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Regional variability of climate–growth relationships in *Pinus cembra* high elevation forests in the Alps

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Summary

1. The tree-ring growth response of stone pine (*Pinus cembra* L.) to climatic variability was studied in the Alps. The aims were (i) to assess tree-ring growth patterns at different spatial-temporal scales; (ii) to identify the climate parameters that explain most of the variability in radial growth at different time domains; and (iii) to study past and current trends in radial growth and climate–growth relationships at different locations.

2. High- and low-frequency stone pine chronologies were compiled for 30 treeline sites on the French and Italian Alps. We used gridded climate data computed from 200 years of instrumental records from an extensive Alpine network. Climate–growth relationships were computed with bootstrap correlation functions and their stationarity and consistency over time assessed with moving correlation.

3. No spatial patterns were detected in stone pine chronology statistics despite the regional clustering observed in tree-ring series and climate responses. This can be attributed to (i) local weather variability; (ii) different biophysical conditions caused by soil moisture, solar radiation, snowmelt dynamics and growing season length; and (iii) forest stand history and age structure, the expression of long-term land use and disturbances.

4. The exceptionally long-term climate records allowed significant stone pine growth response changes to be assessed at both annual and decadal time scales. Winter conditions and spring–summer temperatures mainly affected the growing season length, in addition to site carbon and water balance. Most of these limiting factors varied spatially and temporally along the latitudinal and longitudinal gradients in response to the corresponding changes in local conditions.

5. Our results show evidence of a clear response variability of *Pinus cembra* to climate limiting factors, at both spatial and temporal scale. Such knowledge extended to other species and regions will provide better estimates of the effect of climate variability on species distribution and dynamics within global change scenarios and more accurate past climate reconstruction and forest ecosystem modelling.

Key-words: dendrochronology, European Alps, global change, global warming, limiting factors, moving correlations, treeline, tree-rings to climate relationships, spatial-temporal scales

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Introduction

High altitude and high latitude forests are sensitive to climate variability due to their location at the edges of their tree species distribution areas (Grace *et al.* 2002). Indeed, treelines occur where harsh environmental conditions inhibit tree establishment, growth and survival (Tranquillini 1979). Although both the specific and general mechanisms controlling alpine treelines are under debate, the direct or indirect negative influence of decreasing air and soil temperatures with increasing altitude is considered to be the primary constraint on the upper altitudinal limit of tree establishment in most mountain regions (Korner & Paulsen 2004; Korner & Hoch 2006).

High altitude forests are frequently investigated in palaeoecological studies to determine the influence of climate variability on present-day tree growth and forest productivity. They are also the source of valuable proxy records and reveal climate changes at different temporal (years to centuries) and spatial (local, regional to hemispherical) scales (Briffa *et al.* 1995; Gedalof & Smith 2001; Hofgaard & Wilmann 2002; Briffa *et al.* 2004; Guiot *et al.* 2005).

Within the geographical range of a species, environmental features vary along physiographic and ecological gradients at different scales, creating the conditions for spatial variability in the limiting factors, and consequently the species sensitivity to climatic variability. More detailed studies at regional and subregional scales are therefore needed to detect local patterns of the individual species' responses and their main constraints (Oberhuber & Kofler 2000; Peterson *et al.* 2002; Bunn *et al.* 2005). This is particularly true in the Alps, where the climate varies from maritime in the south-west to more continental in the central and eastern areas. In addition, there is a considerable physiographic variability in mountain structure, from higher peaks of granite bedrock in the western Alps to lower peaks on dolomite bedrock in the east (Ozenda 1985; Böhm *et al.* 2001). The Alps also offer unique possibilities for climatological studies as over two centuries of instrumental weather records are available for the region (Auer *et al.* 2005; Casty *et al.* 2005). This permits (i) detailed analysis of the tree ring–climate relationships on a centennial scale, and (ii) thorough testing of their temporal stability since preindustrial times (Büntgen *et al.* 2005; Frank & Esper 2005; Carrer & Urbinati 2006).

Swiss stone pine (*Pinus cembra* L.) and European larch (*Larix decidua* Mill.) are the two most important high-altitude tree species in the Alps and have both proved very suitable for different kinds of tree-ring analysis (see Schweingruber (1996) for a review). Nonetheless stone pine is more suited to climate-related studies over the whole Alpine range because its ring-width pattern is never affected by growth disturbances due to bark-boring or defoliating insects, such as larch budmoth (*Zeiraphera diniana* Guénée). In contrast, the climatic signal seen in larch may periodically be altered by larch budmoth outbreaks, especially in areas of high outbreak frequency (Rolland *et al.* 2001; Büntgen *et al.* 2005; Nola *et al.* 2006).

Based on a wide network of sites, and a very long climate data set for the whole Alpine region, we used a dendroecological approach to study the growth responses of stone pine to climate variability. Our aims were to (i) assess tree-ring growth patterns of stone pine at different spatial-temporal scales; (ii) identify the climate variables that explain most of the variability in radial growth at different time domains; and (iii) study past and current trends in radial growth and climate–growth relationships at different locations.

Methods

STUDY AREA

Stone pine ring-width chronologies were compiled for 30 sites in the French and Italian Alps. Sites were chosen to span the latitudinal and longitudinal distribution of the species ranging from the southern edge of the Maritime Alps (44°13′ N, 7°23′ E) to the eastern Italian Dolomites (46°51′ N, 12°21′ E) (Fig. 1).

All sites sampled were in high-altitude (1900–2300 m a.s.l.) open forest stands with canopy closure ranging between 5% and 40% and minimal human disturbance (e.g. logging, livestock grazing, fire, etc.). Bedrock and soil types vary according to site location, from dolomite and limestone with shallow rendzic leptosols, to igneous, volcanic and metamorphic silicates (i.e. granite, porphyry, gneiss and phyllite) with spodosols and podzols.

