

Site-aspect influence on climate sensitivity over time of a high-altitude *Pinus cembra* tree-ring network

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Abstract Recently a divergence between tree-ring parameters from temperature-limited environments and temperature records has been observed worldwide but comprehensive explanations are still lacking. From a dendroclimatic analysis performed on a high-altitude tree-ring network of *Pinus cembra* (L.) in the Central Italian Alps we found that site aspect influences non-stationary growth-climate relationships over time. A general increasing divergence between ring width and the summer temperature record (J–A) has been observed especially for chronologies from SW-facing slopes, whereas chronologies from N-facing sites showed stable relationships over time. The monthly analysis revealed that the decrease in sensitivity was mostly accounted for by the changes in the relationships with June temperature (decreasing correlations especially for S- and W-facing site chronologies), whereas trees from N-facing sites showed an increasing sensitivity to July temperatures. Our data suggest that at high altitudes, low temperatures at the beginning of the growing season no longer limit growth. We also found that our temperature-sensitive trees did not linearly respond in radial growth to the extreme heat event of summer 2003, and formed an annual ring of average width, resulting in a strong divergence from the temperature record. Our findings underline the importance of site ecology for tree-ring based climate reconstructions using temperature-sensitive ring-width chronologies, and may help in solving the ‘divergence problem’.

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1 Introduction

Past climate reconstructions have acquired an important position inside the scientific community since policy makers from different sectors of society require reliable predictions of future climate change impacts (IPCC 2001, 2007). The role of climatic reconstructions is crucial since they help to assess the past natural natural variability of climate and, therefore, they provide essential information for climate predictions. Climate reconstructions are based on two main approaches. The first relies on models based on historical records of meteorological instrumental data. The second is based on the analysis of proxy data from natural archives (e.g., tree rings, pollen profiles, varves, sediment stratigraphy, glaciers and ice cores) or from the landscape's morphology (e.g., moraines and glacial drifts). The study of proxies allows the extensions of climate reconstruction back to periods before instrumental data, and proxies have been successfully used in the construction of many long climate records worldwide (Jones et al. 1998; Mann et al. 1998; Pauling et al. 2003; Bradley et al. 2003; Luterbacher et al. 2004). In many different proxy-based reconstructions of climate, dendrochronology plays an important role, because trees are able to record long series of annual environmental information in the tree rings (e.g. IPCC 2001; Hughes 2002).

The classical approach to dendroclimatic reconstructions is based first on the definition of the relationships between tree-ring data and meteorological records over the common period. Before performing the reconstruction, the period with meteorological data is usually split into a calibration period, where the model is calibrated, and a verification period, where the model's strength is tested (Fritts 1976). This approach assumes that growth-climate relationships are stable over time, i.e. it is based on the uniformitarian principle. Several authors (e.g. Jacoby and D'Arrigo 1995; Briffa et al. 1998; Wilson and Luckman 2003; D'Arrigo et al. 2007) however, have reported a general increasing divergence between tree-ring parameters (i.e. ring width and maximum density) and temperature records in the recent decades, which has serious implications for tree-ring based reconstructions. Briffa et al. (1998) reported a decreasing sensitivity of wood density and ring width to summer temperature records on a global scale especially at high-latitude sites. Various reasons for this phenomenon have been suggested: an increase in spring temperatures, a decrease in solar radiation, an increase in atmospheric carbon dioxide and pollution (tropospheric ozone, nitrogen or acidic deposition). Frank and Esper (2005) reported a divergence between a multispecies high altitude tree-ring network in the European Alps and instrumental records of summer temperatures. Büntgen et al. (2006) analyzed tree-growth responses to summer monthly temperatures and precipitation at high-altitude sites of *Picea abies* (L.) Karst. and they found a strong decreasing sensitivity to summer temperatures and even a negative correlation with August temperatures in the recent decades. Carrer and Urbinati (2006), analysed the monthly responses of *Larix decidua* (Mill.) in a high-altitude tree-ring network, also in the European Alps, and suggested there has been a recent deviation from the uniformitarian principle traditionally applied to dendroclimatology. They found significant changes in growth-climate relationships over time, with trees showing long-term trends in their sensitivity to climate. In a recent publication Carrer et al. (2007) reported varying growth-climate relationships over time for a *Pinus cembra*

tree-ring network from the Eastern and Western Italian Alps, but in their analysis they did not differentiate the chronologies by site characteristics.

