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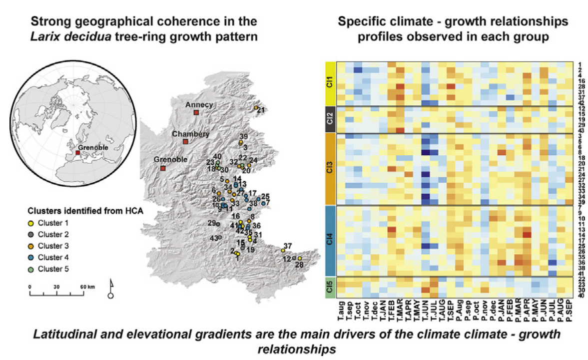
HIGHLIGHTS

- We determine climatic drivers for a *L. decidua* tree-ring network of the French Alps.
- We illustrate variability of climate-radial growth relationships along latitudinal and elevational gradients.
- Higher summer temperatures increase growth at high-altitude sites but act as a limiting factor at lower elevations.
- Climate change exacerbates sensitivity of the Northernmost populations to mean summer temperatures.
- High growth-rate plasticity was proved in response to local climatic conditions.

GRAPHICAL ABSTRACT



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ABSTRACT

A better understanding of the respective role of key climatic variables on tree growth is crucial for an accurate assessment of how ongoing global changes may affect both dynamics and distribution of forest tree species in the future. The aim of this study was (i) to explore growth patterns of European larch (*Larix decidua* Mill.) through a network of tree-ring chronologies developed for the French Alps and (ii) to identify the main climatic drivers explaining radial growth. Climate-growth relationships were coupled with a hierarchical analysis. This relationship revealed significant variability expressed spatially by the existence of five clusters, initially discriminated by an elevational contrast related to (i) a negative correlation between summer temperatures and larch growth at lower elevations and (ii) a stronger response of low-elevation larch stands to winter precipitation. In the high-elevation clusters, tree growth depends on previous autumn and current summer temperatures and water supply in July. The differentiation, that portrays a strong geographical coherence, is mainly related to the latitudinal gradient; (i) the northwestern stands are mostly sensitive to high temperatures in summer; (ii) the growth of the southernmost clusters is equally driven by temperatures during autumn, winter, and summers; (iii) the populations of a cluster located in a transitional zone of the inner French Alps, subject to both

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1. Introduction

European larch (*Larix decidua* Mill.) is a coniferous tree species endemic to Europe, characterized by its strong disjunctive distribution within two regions, the Carpathians and the European Alps (McComb, 1955; Geburek, 2010; Danek et al., 2017). In the Carpathians, the species' distribution is scattered and extends to lowland sites (Caudullo et al., 2017). The Alps are the natural and largest continuous habitat of *L. decidua* where its distribution ranges from around 450 meters above sea level (m a.s.l.) to >2300 m a.s.l. European larch mainly grows in pure stands but can also occur in mixed forest stands along with Norway spruce (*Picea abies* (L.) Karst.), stone pine (*Pinus cembra* L.) and silver fir (*Abies alba* Mill.). In the Alps, the climate, along with both natural and anthropogenic disturbances (Courtois, 1960; Fauquette and Talon, 1995; Nakagawa, 1998; Nakagawa et al., 2000; Mocci et al., 2005; Walsh et al., 2005), determines both the distribution limits of *L. decidua* and the structure of larch forests. These factors also influence physiological and phenological processes of the species, yet the relationships between tree growth and climate can vary rapidly due to sharp natural environmental gradients (e.g. Frank and Esper, 2005).

Considered as a species with high dendrochronological potential due to its high longevity (>1000 years, Tranquillini, 1979; Rolland et al., 1998) and high temperature sensitivity (Frank and Esper, 2005), *L. decidua* trees growing at high-elevation sites in the Alps have been used repeatedly for climatic reconstructions (e.g., Büntgen et al., 2005; Corona et al., 2010a, 2010b; Daux et al., 2011; Büntgen et al., 2011; Coppola et al., 2013). At the same time, detailed studies have been undertaken to understand the response of *L. decidua* to climate in the Eastern Italian (Anfodillo et al., 1998; Carrer and Urbinati, 2004, 2006), Eastern Austrian (Nicolussi et al., 2009), Swiss (Büntgen et al., 2005; Garbarino et al., 2013), Southeastern German (Hartl-Meier et al., 2014), Southeastern Slovenian Alps (Hafner et al., 2011), and in lowland sites of Poland and Lithuania (Koprowski, 2012; Vitas, 2018). In addition, several studies have investigated complex and nonlinear larch growth responses to changing climatic conditions (i.e. the so-called divergence phenomenon, Carrer and Urbinati, 2006; Büntgen et al., 2008, 2012) or to tree age (Carrer and Urbinati, 2004) in several alpine regions.

In the French Alps, climate-growth relationships have been computed mostly at the local scale (Serre, 1978; Rolland et al., 1998). The most comprehensive dendrochronological analysis of *L. decidua* in the French Alps is limited to 12 sites and focused on the teleconnections between tree-ring width (TRW) chronologies (Rolland, 2002). To date, and by contrast to other alpine regions, studies addressing the large-scale, spatial variability of tree-ring–climate relationships is missing for the French Alps. This lack is all the more detrimental as, in the case of the French Alps, *L. decidua* is subjected to a latitudinal climatic gradient exceeding that of other alpine countries. More specifically, the French Alps offer a unique opportunity to analyze climate–growth relationships at the western and southernmost limits of the species' distributions in alpine massifs that are, in addition, subjected to oceanic and Mediterranean climatic influences.

In this context, this study analyzes the relationship between larch growth and climate at large spatial scales and for a wide elevational range. Our study area covers the entire French Alps and extends from the Mercantour to the Vanoise Massif (from 43°N to 46°N and from 6.5°E to 7.5°E). Our objectives are (i) to determine climatic parameters that control tree growth over the entire study area and (ii) to analyze spatial variability of relationships between tree-ring growth and climate. We hypothesize that the broad range of climatic conditions throughout the French Alps likely leads to regional differences in larch climate-growth relationships. By doing so, this study thereby sheds light on *L. decidua* response to climate especially at the western and southern margins of its distribution area in the European Alps.

2. Materials and methods

2.1. Materials

The tree-ring network studied here consists of 620 TRW series from 43 sites ranging from 1050 to 2300 m a.s.l. The longest TRW chronology is from the Merveilles Valley (Southern French Alps) and spans the period 933–1974, whereas the shortest chronology is restricted to the period 1830–1983 (see Fig. 1 and Table 1 for details). For the first time, the relationships between larch growth and climate were explored using this large dataset across the French Alps, using a network of chronologies that has been collected by successive research programs since 1974 (Serre, 1978; Tessier, 1986; Guibal unpublished; Edouard et al., 2002, 2009, 2010; Corona et al., 2011; Saulnier, 2012; for detailed sources of each chronology, please refer to Saulnier et al., 2017).

Importantly, the study sites cover the north–south and west–east climatic gradients (44° 06′–45°53′ N, 6°40′ E–7°45′ E, Fig. 1) commonly observed in the French Alps. According to the Köppen Geiger climate maps established from monthly HISTALP temperature (Böhm et al., 2001; Chimani et al., 2013) and precipitation fields (Efthymiadis et al., 2006; Chimani et al., 2011), the tree-ring network covers regimes from warm temperate (Cfb) to alpine frost (EF) climates, with most of the study sites located in the Boreal and Alpine climate zones (Rubel et al., 2017) (Fig. 1b). The sampled sites are mainly characterized by open forest stands with different slope exposures. Although human activities largely modeled the French Alps (Courtois, 1960; Fauquette and Talon, 1995; Nakagawa, 1998; Nakagawa et al., 2000; Mocci et al., 2005; Walsh et al., 2005), they occurred in a disjoined and asynchronous way. The use of such an extensive network minimizes the effects of human disturbances.

