to reduced growth. There were two exceptions during the driest years: in Le Treps for the 1106 provenance in 2003 and for the 1150 provenance in 2004. In 2003, northern interior provenances appeared to be less affected in growth on both sites (+7 % to −16 %), while southern interior provenances had a medium to high reduction in growth (−6 % to −36 %); the reduction in growth of coastal Californian provenances was intermediate (−8 % to −25 %) (Fig. 3c and d). In Félines, GI was on average lower in 2004 and had higher inter-provenance differences when compared to 2003 (Fig. 3c), due to a sharper GI decrease in 2004 for southern interior provenances.

In the Le Treps trial, north interior provenances showed the highest growth reduction between 2003 and 2004 (Fig. 3d).

3.4 Provenances classified according to growth and wood properties

The first two principal components explained up to 88 %–89 % of the total variance of the provenance variation depending on the site (Fig. 4). For the Félines trial (Fig. 4a), the first component (PC1) explained 67.9 % of total variation, and it was overall positively correlated to the growth index in 2003 ($r=0.76$) and in 2004 ($r=0.89$), and negatively correlated to earlywood mean density ($r=-0.95$) and AHM ($r=-0.55$). Positive correlations were found for PC2 with the two other supplementary variables, MAP ($r=0.68$) and MAT ($r=0.74$).

In the Le Treps trial, the first component (PC1) explained 60 % of the total variance and was positively correlated to basal area ($r=0.93$), and to growth index in 2004 ($r=0.85$), and negatively correlated to earlywood mean density ($r=-0.89$). The supplementary variables were mainly positively correlated with the first component for MAT ($r=0.85$) and MAP ($r=-0.72$). The second component (PC2) was overall negatively correlated to the growth index in 2003 ($r=-0.98$).

The clustering classification grouped provenances into four main groups for the Félines trial (Fig. 4a), and into five main groups for the Le Treps trial (Fig. 4b). In Félines, the group constituted in part of the Californian and Oregon coastal provenances (1138, 1144, 1148 and 1115) was characterized by high basal area at 30 years old (889 cm^2±28), medium growth reduction in 2003 (−20.1 %±1.6) and in 2004 (−24.3 %±5.5), and low earlywood density (0.310 g.cm^{-3}± 0.005). The group consisted of northern provenances from British Columbia (1106, 1109, 1110, 1111, and 1112) and two provenances from the more continental part of California (1131 and 1050), and was characterized by small growth reduction in 2003 (−11.7 %±1.0), contrasted response of growth in 2004 (−16.7 %±4.1), medium to low basal area (468 cm^2±67), and low earlywood density (0.315 g.cm^{-3}±0.004). The third group comprised southern interior provenances (1155, 1160, 1161, 1168, 1169, and 298302) showing intermediate values for growth reduction in 2003 (−18.8 %±1.3), large growth reduction in 2004 (−40.3 %±4.4), a high earlywood density (0.355 g.cm^{-3}±0.005), and very low basal area (298 cm^2±30). The fourth group comprised only two provenances from the southern part of the interior variety area (1158 and 282286), and showed the highest values of earlywood (0.382 g.cm^{-3}±0.007) and contrasted values of basal area (349 cm^2±114), and a large growth reduction during 2003 (−35.4 %±0.7) and 2004 (−57.4 %±3.2).