TREE-RING CHRONOLOGY COMPILATION

In each site, 12–78 undamaged dominant or co-dominant standing trees were selected; in some cases additional samples were taken from snags or logs. From each living tree, two cores were extracted with an increment borer at breast height on the cross-slope sides of the trunk. In the laboratory all the cores were fixed to wooden supports and smoothed with a razor blade or by sanding with progressively finer grade sandpaper until optimal surface resolution allowed annual rings to be recognized easily under magnification. Ring width was measured to the nearest 0.01 mm using a sliding stage micrometer interfaced with a personal computer, crossdated using standard dendrochronological procedures (Stokes & Smiley 1968) and checked for dating and measurement errors with the COFECHA computer program (Holmes 1983).

Tree-ring growth chronologies were created from the crossdated ring-width time series by a two stage detrending procedure using the program ARSTAN (Cook & Holmes 1997). Individual series were first standardized to remove trends in mean ring width that typically occur due to increasing tree circumference. We fitted a negative exponential curve to the raw data series and divided the observed ring widths by the

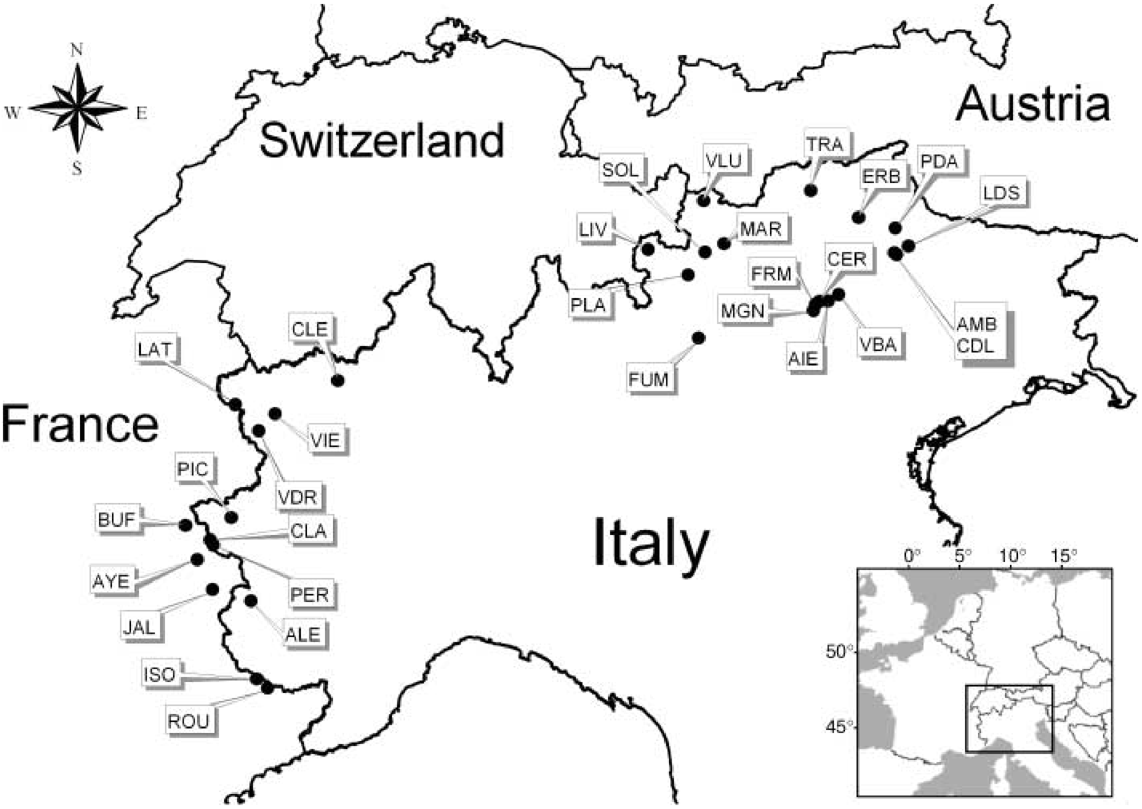

Fig. 1. Location of the study sites

expected values to obtain dimensionless tree-ring indexes. Two different standardization methods were then applied:

(A) To emphasize higher interannual frequency variations, a spline function with a 50% frequency response of 20 years was fitted to individual indexed series and the ratio between observed and expected values computed again. Flexible cubic spline curves can remove both the long-term trend and the effect of localized disturbance events very efficiently, but with the risk of removing possible low-frequency climate information (Cook & Peters 1981; Cook *et al.* 1990). Autoregressive modelling (Box & Jenkins 1976) was then used to remove a significant serial autocorrelation often retained after the spline indexing. The residual series were then averaged site by site or regionally, adopting a robust estimation of the mean value function to enhance the common signal and downweighting the effect of outliers (Cook 1985).

(B) In order to preserve common interdecadal and lower frequency variations after the first negative exponential curve fitting and indexing, we simply computed the robust mean chronologies using the same method as in point A.

Several descriptive statistics, commonly used in dendrochronology, were computed to compare site chronologies. These included the standard deviation (SD) that estimates the variability of measurements for the whole series and the mean sensitivity (MS), which is an indicator of the mean relative change between consecutive ring widths and is calculated as the absolute difference between consecutive indices divided by their mean value. Both SD and MS permit the assessment of high-frequency variations in the chronologies (Fritts 1976). Other statistics computed were the first order serial autocorrelation (AC) to detect the persistence retained before and after the standardization, the mean correlation between trees (r_{bt}) and the variance explained by the first principal component (PC1) to estimate the level of year-by-year growth variations shared by trees in the same site. Higher values of r_{bt} and PC1 indicate greater similarity in the annual growth patterns among sampled trees and better representation of overall stand growth by the mean growth chronologies (Fritts 1976; Peterson & Peterson 2001).