2.2. Sampling strategy and detrending

At each of the 43 sites, between five and 32 samples were taken from undamaged, dominant or co-dominant trees (Table 1). At least two cores were extracted per tree, perpendicular to the slope direction, in order to avoid reaction wood formation. Samples were taken systematically at breast height with a Pressler increment borer. The samples obtained in the field were analyzed and data processed following standard dendrochronological procedures (Bräker, 2002). Single steps of surface analysis included sample mounting on a slotted mount, drying, and surface preparation with a razor blade or by fine sanding the upper core surface up to grit size of 600 that allowed the annual rings to be easily recognized under magnification. In the laboratory, tree rings were counted and rings measured to the nearest 0.01 mm using a digital LINTAB positioning table connected to a Leica stereomicroscope and cross-dated using TSAP-WIN Scientific software (Rinn, 1996). Prior to

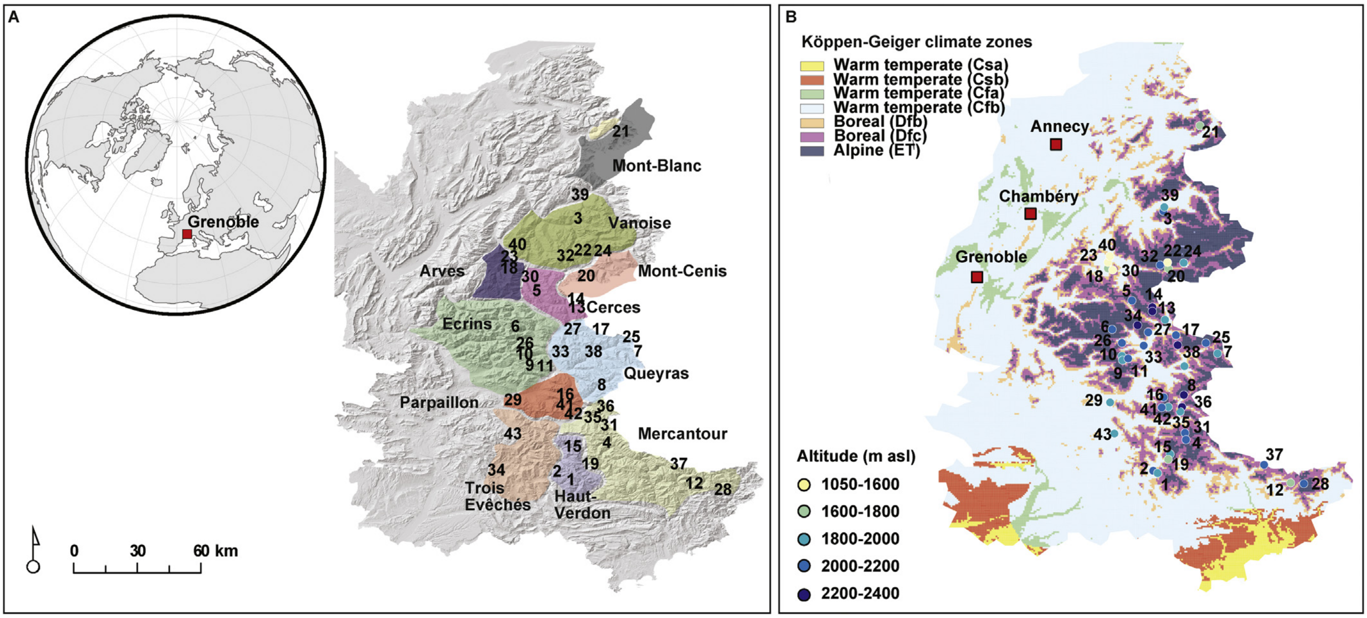

Fig. 1. Maps of the larch sites throughout French Alps with (a) the main Alps region as referred in the text and (b) the distribution of the Köppen Geiger climate regimes.

Table 1
Sites location and descriptive statistics of the larch tree ring chronologies. Lat: latitude; Long.: longitude; Alt.: elevation; MRW: mean ring width; SD: standard deviation; AC and AC b.s.: autocorrelation and autocorrelation before standardization; n: number of individus; M.T.A.: mean tree age; MS: mean sensitivity; rbar: running bar; EPS: expressed population signal.

Label	Pop	Lat.	Long.	Alt.	MRW	SD	AC	n	Length	M.T.A	AC b.s	MS	rbt	EPS
1	Beauvezer_2	44.12	6.65	1950	0.68	0.33	0.76	8	1421–1993	355	0.21	0.22	0.40	0.84
2	Beauvezer_4	44.12	6.65	1950	0.50	0.18	0.66	22	1160–1994	292	0.14	0.22	0.40	0.94
3	Bellecote	45.51	6.70	2030	1.61	0.64	0.63	12	1812–1993	95	0.19	0.27	0.60	0.95
4	Braisse	44.29	6.82	2150	0.80	0.36	0.72	16	1417–1995	391	0.24	0.24	0.69	0.97
5	Chardonnet	45.03	6.54	2180	0.68	0.36	0.72	18	1492–1989	373	0.23	0.30	0.64	0.97
6	Clapouse	44.87	6.43	2150	0.77	0.36	0.71	16	1557–1995	290	0.27	0.27	0.62	0.96
7	Echalp	44.76	7.00	1930	0.80	0.45	0.73	32	1338–1995	342	0.39	0.32	0.69	0.98
8	Fouillouse	44.51	6.81	2300	0.99	0.41	0.69	13	1669–1981	189	0.24	0.26	0.52	0.93
9	Fres1A	44.73	6.51	1930	0.71	0.35	0.71	11	1632–1990	267	0.36	0.31	0.55	0.93
10	Fres1B	44.73	6.51	1930	0.80	0.53	0.82	10	1542–1961	374	0.44	0.29	0.66	0.95
11	Fres2	44.73	6.51	2100	0.92	0.46	0.73	18	1474–1992	357	0.31	0.28	0.57	0.96
12	Gordolasque	44.06	7.38	1750	1.44	0.72	0.72	10	1830–1983	113	0.39	0.31	0.71	0.96
13	Granon1	44.97	6.63	2230	0.88	0.43	0.72	12	1710–1993	229	0.39	0.31	0.73	0.97
14	Granon2	44.97	6.63	2230	0.65	0.35	0.73	8	1734–1993	222	0.34	0.32	0.64	0.93
15	HautGarreton	44.21	6.73	1900	1.57	0.98	0.78	10	1824–1981	144	0.42	0.33	0.60	0.94
16	Infernet	44.51	6.70	2100	1.20	0.55	0.73	18	1654–1986	248	0.34	0.25	0.54	0.96
17	Izoard	44.84	6.73	2150	0.70	0.38	0.78	12	1734–1993	229	0.29	0.31	0.80	0.98
18	Karellis	45.22	6.40	1650	1.56	0.75	0.86	5	1755–1983	162	0.38	0.20	0.54	0.85
19	LaColle	44.18	6.72	1800	1.96	1.07	0.72	10	1732–1981	153	0.39	0.31	0.38	0.86
20	LaRepose	45.20	6.73	1790	1.00	0.48	0.81	10	1700–1983	214	0.30	0.24	0.65	0.95
21	Lavancher	45.96	6.89	1750	1.95	0.91	0.75	20	1775–1994	125	0.34	0.26	0.36	0.92
22	LeBesseil	45.21	6.73	1450	1.08	0.54	0.73	10	1732–1983	190	0.25	0.29	0.62	0.94
23	LeBochet	45.24	6.40	1050	1.21	0.80	0.83	10	1791–1984	145	0.32	0.31	0.52	0.93
24	LeJeu	45.23	6.81	2000	0.88	0.40	0.81	12	1665–1994	191	0.34	0.23	0.61	0.95
25	LesBans	44.92	6.70	2000	0.70	0.35	0.71	13	1640–1995	270	0.21	0.30	0.69	0.97
26	LesClots	44.82	6.47	2100	1.35	0.61	0.65	15	1748–1995	192	0.31	0.31	0.74	0.98
27	Melezet	44.87	6.63	2150	1.17	0.56	0.79	13	1752–1995	189	0.28	0.24	0.57	0.95
28	Merveilles	44.05	7.45	2200	0.35	0.14	0.56	37	933–1974	486	−0.01	0.28	0.59	0.98
29	Morgon	44.49	6.42	1930	0.97	0.54	0.78	18	1679–1989	262	0.29	0.28	0.71	0.98
30	Moulins	45.23	6.41	1400	0.87	0.74	0.83	5	1830–1983	149	−0.02	0.35	0.65	0.90
31	Moutieres	44.30	6.82	2150	0.71	0.36	0.74	17	1414–1995	405	0.15	0.26	0.66	0.97
32	Orgeres	45.22	6.68	2100	1.00	0.47	0.77	26	1353–1973	319	0.16	0.24	0.48	0.96
33	Oriol	44.80	6.60	2180	0.62	0.35	0.76	19	1381–1989	447	0.22	0.26	0.65	0.97
34	PasArchais	44.16	6.36	1600	2.58	1.16	0.65	11	1815–1989	72	0.20	0.28	0.58	0.94
35	Roche1	44.68	6.80	2100	1.10	0.49	0.68	14	1782–1989	178	0.37	0.29	0.70	0.97
36	Roche2	44.68	6.80	2100	0.59	0.35	0.78	12	1617–1990	253	0.26	0.31	0.64	0.96
37	Salese	44.15	7.24	2150	1.12	0.68	0.76	17	1701–1980	238	0.13	0.32	0.57	0.96
38	Souliers	44.48	4.46	2250	0.81	0.42	0.73	14	1448–2009	308	0.37	0.29	0.23	0.98
39	StJacques	45.53	6.70	1990	0.97	0.37	0.62	12	1737–1993	173	0.24	0.26	0.71	0.97
40	Tourmentier	45.27	6.41	1450	0.88	0.63	0.86	5	1784–1983	183	0.15	0.27	0.62	0.95
41	Tournoux1	44.47	6.74	2000	1.03	0.64	0.76	6	1747–1990	182	0.35	0.28	0.55	0.86
42	Tournoux2	44.47	6.74	2000	1.14	0.52	0.73	10	1724–1990	221	0.17	0.24	0.56	0.88
43	Tourtourel	44.32	6.44	1820	1.33	0.65	0.69	19	1728–1989	195	0.26	0.29	0.64	0.95