In the Le Treps trial, Californian and Oregon coastal provenances were divided into two groups. The first comprised mostly southern coastal Californian provenances from the trial (1144, 1148 and 1150) and was characterized by a high basal area (519 cm^2±34), a medium growth reduction in 2003 (−14.3 %±1.3) and no growth reduction in 2004 (+3 %±2),
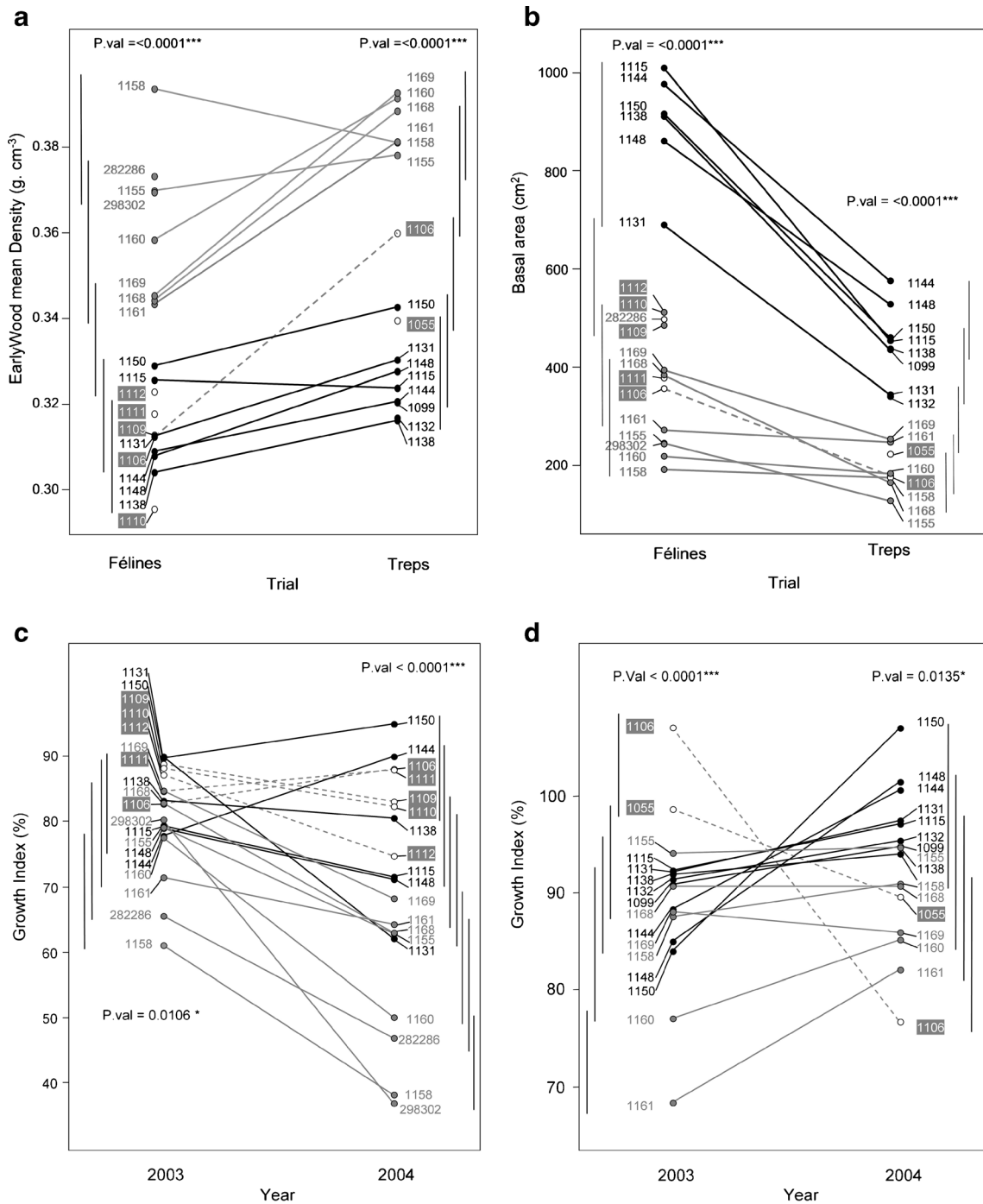
Fig. 3 Provenance ranking for **a** earlywood density (g. cm^{-3}) at each site, **b** basal area at 30 years old (cm^2) at each site, **c** growth index (%) in Félines for the 2 dry years 2003 and 2004, and **d** growth index (%) in Le Treps for the 2 dry years 2003 and 2004. *P.val* corresponds to the probability value of the significant provenance effect for each site, tested by a single-effect variance analysis. The *vertical lines* illustrate the non-significant difference among provenances assessed by a Duncan test. *Boxed codes* indicate the IUFRO code of provenances, *colours* indicate different geographical origins: *black* for Californian and Oregon coastal provenances, *grey* for south interior provenances, *white* and *dashed gray* for northern provenances from British Columbia

and by a low earlywood density (0.330 g.cm^{-3}±0.007). The second group of coastal provenances (1115, 1099, 1131, 1332, and 1138) showed a low reduction growth in 2003 (−8.3 %±0.3) and in 2004 (−4.3 %±0.6), medium value of basal area (405 cm^2±29), and low earlywood

density (0.320 g.cm^{-3}±0.003). The group comprised provenances from the northern part of the interior area (1106 and 1055), and was characterized by the absence of growth reduction in 2003 (+2.8 %±4.2) but a large growth reduction in 2004 (−16.8 %±6.4), low basal area