COMPOSITE CHRONOLOGY DEVELOPMENT

Principal Component Analyses (PCA) of the covariance matrix of the tree-ring network was used to extract common modes of variability in annual radial growth. As discussed in detail in the Results section, the PCA produced three clusters and, accordingly, we computed three composite chronologies averaging the indexed series (method B) of all trees present in the sites pooled in the same cluster. Then, in order to preserve the lower frequency variations in the computed chronologies, a 16-year Gaussian low-pass filter with a 50% frequency response of 20 years was applied to the mean series. This procedure removed all the frequencies shorter than 7 years, leaving all the others of less than 40 years relatively unaffected (Cook *et al.* 1990). For a better comparison among composite and site chronologies we computed the same descriptive statistics as those applied to the site chronologies (SD, MS, AC, r_{bt} and PC1).

The composite chronologies (West1, West2 and East) were compared, for the period 1700–1999, at both high- and low-frequency (after the 16-year filter) time scales, and a 50-year window running-correlation was computed between these tree-ring series at both time scales (Wigley *et al.* 1984; Briffa *et al.* 1996).

CLIMATE DATA

Instrumental data gathered from 192 precipitation and 132 temperature stations throughout the Alps were subjected to homogeneity tests and relative adjustments, to spatial and temporal analyses, and finally gridded on a 1 × 1 degree network (Böhm *et al.* 2001; Auer *et al.* 2005). We preferred these data instead of those available from individual weather stations because of the lack of a station or long-term data set for several sites and the limited representivity of local stations in this mountain area. However, given the temporal span of the records (approximately 200 years), it should be stressed that those data collected before 1840, especially for precipitation, are not as reliable as the later ones (Auer *et al.* 2005; Auer *et al.* 2007).

Given the high climate variability in the Alps, especially for precipitation, we selected the closest grid point to each site with the complete temperature and precipitation data from 1804 to 2000 expressed as anomalies from the 20th century mean, while for the three regional chronologies the previously selected grid series were averaged to create three sets of regional climate variables.

CLIMATE INFLUENCES ON TREE GROWTH

The influence of climate on tree-ring growth was investigated using different approaches. We assessed climate–growth relationships for each site and for the composite chronologies, for the 1804–1994 period, using a correlation function (CF) analysis (Fritts 1976) computed using 32 independent monthly climate variables sequenced from June of the year prior to growth ($t-1$) to September of the year of growth (t). To evaluate the stationarity and consistency of the CF over time, we computed moving CF (MCF) with the software package DENDROCLIM2002 (Biondi & Waikul 2004). With MCF we adopted a 100-year interval progressively shifted over time to compute the correlation coefficients (Biondi 1997, 2000) for the same 32 monthly variables. The statistical significance and stability of the CF and MCF were evaluated with a bootstrap procedure adopting 1000 replications. Each correlation coefficient was considered significant if the mean value was at least twice the standard deviation of its 1000 replications (Guiot 1991). For MCF the Benjamini & Hochberg (1995) False Discovery Rate approach was applied for multiple test correction of the significance levels.

SPATIAL VARIABILITY IN TREE GROWTH PATTERN AND CLIMATE INFLUENCES

Principal Component Analysis (PCA) (Jolliffe 2002) was used as a clustering technique to identify common patterns of growth variability and responses to climate among the 30 ring-width chronologies. PCA is a data reduction technique that transforms a group of variables (in this case the tree-ring chronology statistics reported in Table 1 (i.e. MRW, SD, AC, MS, r_{bt} and PC1), the tree-ring chronology indexes for the period 1804–1994 and the 32 standardized monthly CF coefficients) into a new set of variables called principal components (PCs), which are a linear combination of the original variables. These PCs were calculated on the covariance matrix of variables: in the case of tree-ring chronology statistics that do not share the same unit measures and variances, PCA was performed on previously standardized data (z scores). We decided to retain only the components that expressed at least 5% of the variability of the original variables, a criterion previously used in similar dendroecological studies (Peterson & Peterson 2001; Peterson *et al.* 2002; Case & Peterson 2005). These components were rotated orthogonally according to the Varimax criterion that redefines the PC axes and maximizes the spread of the individual loadings. Generally this procedure provides increased interpretability of the principal components, easier definition of fairly homogeneous areas, and a more suitable spatial interpretation of the loadings (Richman 1986). The weighting coefficients, or eigenvector (factor) loadings, were examined to identify common properties among the variables analysed in a similar way to that used by Brubaker (1980). Scatter plots of the weighting coefficients for the first two PCs displayed the clustering of variables with similar modes.

Results

CHRONOLOGY DESCRIPTIVE STATISTICS

Table 1 lists the locations and descriptive statistics of the 30 tree-ring site chronologies. These series were obtained from 820 mature stone pine trees, with site mean tree ages (at coring height) of 158–344 years. Mean sensitivity and first order serial autocorrelation were 0.13 ± 0.02 and 0.82 ± 0.06 (mean ± 1 SD), respectively. Two useful parameters for evaluating chronology quality are the mean interseries correlation (r_{bt}) and percentage of common variance among trees included in the chronology (PC1): their values were 0.36 ± 0.05 and 39 ± 5, respectively.

None of these statistics displayed a significant correlation with respect to sample size, longitude or latitude and no common association patterns were detected between sites with PCA analyses (Fig. 2a).