detrending, all ring-width series were screened for missing rings and dating errors using COFECHA (Cook and Holmes, 1984).

A hybrid "double-detrending" procedure (Cook and Peters, 1981) was employed to standardize tree-ring data and to conserve high-frequency variations: an initial negative exponential or linear regression was applied for each raw measurement series, followed by a fitting of a 30-year cubic smoothing spline with 50% frequency response cut-off (Cook and Peters, 1981; Cook, 1990). Then, for each site, growth indices were averaged per year using a bi-weighted robust mean to develop a site chronology representing the common high-frequency variation of the individual series (Cook, 1990).

Several descriptive statistics that are commonly used in dendrochronology were then computed to compare site chronologies. High-frequency variations in the chronologies were assessed using both the standard deviation (SD), that estimates the variability of measurements for the whole series, and the mean sensitivity (MS), being an indicator of the mean relative change between consecutive ring widths (Fritts, 1976). Above a threshold of 0.3, MS values indicate that populations are particularly sensitive to climate, while values between 0.2 and 0.3 are considered intermediate with regard to their suitability for dendroclimatological studies (Grissino-Mayer, 2001). The first-order serial autocorrelation, that complements MS to document growth trends (Bunn et al., 2013), was computed to detect persistence (i.e. how much the ring width in year n is correlated with the width in year n − 1) retained before and after detrending in tree-ring patterns. The common variance and signal strength of each chronology can be assessed by values of mean Rbar and Expressed Population Signal (EPS). The EPS quantifies the degree to which a reconstructed chronology portrays hypothetically perfect conditions (Wigley et al., 1984). We used an EPS threshold of 0.85 to determine reliability of our chronologies. Rbar was used as a measure of the strength of the common signal (Wigley et al., 1984) in each population and was calculated as a mean correlation between all overlapping pairs of indexed tree series.

2.3. Cluster analysis

We used a Hierarchical Cluster Analysis (HCA, Ludwig and Reynolds, 1988) to detect sub-divisions among the 43 detrended TRW chronologies. A measure of similarity was calculated using a matrix of Euclidean distance for each year between all mean chronologies for the common period 1920–1987. In a second step, the Ward's minimum variance criterion (Everitt et al., 2001) was used to delineate clusters from the dataset. This technique minimizes the total within-cluster variance and produces compact, equal-sized dendrograms (Nicault et al., 2014). In a last step, we used multiscale bootstrap resampling (10,000 iterations; pvclust package of R; Suzuki and Shimodaira, 2006; Nicault et al., 2014) to assess the uncertainty in HCA. This resampling-based technique provides a level of significance (*p*-value) associated with standard errors (here expressed as a percentage) for each node of the dendrogram.

2.4. Climate-growth analysis

The 43 larch chronologies were regressed against mean monthly air temperature (°C) and monthly precipitation sums (mm) using values from the HISTALP dataset (Auer et al., 2007; Böhm et al., 2001; Chimani et al., 2011, 2013). Climate–growth relationships in *L. decidua* chronologies was explored in three methodological steps: First, partial correlation functions were computed using the seasonal correlation procedure (SEASCORR; Meko et al., 2011) with the aim to disentangle confounding influences of correlated climatic variables. SEASCORR correlates tree-ring series with a primary climate variable and uses partial correlations to investigate a secondary variable controlling for the influence of the primary variable. We selected temperature as the primary and precipitation as the secondary variable because previous work on climate controls in trees at high-elevation sites has identified temperature as the key driver of growth in the Alps (Büntgen et al., 2007; Corona et al., 2011; Saulnier et al., 2011). We then used individual monthly values and considered a 16-month window, assessing a period extending from June of the year preceding growth-ring formation (n − 1) to September of the year of actual ring formation (n); the approach thus analyzes 32 climatic variables. Correlations coefficients were computed for the period 1850–1974 common to all chronologies. Confidence intervals for all correlations were estimated with Monte-Carlo simulations of the tree-ring series (Percival and Constantine, 2006). In addition, we employed the Bonferroni approach for multiple comparison correction of significance levels (Hochberg, 1988). To analyze spatial variability of relationships between tree rings and climate, results of the correlation functions were mapped across the study area.

To further elucidate factors causing differentiation between clusters, a Principal Component Analysis (PCA) was performed with a covariance matrix. This technique replaces original p variables (i.e. the 32 partial correlation coefficients for each site in our case) with a smaller number (q) of derived variables (so-called Principal Components, PCs) representing those linear combinations of original variables retaining most of the variability of the original variables while reducing redundancy. Components expressing at least 10% of variability of the original variables (Peterson et al., 2002; Case and Peterson, 2005; Carrer et al., 2007) were retained and subjected to varimax rotation (Richman, 1986) so as to redefine PC axes and to maximize the spread of individual loadings (Frank and Esper, 2005). Based on comparable dendroecological studies (Frank and Esper, 2005; Carrer et al., 2007; Danek et al., 2017) and on the eigenvalue distribution that flattens after PC-3, varimax rotation was performed for the first three PCs. By doing so, we provide increased interpretability of principal components, easier definition of fairly homogeneous areas, and a more suitable spatial interpretation of loadings (Richman, 1986). Finally, to confirm identification of factors, the first two PCs were plotted against the environmental variables (latitude, longitude, and elevation).

3. Results

3.1. Chronologies characteristics

Time covered by the chronologies ranges from 153 (Sites 12 and 30) to 1041 years (Site 28) (Table 1). Ten chronologies exceed 500 years, whereas six cover less than two centuries (Sites 3, 12, 15, 23, 30 and 40). Mean values of first order autocorrelation (AC, Table 1) computed on raw TRW series range from 0.56 (Site 28) to 0.86 (Site 18), thus indicating a strong relationship between tree-ring growth in the current and the previous year. Mean sensitivity (MS) ranges from 0.20 (Site 18) to 0.35 (Site 30). Thirty out of the 43 TRW chronologies have MS values exceeding 0.2 and thirteen chronologies have MS values exceeding 0.3, thus indicating important relative changes between consecutive ring widths and a potentially strong sensitivity to interannual climate fluctuations. The mean inter-series correlation values (Rbar) vary between 0.234 (Site 38) to 0.744 (Site 26). The mean values of EPS mostly exceed the standard EPS threshold of 0.85, except for site 1 (0.84). No significant pattern, related to e.g. latitude–longitude or elevations, could be retrieved from the spatial repartition of MS, AC, Rbar, and EPS values.