a Félines

b Le Treps
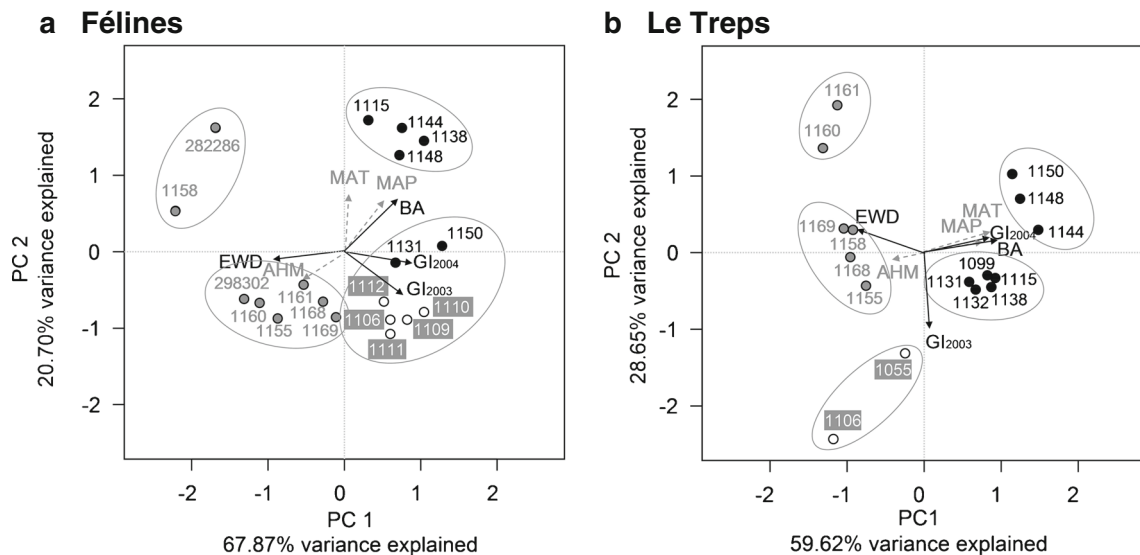
Fig. 4 PCA results showing the factor coordinates of the variables and provenances (•) on the plane defined by the first two principal components (*PC*). The ellipses denote the different groups defined according to hierarchical ascendant classification (*HAC*) on the same variables. Variables are basal area (*BA*), earlywood density (*EWD*), growth index in 2003 (*GI*$_{2003}$) and growth index in 2004 (*GI*$_{2004}$). Supplementary climatic variables from the natural range are represented by a grey dashed line:

mean annual temperature (*MAT*), mean annual precipitation (*MAP*) and annual heat moisture index (*AHM*). *Boxed codes* indicate IUFRO provenance codes, *colours* indicate different geographical origins: *black* for Californian and Oregon Coastal provenances, *grey* for south interior provenances, *white and gray* for northern provenances from British Columbia

(200 cm^2±21), and medium earlywood density (0.346 g.cm^{-3}±0.009). The fourth group comprised part of the southern interior provenances (1155, 1158, 1168, and 1169) and showed intermediate values for growth reduction in 2003 (−9.9 %±1.5) and in 2004 (−9.4 %±1.8), high value of earlywood density (0.382 g.cm^{-3}±0.004), and low basal area (184 cm^2±28). The last group comprised only two provenances of the southern part of the area occupied by the interior varieties (1160 and 1161), and showed the same pattern as the previous group for earlywood density (0.382 g.cm^{-3}±0.004) and basal area (218 cm^2±35), but a higher growth reduction in 2003 (−26.0 %±3.1) and in 2004 (−16.4 %±1.5).

4 Discussion

4.1 Contrasting behaviour among provenances during dry years

The approach we proposed in this study allowed us to take into account not only mean growth performance of provenances, but also growth response to soil-water deficit events. This is of particular interest for the selection of provenances that are adaptable to potential increase of frequency and intensity of future drought episodes. Significant differences among provenances have been detected for all wood density variables as well as for basal area and for growth reduction during extremely dry years. The observed differences among provenances were consistent with genetic differences

previously reported for growth, morphology, and phenology in Douglas-fir (Birot and Ferrandes 1972; Ching and Hinz 1978; Christophe and Birot 1979; White 1987). In a few cases, it has been suggested that these variations are related to environmental or climate causes (Sweet 1965; Irgens-Moller 1968; St Clair et al. 2005). In our study, the observed differences among provenances reflected wide climatic variation in the natural range—Coastal, Northern, and Southern Interior. This could result from the past evolutionary history of the species distribution. Gugger and Sugita (2010) suggest that the last glaciations led to a geographical separation between Coastal and South Interior varieties. As a result of this separation, genetic differentiation could have appeared between the newly formed populations that were growing under contrasted climates due to both adaptive and evolutionary trends. This is expected in a species covering such diverse conditions and with a limited capacity for seed dispersal (Silen 1962).

The observed variability in our trials inside provenances from each geographical area is high, leading to few significant differences. Several reasons may be involved. Firstly, in Douglas-fir, within-provenance variability is known to be high for growth (Rozenberg et al. 1997) and for wood density. Secondly, our sampling suffers from having a limited statistical power due to the low number of standing trees per provenance according to the relatively old age of the studied trials. Thirdly, some authors have hypothesized a lack of variability between provenances within a given region, especially for interior Douglas-fir (Cown and Parker 1979; Kung and Wright 1972).