Table 1. Site location and descriptive statistics of stone pine tree-ring chronologies

Site code	Lat.	Long.	MRW	SD	AC	Number of trees	Chronology time span (no. of years)	Mean tree age	MS	r_{bt}	PC1
BUF	45.01	6.58	0.94	0.43	0.82	78	1594–2000 (407)	226	0.13	**0.47**	48
AYE	44.83	6.68	**0.72**	0.36	0.81	50	1475–1998 (524)	335	0.12	0.33	35
CLA	44.93	6.77	0.82	**0.22**	0.81	24	1472–1995 (524)	280	0.12	0.36	40
PER	44.91	6.79	1.13	0.34	0.78	16	1709–1998 (290)	191	0.15	0.45	**49**
JAL	44.67	6.80	0.90	0.44	0.84	15	1575–1998 (424)	282	0.13	0.43	45
PIC	45.06	6.93	**1.45**	0.56	0.87	15	1723–1998 (276)	189	0.13	0.37	41
LAT	45.68	6.94	0.91	0.58	**0.94**	19	1472–1997 (526)	344	0.12	0.31	35
ALE	44.61	7.09	0.82	0.31	0.88	23	1453–1994 (542)	278	0.13	0.37	39
VDR	45.54	7.12	0.78	0.29	0.89	25	1478–1994 (517)	257	0.13	0.32	35
ISO	44.18	7.15	0.88	0.35	0.81	31	1637–2000 (364)	233	0.12	0.37	40
ROU	44.13	7.23	**0.65**	0.28	0.74	14	1541–2001 (461)	254	0.17	0.43	48
VIE	45.63	7.25	1.14	0.43	0.90	15	1584–2002 (419)	188	0.14	0.4	45
CLE	45.82	7.73	0.89	**0.21**	0.77	17	1599–1999 (401)	268	0.12	0.31	34
LIV	46.54	10.16	1.02	**0.72**	**0.96**	15	1585–2000 (416)	319	0.12	0.36	38
PLA	46.40	10.47	1.11	0.23	**0.72**	16	1634–2000 (367)	244	0.13	0.34	37
FUM	46.05	10.55	1.06	0.43	0.91	14	1584–1996 (413)	211	0.14	0.35	40
SOL	46.52	10.61	0.91	0.34	0.80	16	1490–1999 (510)	274	0.11	0.33	36
VLU	46.80	10.61	0.79	0.41	0.85	15	1579–1999 (430)	307	0.14	0.38	41
MAR	46.56	10.76	1.04	0.47	0.84	13	1666–1999 (334)	224	0.11	**0.24**	**28**
MGN	46.18	11.45	1.04	0.50	0.84	29	1488–1996 (509)	235	0.12	0.34	37
TRA	46.79	11.46	0.87	0.38	0.80	52	1365–2003 (639)	224	0.11	0.30	33
FRM	46.22	11.47	0.82	0.33	0.75	91	961–1997 (1037)	173	0.11	0.33	35
CER	46.23	11.50	1.12	0.47	0.78	30	1552–1998 (447)	171	0.16	0.35	38
AIE	46.23	11.57	1.27	0.58	0.80	27	1342–1997 (656)	184	0.17	0.36	41
VBA	46.27	11.65	1.07	0.47	0.80	20	1567–1997 (431)	179	0.17	0.32	38
ERB	46.68	11.83	0.84	0.38	0.85	17	1581–1999 (419)	269	0.11	**0.28**	**32**
CDL	46.48	12.10	0.78	0.37	0.74	36	1409–1994 (586)	235	0.14	0.41	43
AMB	46.47	12.12	0.89	0.45	0.84	58	1425–1997 (573)	219	0.14	0.37	38
PDA	46.62	12.12	1.15	0.53	0.77	15	1749–1995 (247)	188	0.16	**0.48**	**51**
LDS	46.52	12.22	**1.31**	**0.65**	0.82	14	1760–1997 (237)	158	0.12	0.37	42
WEST1	44.63	6.90	0.91	0.42	0.81	163	1472–2001 (530)	234	0.19	0.32	34
WEST2	45.23	7.07	0.91	0.43	0.83	179	1453–2002 (550)	282	0.18	0.23	25
EAST	46.44	11.41	0.95	0.43	0.81	478	961–2003 (1043)	214	0.19	0.25	26

Note: Chronology statistics include mean ring width (MRW), standard deviation (SD) and first-order serial autocorrelation (AC) computed on the raw tree-ring series, mean sensitivity (MS), mean interseries correlation (r_{bt}) and the variance explained by the first principal component (PC1) computed on the indexed tree-ring series. Bold values highlight statistics outside the 10th or 90th percentile. See Fig. 1 for site locations. Latitude and longitude for composite chronologies (WEST1, WEST2 and EAST) are the mean values derived from the single sites.

SPATIAL VARIABILITY OF TREE GROWTH AND CLIMATE RESPONSE PATTERNS

When applied to the tree-ring growth indexes and climate responses (CFs) for the period 1804–1994, PCA analyses yielded significant and consistent clusters (Fig. 2a–c), which were confirmed by *K*-means clustering and ANOVA (degrees of freedom = 2, 27, $F > 31$, $P < 0.001$ for both analyses) (STATISTICA software, Statsoft 2001). The clear site distribution along a diagonal in the scatterplots suggested that both PCs contributed (with different weights) to the characterization of the site-specific tree-ring growth pattern and climate response.

When PC1 and PC2 loadings were plotted against site latitudes and longitudes, the clusters reproduced the site locations in the Alps (Fig. 3). All of these correlations (except for PC2 vs. longitude: –0.55) remained significant even after either the longitude or latitude effects were removed (partial correlation).

Statistics of the composite mean chronology were coherent with the single site values, and the relatively high values of r_{bt} and PC1 indicated that common variance of tree growth patterns between sites was good (Table 1).

Figure 4 clearly shows that the different patterns of the three composite chronologies in the two time domains significantly and stably match, both visually (Fig. 4a) and statistically, through a 50-year window running-interseries correlation (Fig. 4c, dark grey line), at the high frequency time scale only. There is higher variability in the low-frequency time scale (Fig. 4b), with an increase and a corresponding decline of a common signal during the last century (Fig. 4c, light grey line).