3.2. Hierarchical cluster analysis (HCA)

The hierarchical cluster analysis (HCA, Fig. 2) of the matrix of detrended TRW chronologies resulted in a division of *L. decidua* into five main groups (Fig. 2). Cluster 5 is significant with >99% confidence, three clusters are significant at 95% (Cl2–Cl4), and Cluster 2 is significant at 89%. Fig. 3 illustrates the geographical distribution of TRW chronologies according to the HCA. Clusters are mainly dissociated by their latitudinal geographical context, with the exception of cluster 5 in

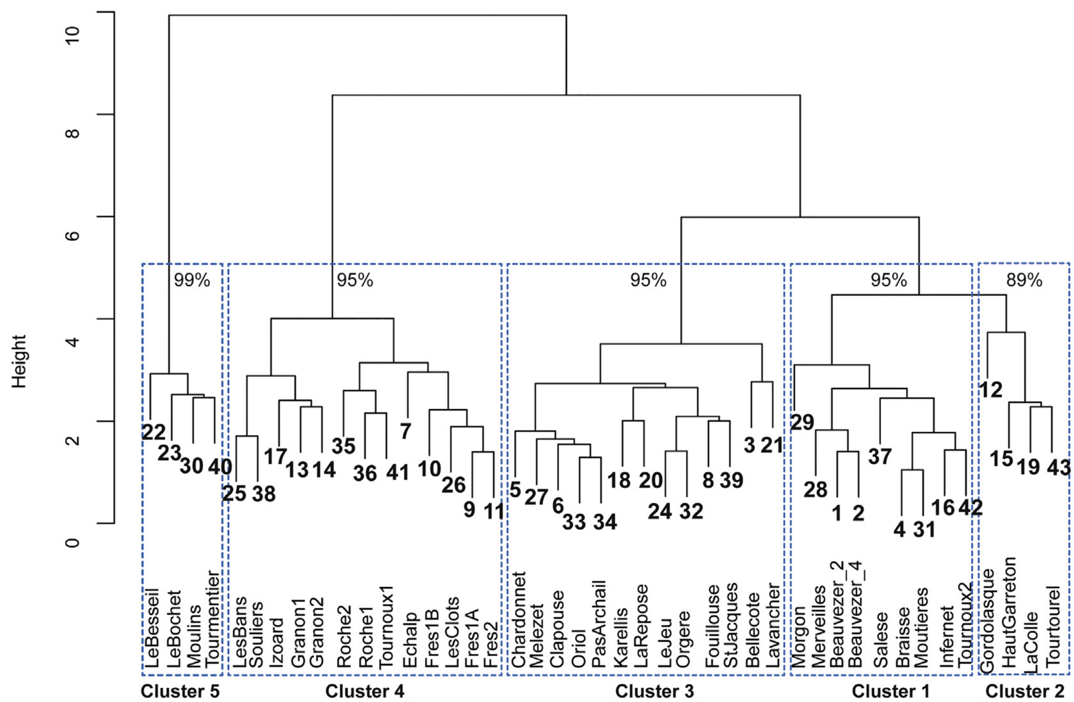

Fig. 2. Results of the hierarchical analysis: affinities between mean tree-ring chronologies calculated for the 1920–1990 period. Significance level and standard error (% and decimal, respectively) were performed for the five main clusters (dashed rectangles). The numbers refer to the site number indicated in Table 1.

which *L. decidua* sites are located at the lowest elevations (Fig. 4). In detail, clusters 1 (9 sites) and 2 (4 sites) include the southernmost TRW chronologies (lat. <44.5°), with sites being located primarily in the Mercantour, Haut-Verdon and Trois Évéchés massifs. Both clusters are separated by elevation with chronologies from cluster 1 being located between 1920 and 2200 m a.s.l. whereas larch sites from cluster 2 are situated below 1930 m a.s.l. (Fig. 4). The 13 sites aggregated in cluster 4 are located, in the Écrins, Queyras and in the southeastern part of the Cerces massifs, and thus in a region of transition between the Northern and Southern French Alps. Cluster 3 groups 13 sites from the northern regions of the network, namely the Briançonnais, Maurienne, Vanoise, and Mont-Blanc massifs. Finally, cluster 5 is exclusively composed of four low-elevation (1050–1450 m a.s.l.) sites from the Vanoise massif (Figs. 3 and 4).

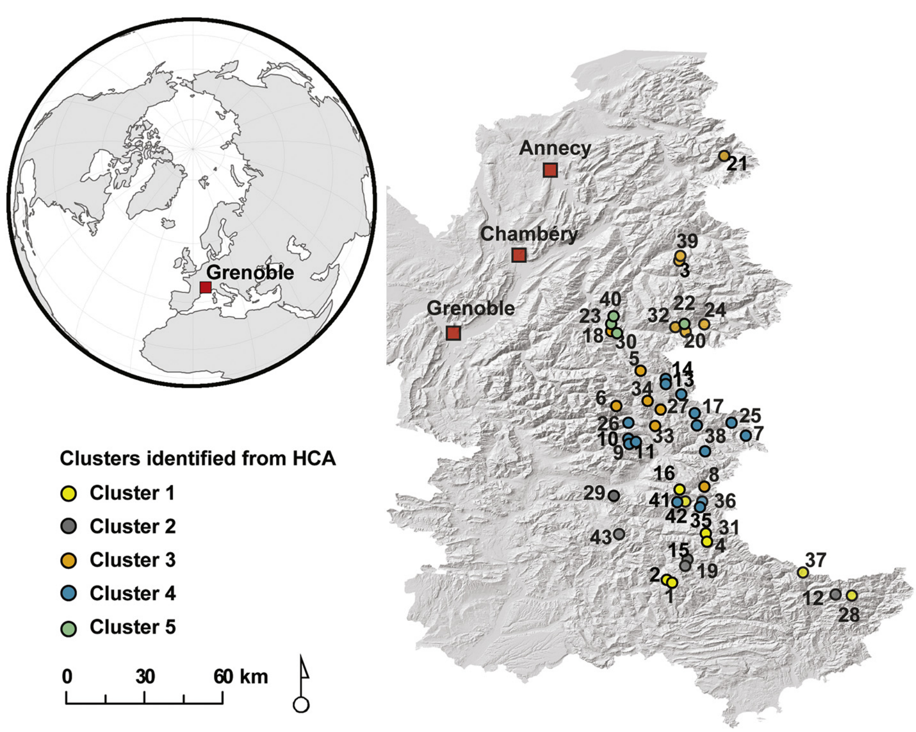

Fig. 3. Distribution of the larch sites according to the clustering classification based on the ring-width chronologies.

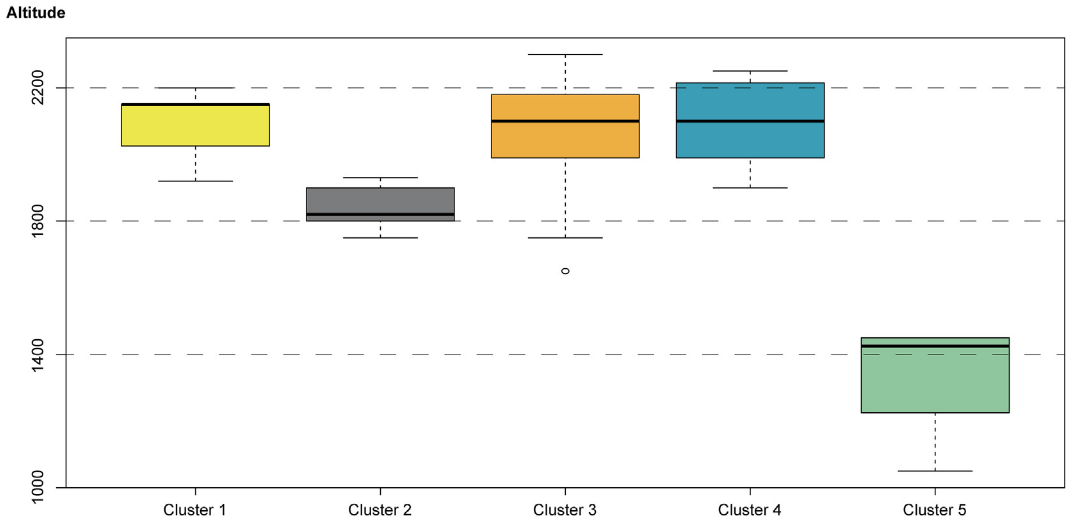

Fig. 4. Boxplot of the elevational distribution of the larch sites classified according to the clustering analysis.