In this paper we test the sensitivity to climate of a *Pinus cembra* (L.) high-altitude tree-ring network over time, comparing ring-width chronologies with seasonal and monthly instrumental data. We focus especially on finding out whether significant long-term changes in growth-climate relationships are taking place at high altitudes in the European Alps, and if trees from different slope-aspect sites show different variations in sensitivity to climate over time. We also are interested in determining the periods of year that are mostly involved in these changes. Moreover, we will analyze growth responses of the high-altitude trees to the heat wave that took place in Europe and the European Alps during summer 2003, which affected vegetation growth in the Alps in different ways, especially according to site altitude (Jolly et al. 2005).

2 Materials and methods

Thirteen tree-ring chronologies of *Pinus cembra* were built from living trees in high-altitude sites in six Italian valleys of the Central Italian Alps (Fig. 1). Sites with different slope aspects were selected, at an altitude between 2,100 and 2,250 a.s.l.

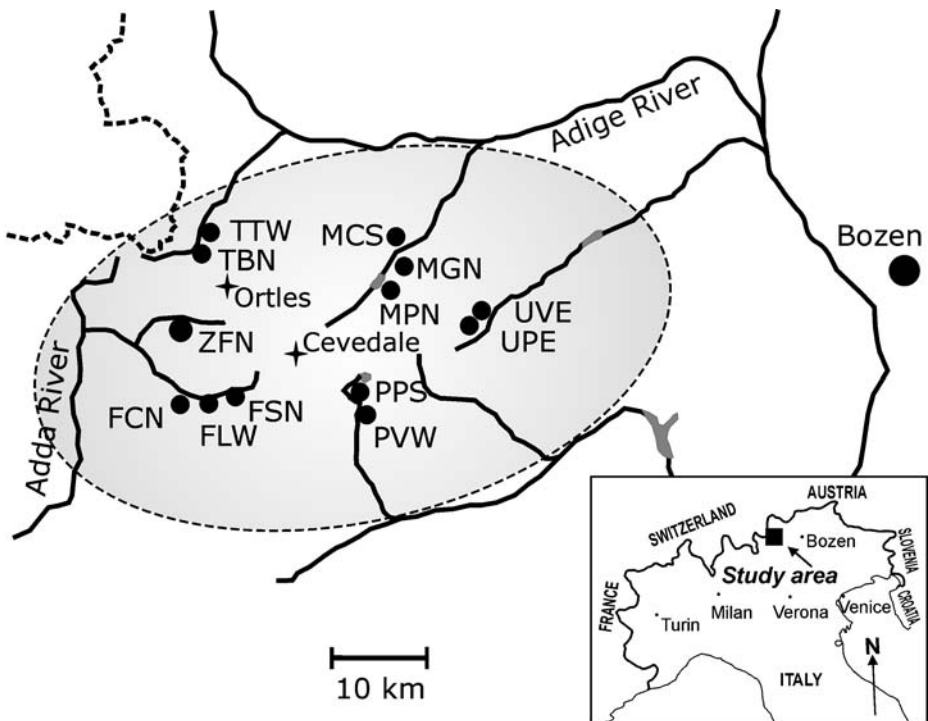


Fig. 1 Sketch map of the study area and the 13 selected sites. Hydrography of the main rivers and position of the two highest peaks (Ortles, 3,902 m a.s.l., and Cevedale, 3,769 m) are also reported

(Table 1). At each site we selected 15 dominant trees with undisturbed canopies, and extracted two opposite cores per tree from opposite sides of the stems at breast height (1.3 m from the ground), perpendicular to the slope direction to avoid possible compression wood and minimize stem eccentricity. The samples were prepared according to standard procedures (Stokes and Smiley 1968), and ring widths were then measured with 0.001 mm precision using the WINDENDRO (Regent Instruments, Quebec, Canada) image-analysis system.