CLIMATE INFLUENCES ON TREE GROWTH

Although the regional responses to monthly temperatures exhibit different magnitude, they express a synchronous pattern, whereas monthly precipitation responses

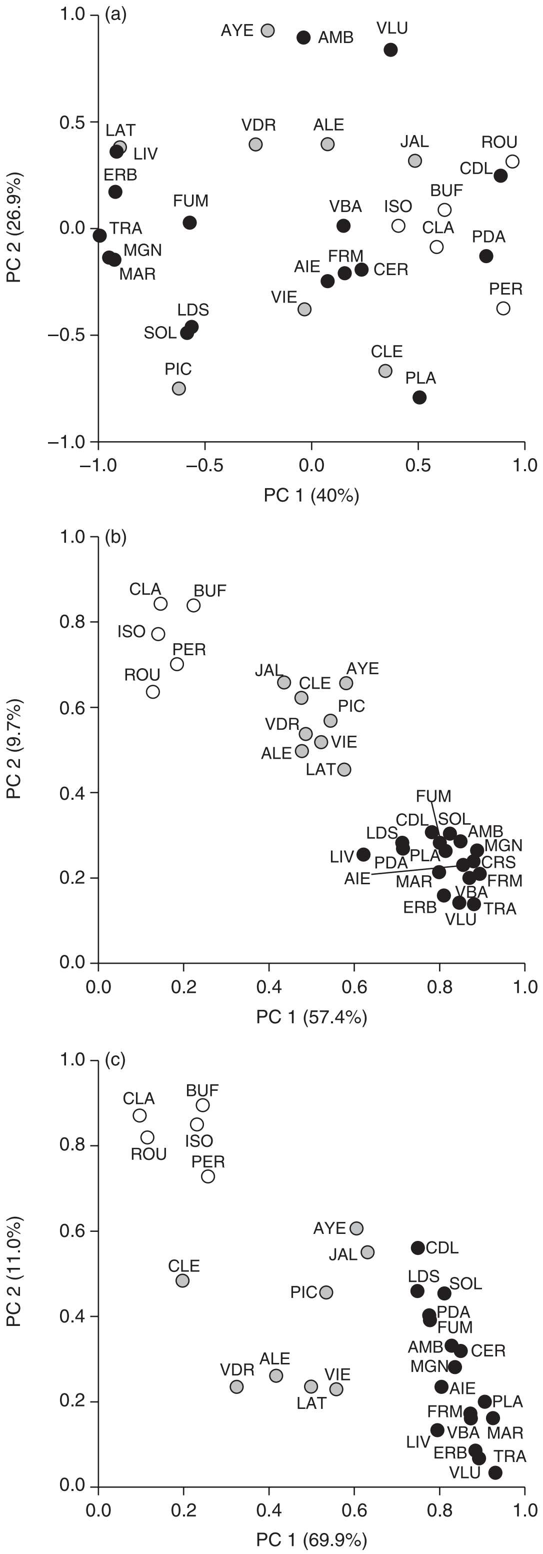

Fig. 2. Scatter plots of weighting coefficients for PC1 and PC2 calculated considering (a) the tree-ring chronologies statistics, (b) tree-ring indexed chronologies for the period 1804–1993, and (c) climate–growth relationships expressed by the 32 monthly correlation functions coefficients. Sites belonging to the same clusters in (b) are the same shade. Axis labels report the percentage of variance expressed by each component.

appear to reflect the well-known higher variability of rain (and snow) distribution in complex mountain regions (Fig. 5). For West2 and most East chronologies, temperature seems to be the key factor for tree-ring growth, while precipitation plays a major role in West1. Significant responses converge during three periods: (i) the growing season (May to August) of the year of ring formation (*t*), with positive temperature correlations especially in the eastern Alps; (ii) the autumn (September to December) prior to the year of ring formation (*t* – 1), again with positive responses to temperature for West2 and East, and a positive response to precipitation for West1; in the latter, significant responses shift from November to the winter months (January to March); (iii) the late winter/early spring months (February to April) just prior to the growing season, with a negative response to temperature which converges in March for all regional chronologies.

CFs can appropriately assess the year-by-year climate–growth responses of stone pine, but are unable to detect changes over time. MCF coupled with a very long-term weather data set allowed us to understand and reliably test the dynamic features of the long-term growth responses.

MCF monthly precipitation (Fig. 6) and temperature patterns (Fig. 7) generally confirm the results obtained with CF (Fig. 5). In many cases non-significant variables in CF analysis exhibit a stationary response over time (e.g. *t* – 1 September and October precipitation, *t* May and September precipitation, *t* – 1 June and July temperatures, *t* January, February and April temperatures). However, some variables to which the chronologies exhibit a significant response to climate, like *t* – 1 December or *t* August temperatures and *t* April precipitation, show dynamic responses with remarkable fluctuations throughout the 200-year period.

When the three curves have similar trends and run almost parallel, MCF (*t* – 1 October and *t* May precipitation, *t* – 1 July and *t* February temperatures) assesses the 'static' distribution of the responses to climate over time, but when the curves diverge (e.g. *t* July and August temperatures or *t* June precipitation) or converge (e.g. *t* – 1 and *t* September temperature or *t* February precipitation), the dynamic behaviour can be assessed between the different regional chronologies. For instance, the influence of *t* August temperature in the three regions has changed widely over time, with a significant increase of the positive effect only in the eastern Alps, a progressive decrease in the West2 region and a more stationary, but recently decreasing, trend in West1. Attention should also be paid to the entry or exit of the lines in the statistical significance threshold zone.