3.3. Climate–tree growth relationships in the French Alps

Fig. 5 shows the number of significant Pearson's partial correlation coefficients calculated between larch sites and monthly climate variables. The largest positive r value (0.47) was obtained between site 8 and average June temperature (44.5°N, 6.75°E) from the HISTALP dataset. Conversely, the largest negative r value (−0.3) was observed between site 14 and May precipitation sums. At the level of the French Alps, it becomes evident that climate–growth relations in *L. decidua* are driven mainly by summer temperatures. That is, 20 chronologies

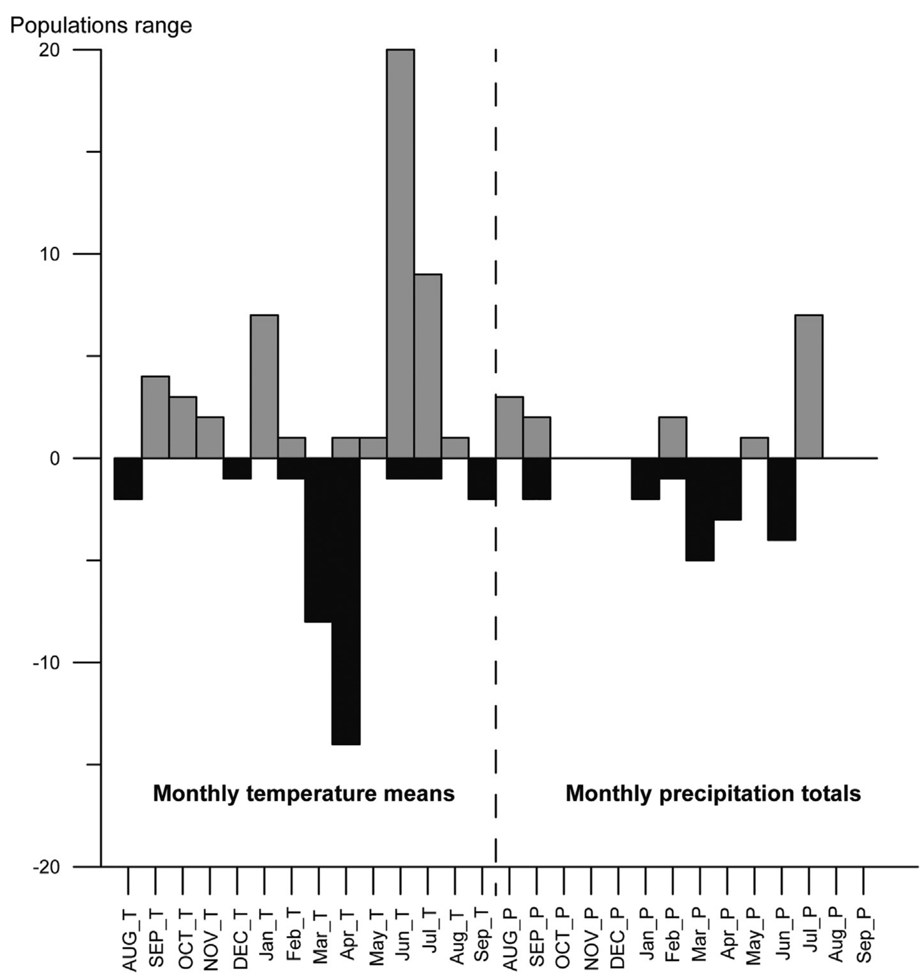

Fig. 5. Histogram showing the number of sites that respond significantly to a monthly climate parameter.

are significantly and positively correlated with June, and 9 chronologies with July temperatures. Significant negative partial correlation coefficients were computed between March (8 TRW chronologies) and April (14 TRW chronologies) temperatures, respectively. To a lesser extent, mild temperatures during previous autumn and winter (from September to December in year n−1) can affect *L. decidua* significantly, but at more local scales.

Our study also highlights that radial growth in *L. decidua* is much less sensitive to precipitation than to temperature. Precipitation in July (positive correlation) and during spring (March or April, negative correlation) appear as the most limiting hydroclimatic variables, but can only be found in 7, 5, and 3 chronologies, respectively.

3.4. Spatial pattern of climate growth relationships

To enhance understanding of the clustering, a PCA was conducted on the 43 × 32 matrix of partial correlation coefficients computed for each stand (Fig. 6a, b). The first principal component explains 20% of the variance whereas the second and third rotated factors PC-2 and PC-3 contribute 13.5 and 11.6%, respectively. The first two rotated axes presented in the PC correlation biplot (Fig. 6a) have highest loadings from mean monthly temperature in previous September (n-1) and October (n-1) as well as present June (n) and July (n) for PC-1 and precipitation sums in previous December (n-1) and present March (n) for PC-2. The four TRW chronologies from Cluster 5 are mainly concentrated within the positive portion of PC-1 whereas sites 3, 8, 31 and 39 from Cluster 3 occupy mostly the negative portion of the same axis (Fig. 6b). PC-1 also discriminates clusters 1 and 2. For PC-2, TRW chronologies from Clusters 1 and 2 are located on the positive portion of the axis, and clearly separated from the 13 sites of Cluster 4 (Fig. 6b).

The main environmental variable linked to the spatial variation of climate–tree growth relationships is elevation as it discriminates stands sensitive to June and July (n) temperatures from those sensitive to June (n) precipitation sums. Interestingly, latitude and longitude play only a minor role by discriminating stands sensitive to winter (i.e. December (n-1), January (n), and March (n)) and July (n) precipitation sums.

Figs. 7 and 8 synthesizes the climate–tree growth relationships in *L. decidua* sites when classified according to the five clusters defined by the HCA. The heatmap presented in Fig. 7 confirms that June (n) temperatures are the key drivers of radial growth throughout the French Alps but also points to stronger correlations in Clusters 1, 3, and 4 (Fig. 8b). In addition, chronologies from Cluster 3 – located at high-elevation in the Northernmost massifs of the French Alps – show significant correlations with July (n) (Fig. 8c) and, to a lesser extent, August (n) temperatures (Fig. 7). By contrast, TRW chronologies from the Mercantour massif (Cluster 1), located above 2100 m a.s.l., in the southern French Alps – where a warm or Mediterranean influence prevails (Fig. 1) – are also sensitive to temperature during previous October (n-1; Fig. 7 and 8a) and November (n-1; Fig. 7). Finally, the low-elevation sites from Clusters 2 and 5 show a correlation profile characterized by statistically non-significant (Cluster 2) or negative (Cluster 5) correlations with summer temperatures.

These results again underline once more that *L. decidua* trees from the French Alps are less sensitive to precipitation than to temperature. Obviously also, the correlation profiles obtained between TRW chronologies and monthly precipitation sums are more complex: July precipitation appears as a common driver in >20% of the chronologies in Clusters 1, 3, and 4 with higher and significant positive coefficients observed at Parpaillon and the northernmost chronologies of the Mercantour massifs (Fig. 8f). In addition, for these clusters, late autumn and early winter precipitation sums, especially in November and December (n−1), are positively and significantly correlated with radial growth (Fig. 7 and 8d). At a more local scale, negative correlations are observed between tree growth and precipitation sums in March–April in the case of the Southern French Alps massifs (Clusters 1 and 4). Interestingly, the stands located at lower elevations in the Northern French Alps (Cluster 5) at lower elevations are largely insensitive to precipitation sums, with positive yet low correlation coefficient values.