The largest differences among provenances were observed for growth. The interior provenances showed a lower growth than the coastal ones, which is consistent with previous observations on seedlings and on young trees (Irgens-Moller 1968; Aitken et al. 1995; Anekonda et al. 2004), and on mature trees in the natural range (Rehfeldt et al. 2006). The results of the PCA showed, in both sites, that basal area at the geographical group level is correlated with mean annual precipitation within the natural range. The group of provenances originating from the wetter climate showed a much higher growth rate. In contrast, a high earlywood density was observed for the group of provenances originating from the area with a high annual heat moisture index (AHM). This link between AHM and EWD supports the hypothesis of an adaptive advantage regarding resistance to cavitation for trees with a high earlywood density. One might further assume that those provenances with a high earlywood density suffer less growth reduction during dry conditions. Our results, however, did not support such reasoning. Levitt (1980) advanced two mechanisms involved in drought resistance: drought hardiness and drought avoidance. The former is characterized by the ability to withstand a dry internal environment resulting in severe tissue dehydration, while the latter mechanism arises from developing deep rooting or low transpiration rates. Our results showed a higher growth reduction during dry years on provenances with a higher earlywood density and originating from the driest part of the natural range. This higher growth reduction could be the result of earlier or stronger stomatal regulation (Aussenac et al., 1989) enabling the prevention of cavitation but leading to earlier growth cessation. Growth reduction under adverse condition could be an expression of a trade-off between growth and drought resistance. This could explain why provenances from dry areas did not show any growth advantage over wetter provenances under drought events in our study. Ferrell William et al. (1966)) argue that southern interior seedlings have a consistent drought-resistance advantage (both with more efficient drought-hardiness and drought-avoidance) over seedlings from Pacific coastal sources. Furthermore, the southern interior Douglas-fir provenances have been shown to stop growing earlier at the end of the growing season than those of the coastal provenances (Irgens-Moller 1968).

4.2 Implication and potential interest of these provenances for future breeding programmes in the context of increasing drought risk

No mortality was observed in any of the studied trials during the period after 2003, despite the high soil-water deficit index in these trials (84 in Félines and 114 in Le Treps). This absence of mortality may point to a high resistance of all provenances tested to two successive drought events, but also to a lack of selective strength in these events.

On the other hand, we have seen that the relationships between growth and soil-water deficit are globally negative, confirming previous dendrochronological studies indicating that Douglas-fir radial growth is limited by growing season precipitation and heat moisture indices (Robertson et al. 1990; Greisbauer and Green 2010; Littell at al. 2008; Chen et al. 2009; Sergent et al. 2014). Nevertheless, in our study some extremely wet years deviated from that trend, indicating that growth of provenances in Le Treps and Félines may also have been affected by the excess of water. The reason could be that the provenances tested in the Le Treps and Félines trials which are exposed to low precipitation in their natural range (mean 828 mm) are not well-adapted to the high levels of precipitation observed in these trials in 1996 (Félines, 2,638 mm) and 2002 (Félines, 1,795 mm and Le Treps, 1,649 mm).

The ranking and clustering classification of provenances points to new suggestions for the ongoing Douglas-fir improvement programme. The coastal Californian provenances have not only shown a high overall production but also a high growth during the 2 successive years of drought. In the climate conditions observed in both trials, coastal Californian provenances appear to be the best choice for forestation. The northern interior provenances also showed high performance in 2003 but a contrasting response in 2004. Furthermore, overall production for this latter group of provenances was relatively low. The Southern Interior provenances showed the lowest productivity, the highest earlywood density, and also the lowest growth during the drier years. As a consequence, interior provenances could provide a trade-off between growth and vulnerability to drought, as they are potentially better adapted to drier conditions than the provenances observed previously. These are preliminary indications, and this dendro-climatic approach should be used on a larger scale for more robust conclusions on provenance differences.

5 Conclusion

Stand water balance was calculated daily for quantifying drought events at both site and year level. Soil-water deficit has been shown to control radial growth whatever the provenance. This study has also shown that growth, earlywood density, and growth reduction as a response to soil-water deficit are geographically structured. In the pedoclimatic conditions of the study sites, coastal Californian provenances performed best for both basal area and growth reduction during dry years. The Southern Interior provenances, which originated from the driest environments, showed the highest growth reduction during the driest years. To confirm the interest of these provenances and to investigate vulnerability to drought with a functional point of view, ecophysiological measurements are requested before these provenances are proposed for a future integration in the breeding programme.

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