Discussion

While the 30 stone pine tree-ring chronologies compiled for high altitude sites in the French and Italian Alps display similar statistics, no spatial patterns were detected with these variables. This suggests that stone

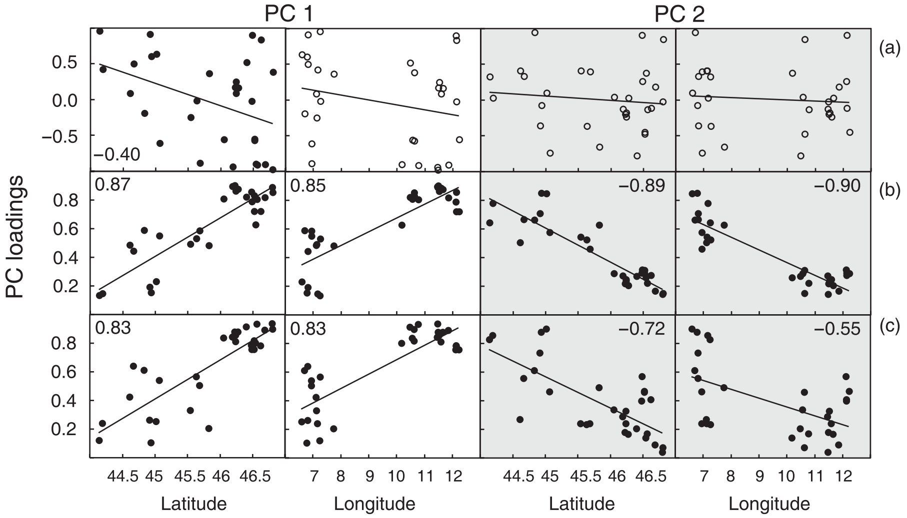

Fig. 3. Relationship between weighting coefficients for PC1 (not shaded) and PC2 (shaded) with sites latitude and longitude, considering (a) the tree-ring chronologies statistics, (b) tree-ring indexed chronologies for the period 1804–1993, and (c) climate–growth relationships expressed by the 32 monthly correlation functions coefficients. Open dots represent a non-significant relationship ($P > 0.05$); in all other cases the number in each plot corner represents the Pearson correlation coefficient ($P < 0.05$).

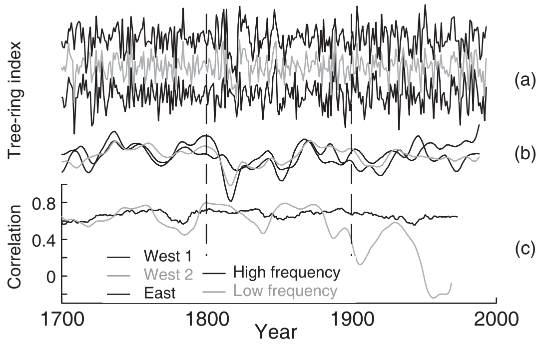

Fig. 4. (a) High-frequency and (b) low-frequency tree-ring indexed chronologies for each region. (c) Mean 50-year window running correlations of the three regional chronologies drawn in (a) and (b).

pine has a uniform mechanism to respond to the many environmental factors influencing tree-ring growth at different sites. On the other hand, the appearance of significant and clear clusters with PCA, computed for indexed site chronologies and their climate responses, are related to the well known capacity of this pine to retain evidence of varying climate in its tree-ring growth series (Motta & Nola 1996; Urbinati *et al.* 1997; Rolland 2002; Oberhuber 2004). A few intracluster differences in tree-ring growth patterns and responses to climate are present but these are likely to be irrelevant. Furthermore, intercluster differences can probably be attributed to: (i) the variable local weather conditions typical of Alpine areas; (ii) site characteristics in terms of soil moisture, solar radiation, snowmelt dynamics and length of growing season; and (iii) forest stand history and chronological structure, which in the Alps derives from millennia of human disturbances and land-use changes.

The same climatic factors appear to limit growth at many sites, and the magnitude of this appears to be synchronously influenced by regional climate variability. Climatological studies from instrumental time series confirm this hypothesis, describing similar regional features for both temperature (Böhm *et al.* 2001) and precipitation variability in the Alps (Brunetti *et al.* 2006).

The separation of high- and low-frequency components in the tree-ring series provided a better visual and statistical understanding of their influence on the spatial clustering of sites, which seems to be determined primarily at low frequency rather than at an annual scale. Moreover, the recent drop in the site intercorrelation curve at low frequency following two centuries of relative stability would suggest climate-driven rather than species-specific or disturbance-induced behaviour. Büntgen *et al.* (2005) reached the same conclusion for high altitude larch (*Larix decidua* Mill.) in the northern Alps since the lowest values of the cross-chronology correlation over 400 years were in the last decades of the 20th century. Auer *et al.* (2006) and Brunetti *et al.* (2006) confirm the distinct climate in the western and eastern Alps in recent decades, with precipitation showing the highest regional and seasonal differences and remarkably opposed dynamics. Another overall factor related to regional variability has been changes to land use since the mid-19th century, which has had a significant effect on the traditional management of high altitude silvo-pastoral systems in the Alps. Many areas were progressively abandoned and human disturbance to timberline forests greatly diminished (Didier 2001; Motta & Nola 2001; Motta & Lingua 2005).

The climate system in the Alps is very complex and so are its changes and dynamics at the different time scales (global seasonal, decadal and interannual). This is due largely to (i) the position of this mountain range between the Atlantic Ocean and a vast continental land mass, to the south-east of the mean axis of the polar-front jet stream over the North Atlantic; (ii) the existence of two main climatic regimes, those of the Mediterranean

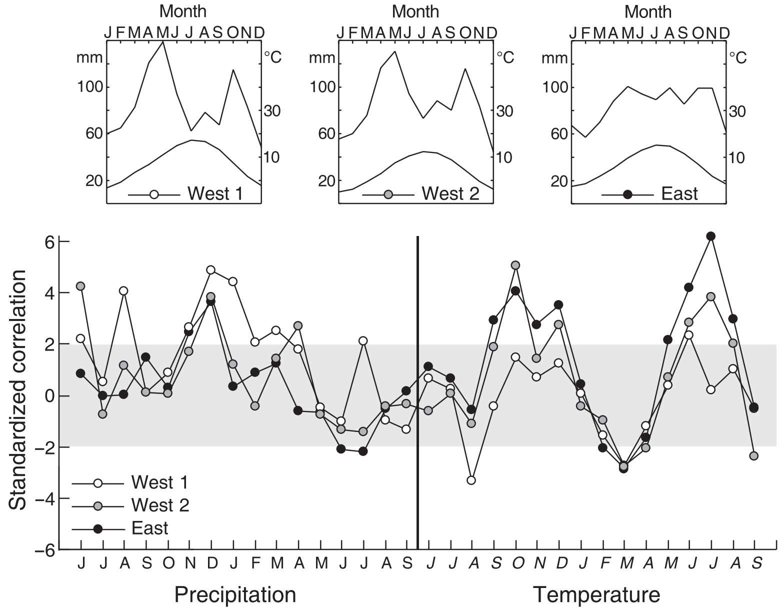

Fig. 5. Correlation functions between regional tree-ring indexed chronologies and total monthly precipitation and mean monthly temperatures for the previous (June to December) and current (January to September) growth year. Standardized coefficients were obtained by dividing the mean correlations by their standard deviations after the bootstrap replications. They express the significance of monthly parameters. Values above |2| are significant at $P < 0.05$. The three small plots show the typical average course of mean monthly temperatures and precipitation regimes linked with the three regional chronologies.