4. Discussion

The study presented here analyses climate–tree growth relationships of *L. decidua* in the French Alps and provides insights into (i) the strong geographical coherence of patterns and (ii) the spatial variability of relationships according to elevational and latitudinal gradients. On the basis of detrended TRW chronologies, HCA and PCA exhibit significant differences among the stands and definition of five clusters characterized by geographical coherence and specificities in their relation with climate variables.

4.1. High- vs low-elevation stands

The major dichotomy observed in this study is related directly to an elevational gradient as it discriminates high-elevation (Clusters 1–4) from low-elevation stands (Cluster 5, <1400 m a.s.l.), with the latter being located in the northern French Alps. Chronologies from Cluster 5

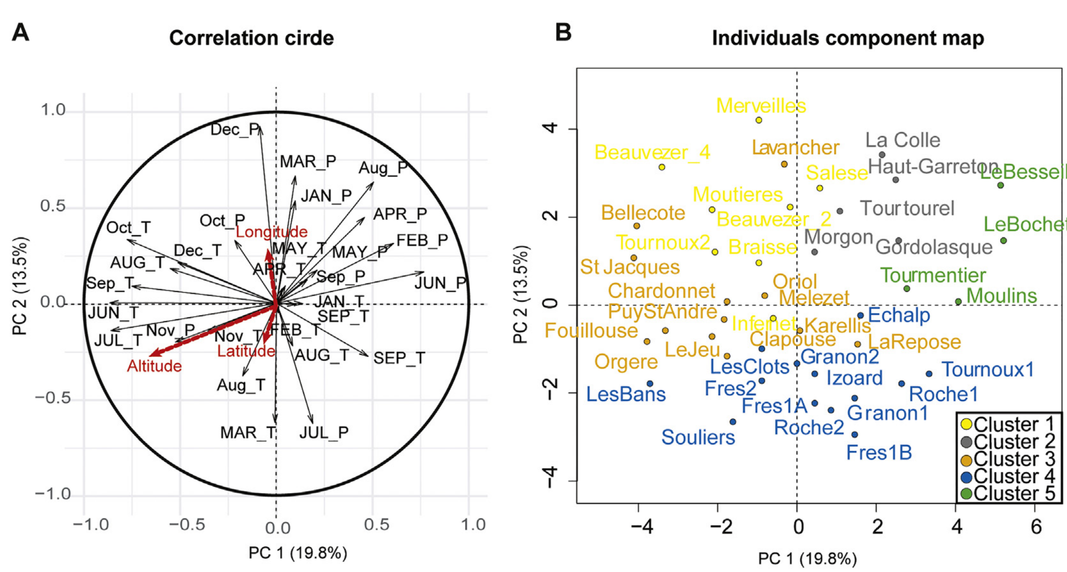

Fig. 6. Results of the principal component analysis performed on the Pearson correlation coefficients.

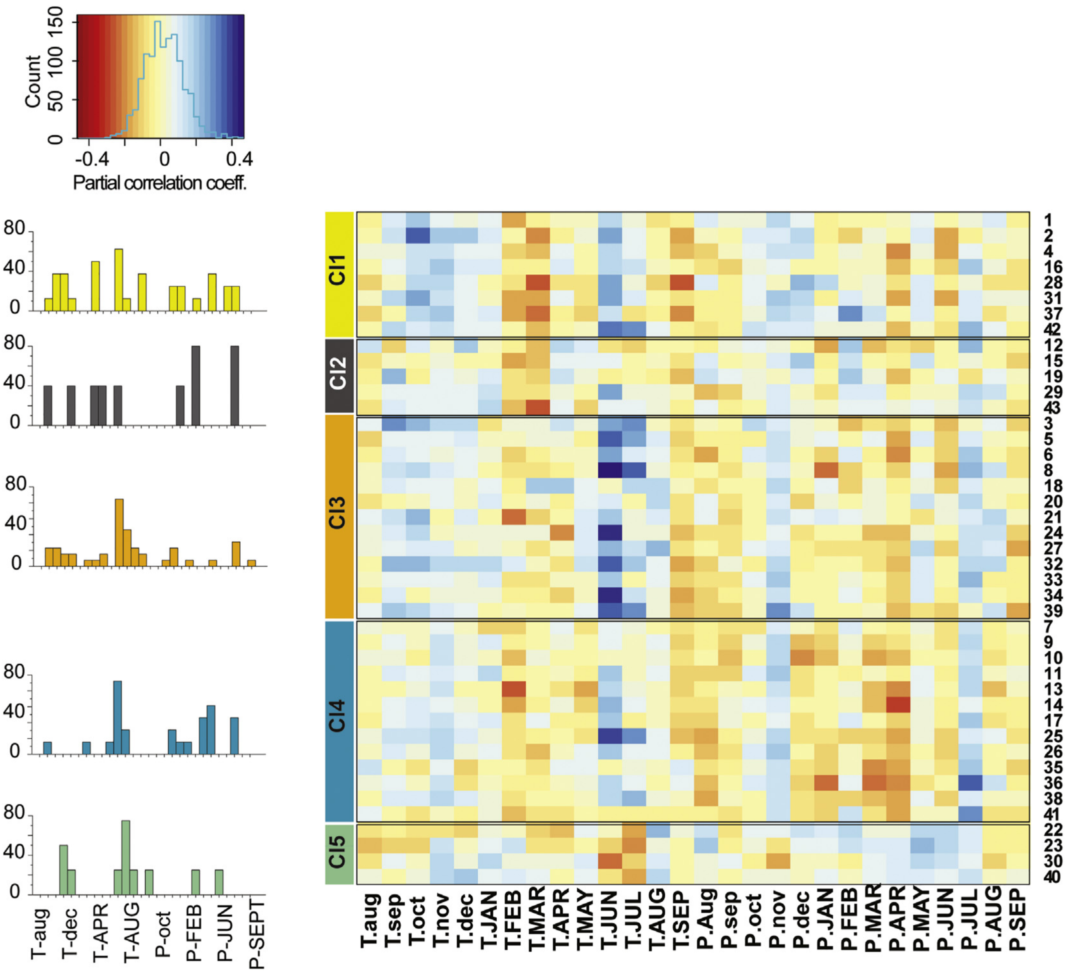

Fig. 7. Heatmap of the Pearson correlation and partial correlation coefficients for each site classified according to the results of the clustering analysis. The numbers on the right refer to the site number indicated in Table 1. The power spectrum on the top left gives color spectrum for the correlations in the heatmap. Diagrams on the left highlight the significant correlations identified by cluster expressed as the percentage of sites with significant correlation values. The labels of the abscissa axis are the same as those of the heat map. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

are characterized by specific correlation profiles differing starkly from the other chronologies. Contrary to the other clusters, in the case of Cluster 5, above-average summer (June and July) temperatures are a limiting factor whereas abundant precipitation during the growing season (i.e. from May–June to September–October, depending on the elevation) has a dominant positive influence on radial growth. Similar positive and significant correlations with spring precipitation sums have been reported for several conifer species at dry sites in Valais (Switzerland, Rigling et al., 2002), Tyrol (Austria, Oberhuber and Kofler, 2002) and the Southern French Alps (Saulnier et al., 2011). Whereas *L. decidua* has been shown to develop a specific drought avoidance strategy by osmotic adjustment resulting from the accumulation of solutes (Rolland et al., 1998; Carrer and Urbinati, 2004, 2006), these profiles suggest a sensitivity of low-elevation sites to water stress, especially during the summer months. This assumption is supported further by several studies attributing a strong rainfall-dependence of *L. decidua* to its anisohydric strategy, i.e. the maintenance of high transpiration rates under conditions of low water availability by opposition to species with an isohydric behavior that close stomata to maintain leaf water potential despite declining soil and root water potentials (Eilmann and Rigling, 2013; Lévesque et al., 2013; Oberhuber et al., 2015).

Common forcing factors of radial tree growth have been evidenced at high-elevation Clusters 1–4. Here, summer (June–July) temperatures play a key role, which is in line with findings on radial growth in *L. decidua* or, more generally, high-elevation tree species across the Alps (Fourchy, 1952, 1968; Carrer et al., 2007; Rossi et al., 2006). High temperatures in summer have been reported to favor cambial division and wood formation (Frank and Esper, 2005; Carrer and Urbinati, 2004; Carrer et al., 2007; Büntgen et al., 2007; Hafner et al., 2011). Monitoring studies aimed at intra-annual ring formation confirm that cell differentiation and tracheid production mostly occur from May to early August (Camarero et al., 1998; Rossi et al., 2003; Schmitt et al., 2004), but that growth rate varies with summer weather conditions. Moser et al. (2010) analyzed the effect of elevational gradients on the timing and duration of the growing season in *L. decidua*, and reported a delay in the onset of the growing season by 3–4 days per 100 m difference in elevation. Moreover, Busetto et al. (2010) studied the relationships between inter-annual variability of the *L. decidua* phenological cycle and climate, thereby showing a strong linear relationship between mean spring temperatures and mean growth onset dates. The authors concluded that an increase of 1 °C in late spring temperatures would lead to a 7-day anticipation of mean larch budburst dates.

In addition, some positive correlations were observed at the high-elevation sites between *L. decidua* chronologies and previous September–November (n-1) temperatures. Similar dependencies of *L. decidua* radial growth to previous fall temperatures were reported for the Northeastern, Central, and Eastern European Alps (Rolland et al., 1998; Carrer et al., 2007; Oberhuber et al., 2008). This dependence of *L. decidua* to previous fall conditions has been attributed to the deciduous character of its needles and to the storage of carbohydrates for early shoots, new sets of needles and growth resumption in the next season (Wieser et al., 2009). In the absence of such reserves, low rates of photosynthesis in early spring can thus be expected to limit the supply of sucrose to the stems (King et al., 2013; Jochner et al., 2017). In addition, analysis of $^{13}CO_2$ pulse-labeled photoassimilates showed that compounds for the synthesis of cell walls of earlywood are derived from the previous year photoassimilates (Kagawa et al., 2006) during late winter to early spring – i.e. during a time when photosynthesis is at its minimum or almost non-existent.

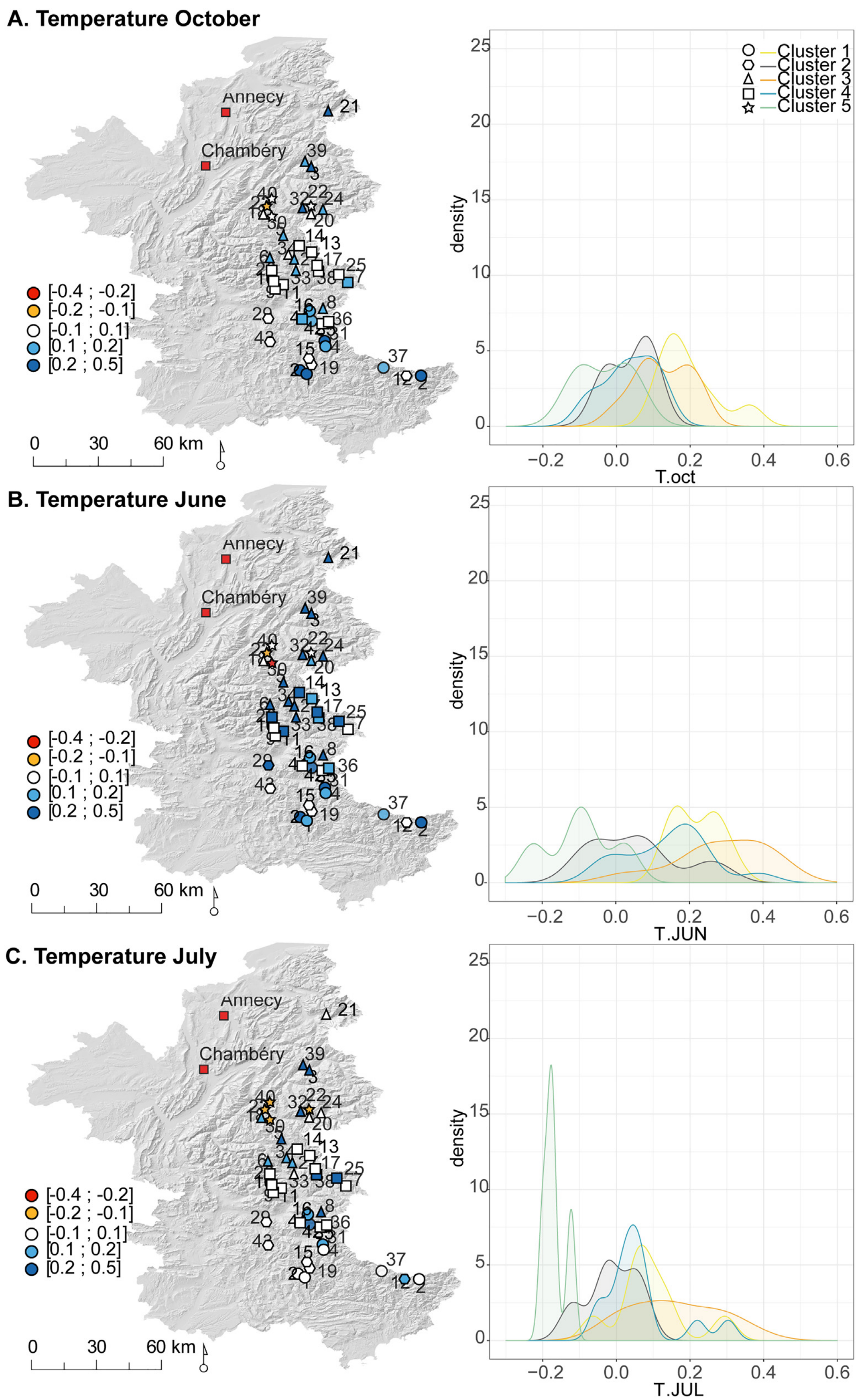

Fig. 8. Geographical and ecological distribution of the correlation values between each site and the main identified monthly climate parameters. The diagram on the right represents the range of the distribution of correlations according to clusters.