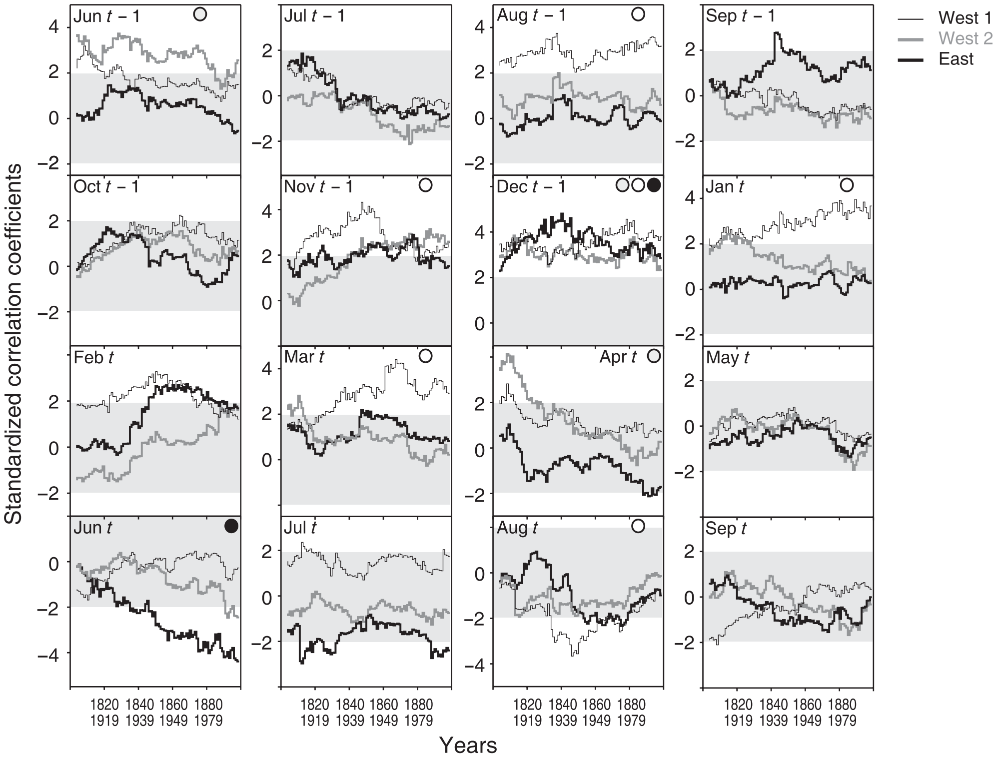

Fig. 6. Monthly precipitation effect on tree-ring growth during the period 1804–1999, using moving correlation function with a 100-year time window (represented in four cases by the labels on the *x*-axis). Values outside the shaded area are significant ($P < 0.05$) with the standard approach (i.e. considering each test as independent); filled circles indicate significant curves according the False Discovery Rate adjusted significance levels. *x*-axis range is the same for all plots, but ordinate axis scale can change according to absolute values.

and the North Atlantic; and (iii) the very heterogeneous and irregular topography (Wanner *et al.* 1997; Böhm *et al.* 2001; Auer *et al.* 2005). The biologically mediated responses of stone pine obtained with CFs globally reflect this situation and confirm once again the ability of this species to capture low-scale environmental variability in its tree-ring series (Urbinati *et al.* 1997; Oberhuber 2004). A few climatic factors appear to control tree growth in the southern Alps: winter precipitation in the West1 sites, and summer (*t*) and late

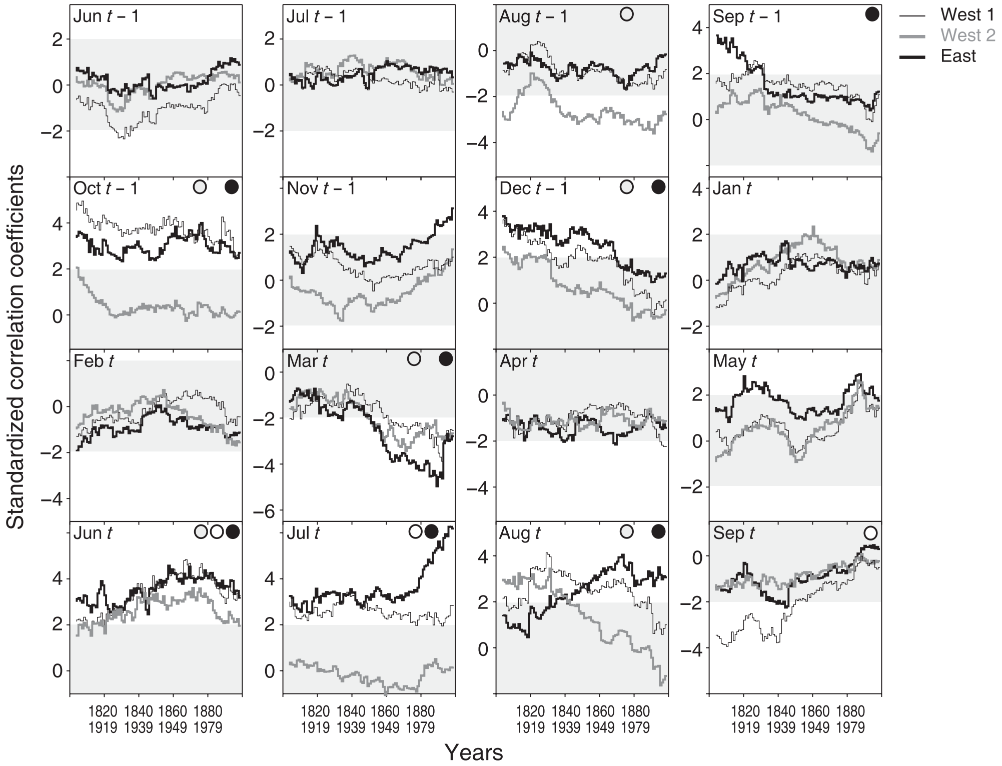

Fig. 7. Monthly temperature effect on tree-ring growth during the period 1804–1999, using moving correlation function with a 100-year time window. See Fig. 6 for further explanations.

autumn/early winter (t – 1) temperatures in the West2 and East sites. The relatively drier summer conditions in the westernmost district of the Alps (mean June to September precipitation in West1 vs. East sites is 302 mm vs. 369 mm, respectively, $P < 0.0001$) make stone pine particularly sensitive to winter precipitation in the West1 sites, i.e. to snow cover that provides an essential reservoir for water storage in these high-elevation shallow and coarse-textured soils (Beniston *et al.* 2003). The different responses between West1 and West2 sites, despite their relative proximity, could be explained by: (i) the area astride the Italian/French border is in the transition zone between two different climatic regions (mean June to September precipitation in West2 vs. West1 sites is 336 mm vs. 302 mm, respectively, $P < 0.0001$) (Böhm *et al.* 2001; Brunetti *et al.* 2006), and (ii) the accuracy of stone pine in recording climate signals caused by topographical differences (e.g. aspect and slope), especially in limiting conditions such as at the treeline (Urbinati *et al.* 1997; Oberhuber 2004). In contrast, the negative influence of June and July precipitation on growth in East sites is probably associated with a reduction in available solar radiation (more cloudy days) and reduced photoinhibition following cold night temperatures (Grace *et al.* 2002).

The positive correlation of summer temperature in the East and West2 sites supports the hypothesis of growing season length as a major growth limiting factor. Warmer summer temperatures at these sites promote earlier snow-melting and more rapid soil warming, thereby lengthening the growing season. These warmer temperatures may also promote faster leaf, shoot and stem growth (Tranquillini 1979; Korner & Paulsen 2004). On the other hand, the interpretation of the positive correlation in the same sites for the t – 1 late summer/autumn temperatures is not straightforward. A possible explanation is that net photosynthesis and daily carbon balances are still positive, even if they progressively decrease at this time of year until winter dormancy sets in (as a result of shorter days, lower irradiance and near-freezing temperatures), allowing the pine to keep storing carbohydrates available for early shoots and stem growth in the forthcoming season (Fritts & Swetnam 1989; Wieser *et al.* 2005). A similar but reverse process could provide an explanation for the negative growth response in late t winter/early spring, when temperatures rise in parallel with respiratory C losses. Trees may need more than one month to recover these losses, thus increasing the possibility of narrow ring formation (Wieser & Bahn 2004).

Moving correlation functions were used to assess the differences and dynamics of these signals over time. Two main features appeared. First, several months exhibit changing patterns over time (e.g. January, March and June for precipitation; July and August for temperature). This is probably related to regional climate and environmental changes in the Alps, with different interannual variations and long-term trends featuring two main dipolar structures, one north–south and the other east–west. Second, the temporal step-wise increase or abrupt loss of significance in growth sensitivity for certain variables (e.g. February precipitation, July and August temperature for the East chronologies) may indicate the presence of underlying threshold-controlled mechanisms. Some of these effects were detected in high-altitude species in alpine (Carrer & Urbinati 2001) and boreal areas (Wilmking *et al*. 2004), but additional ecophysiological research is needed to fully evaluate these complex feedback mechanisms and to establish whether trees reached these thresholds in the past, or if they are related to some unprecedented environmental conditions affecting tree growth (e.g. atmospheric CO_2, anthropogenic nitrogen deposition or stratospheric ozone concentration). However these changing responses cannot be related to one specific factor, as the synergic and contrasting climate–growth relationships have clearly proven.

Conclusion

Stone pine growth in the French and Italian Alps varied significantly at annual and, mainly, short (> 20 years) time scales, and these changes appeared to be mostly driven by climatic factors. Winter conditions and spring–summer temperatures mainly affected the growing season length and carbon and site water-balances of stone pine. Response patterns to temperature are more homogeneous in the three regional chronologies, whereas those to precipitation exhibit a higher degree of variability, especially in the westernmost sector. Most of these limiting factors varied spatially and temporally along the latitudinal and longitudinal gradients, and most probably arose in response to the regional variations in climate and geographical features present along the 1500-km transect investigated.

Climate–growth relationships based on long-term weather records and extensive site networks provided excellent tools to detect species' spatial and temporal variability in a climatically complex region. More detailed studies, at least for the Alps, should be done on a regional scale in order to accurately evaluate cause–effect interactions between climate change and forest productivity (IPCC 2001). A forest dynamics modelling approach at high spatial–temporal resolution may fail to provide reliable estimates of climate controlled tree-ring growth if the potential variability of this factor over time has not been assessed. In addition, the transfer of climate–growth functions for reconstructions of past conditions could be similarly biased.

Future studies should also consider multiple species sampling along altitude gradients and the collection of stand structure data (density, height and biomass) in the closed forests below the treeline. This will be useful for distinguishing climate from competitive constraints on species ranges, and validating ecosystem model predictions, thereby providing a clearer understanding about the future role of forests in the global carbon cycle (Tardif *et al*. 2006).

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