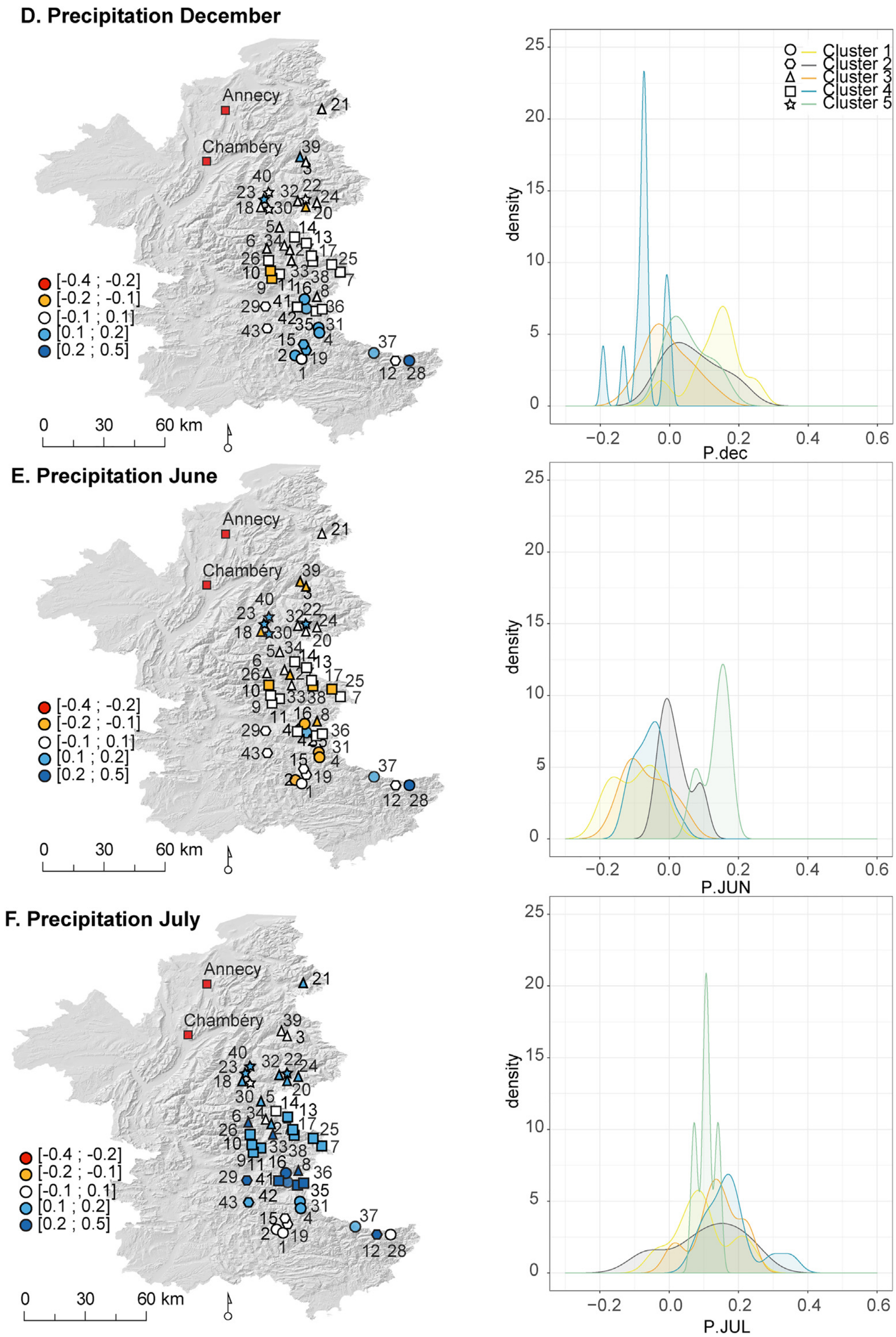

Fig. 8 (*continued*).

Among the monthly precipitation sums tested, we found that July precipitation sums were the most common driver of radial growth of *L. decidua* across the French Alps. This finding is in line with results from high-elevation sites in the inner Austrian, Swiss and Italian Alps, at high elevation sites (Anfodillo et al., 1998; Oberhuber, 2004; Eilmann and Rigling, 2013; Schuster and Oberhuber, 2013), and explain responses of high-elevation conifer trees to precipitation by the discontinuous nature, shallowness, high permeability of soils and thus their susceptibility to become physiologically dry quite rapidly. By contrast to the low minimum water potential evidenced in the Italian Alps for *P. abies* and *P. cembra* (Anfodillo et al., 1998), *L. decidua* trees from the French Alps appear significantly affected by water stress conditions during dry summers.

4.2. Northern vs. southeastern L. decidua stands

We have shown in this study that among the higher-elevation stands, four clusters can be significantly discriminated by the HCA.

These clusters portray a strong regional consistency that clearly evidences a latitudinal gradient. The second dichotomy of the HCA isolates TRW chronologies from Cluster 4 located in the Queyras, Parpaillon, and Ecrins massifs, from other high-elevation sites. At Cluster 4, radial growth is significantly and positively correlated with summer (June–July) temperatures and precipitation sums, as observed in Cluster 1–3. Nonetheless, climate–tree growth relations mainly differ from the other high-elevation clusters due to the stronger negative response to late winter and early spring (March–April) precipitation sums. In this transitional area of the inner French Alps – subjected to both Mediterranean and continental influences (Ozenda, 1985) – extensive and long-lasting snow cover may have a detrimental effect on radial growth of *L. decidua* at the treeline through (i) cooler soil temperatures (Pellizzari et al., 2014), (ii) a shortening of the growing season and (iii) possible delays in the onset of cambial activity at the start of the new growing season, or (iv) even through lower amounts of growing degree-days (Vaganov et al., 1999; Blok et al., 2011).

The third partition differentiates Cluster 3 – containing stands from the Mont Blanc, Vanoise, Arves and Cerces massifs (Northern French Alps) – from Clusters 1–2 (i.e. southeasternmost Alps with Parpaillon, Haut-Verdon, Trois-Evechés and Mercantour massifs). Comparison of correlation profiles from Clusters 1 and 3, although located at comparable elevations (Fig. 4, >2100 m a.s.l.), evidences clear differences between these clusters. The northern *L. decidua* stands (contained in Cluster 3) are subjected to continental influences (Ozenda, 1985) and thus show the highest sensitivity to June–July temperatures. We interpret this exacerbated dependence on summer temperatures to the shorter length of the growing season at higher latitudes, due to the declining gradient in both snow cover duration and thickness from the northwestern to the southeastern inner regions (Durand et al., 2009). By contrast, correlation profiles demonstrate that radial growth of the southernmost sites (Cluster 1), subjected to Mediterranean climatic influences, is significantly and negatively correlated with winter temperatures (February–March). Comparable results have been reported for *L. decidua* trees for the Greater Tatra region (Büntgen et al., 2007) and the eastern Italian Alps (Carrer and Urbinati, 2004). The risk of embolism related to freezing during snow free periods in late winter and early spring has been suggested as an explanation for the limiting effect of temperatures (Mayr et al., 2003) in these cases. In addition, Begum et al. (2013) highlighted the risk of cambium frost damage due to an earlier onset of cambial activity. They also reported that late spring frost occurring after the onset of cambial reactivation could induce a depolymerization of microtubules, which are key components of the cellular skeleton. Furthermore, limited snow depth and limited reserves in above-ground tissues can lead to intense desiccation related to increased needle and shoot transpiration rates, photo-inhibitory stress and short-term shoot temperature fluctuations (Havranek and Tranquillini, 1995; Oberhuber, 2004; Büntgen et al., 2007).

Finally, the last dichotomy of the HCA discriminates Clusters 1 and 2, both including stands in the Southern French Alps. Interestingly, discrimination of clusters in this case is neither explicitly related to an elevational nor to a latitudinal gradient. As such, comparison between the correlation profiles from both clusters reveals similar correlations between TRW and winter temperatures. These profiles yet differ through the absence of significant relation between the five *L. decidua* stands from Cluster 2 – ranging in elevation from 1750 to 1930 m a.s.l. – and summer temperatures. Given the vicinity between the sites in Cluster 1 and 2 (e.g. site 15– site 19 and sites 1–2– site 12), we speculate that topography and/or microclimatic conditions may drive differentiation between these two clusters. Carrer and Urbinati (2004) highlighted TRW responses to climate could also be age-dependent in *L. decidua*. They reported that the climate signal could be maximized in older trees. Average ages of sites in Clusters 1 and 2 are quite different with 561 and 227 years, respectively. Even if the sites of Cluster 2 are younger than those of Cluster 1, they are considered as mature stands. As a consequence, we do not expect tree age to explain the low correlations observed with summer temperatures, and conclude that growth of sites of Cluster 2 are driven mainly by other factors and that local conditions are at the origin of the specific relations of stands in this cluster to climate.

5. Conclusion

The analysis of climate–tree growth relationships of *L. decidua* stands revealed significant spatial variability in the French Alps. This variability was expressed spatially by the existence of five clusters. These clusters are initially discriminated by an elevational contrast apparently related to (i) a negative correlation between summer temperatures and larch growth at lower elevations and (ii) a stronger response of low-elevation larch stands to winter precipitation. In the four high-elevation clusters, tree growth depends mainly on previous autumn and current summer temperatures as well as water supply in July. This dependence does not only portray strong geographical coherence, but is also related mostly to latitudinal gradients insofar as the northwestern stands are mostly sensitive to high temperatures in summer whereas the growth of the southernmost clusters is equally driven by temperatures during autumn, winter and summers. Finally, only the sites located in a transitional area of the inner French Alps, subject to both Mediterranean and continental influences, appear sensitive to late winter and early spring precipitation. We conclude that the significant spatial heterogeneity of climate–tree growth relationships in *L. decidua* clearly underlines the high plasticity of the species to adapt its growth to local climate conditions. As a consequence, the impact of climate change on tree growth will likely vary according to the region considered. As warmer temperatures are predicted (IPCC, 2007), *L. decidua*, whose growth is principally governed by spring and summer conditions at high elevation, may experience increased growth. By contrast, at low elevation sites, we hypothesize that larch stands could suffer from global warming.

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