All tree-ring measurements from each site were visually and statistically cross-dated to avoid potential dating errors and to test the quality of the data set. This procedure was performed with the TSAPWIN (Rinntech, Heidelberg, Germany) and COFECHA (Holmes 1983; Grissino-Mayer 2001) programs, and the data then validated by selecting for further analysis only the ring-width series that correlated well ($r > 0.5$) with their site's mean chronology (Hofgaard et al. 1999; Pelfini et al. 2006).

Site chronologies were built with the program winARSTAN (vers. 41; <http://www.ldeo.columbia.edu>) by detrending ring-width series to remove long-term growth variations related to age and stand disturbances (Fritts 1976; Cook et al. 1990). A first detrending was performed by fitting to the series a linear or an exponential curve or a horizontal line passing through the mean, and a second detrending by fitting a cubic smoothing spline with a 50% frequency-response cut-off at 67% of the series length (Cook et al. 1990). Residual chronologies were computed by applying a robust biweight mean to the detrended indices, derived from autoregressive modelling (Cook and Briffa 1990). Using residual chronologies from autoregressive modelling helps to remove the problem of biological persistence in the resulting series (Fritts 1976).

Considering for each site chronology only the period presenting a minimum sample size of five cores, a hierarchical cluster analysis was performed on the common period 1808–2003 in order to produce clusters of sites. Sites were grouped according to the average linkage method and the Euclidean distance was used as a measure of similarity. The four more distant site chronologies presenting the same site slope aspect were averaged into two composite chronologies ('SouthWest', SW, and 'North', N, as detailed in Section 3), by applying a robust estimation of the mean which reduces the influence of outliers and enhances the common signal (Cook et al. 1990). With the same method another chronology ('All') was computed by including all the 13 chronologies.

For the dendroclimatic analysis we used data from 1865 to 2003 (139 years) comparing the three composite chronologies (SW, N and 'All') and the gridded seasonal and monthly temperature and precipitation anomalies for the grid point 10° N, 46° E from the HISTALP dataset (Auer et al. 2007). Anomalies refer to the twentieth century mean (1901–2000) and were derived only from homogenised data, both for the seasonal and monthly temperature series (2004–11 release; high-altitude record, >1,400 m a.s.l.) and precipitation series (2004–2008 release). For the seasonal analysis, we chose six variables of mean temperatures and six of total precipitation which ranged from the summer (JJA) of the previous year (t^{-1}) to the autumn (SON) of the year of growth (t). For the monthly analysis, on the other hand, we chose 15 variables, both for temperature and precipitation, from July (t^{-1}) to September (t). For both seasonal and monthly analyses we used the program DENDROCLIM2002 (Biondi and Waikul 2004), computing correlation functions over the whole period

Table 1 Site characteristics and corresponding essential statistics for the site chronologies, ordered according to the three groups emerging from the cluster analysis

Site code	Cluster group	Mean altitude	Latitude N	Longitude E	First year of chronology	Last year of chronology	Chronology length	Number of trees	Number of radii	Mean tree age	Mean ring width	Mean sensitivity	EPS	AC order in the 1 ^a	Variance in the PCI
<i>PPS</i>	A	2230	46.41	10.69	1560	2004	445	14	27	231	0.904	0.176	0.947	0.90	0.48
<i>UVE</i>	A	2250	46.48	10.81	1752	2004	253	15	30	157	1.410	0.173	0.926	0.80	0.43
<i>PVW</i>	A	2250	46.4	10.71	1593	2004	412	15	29	201	1.318	0.226	0.918	0.76	0.45
<i>MCS</i>	A	2230	46.56	10.75	1680	2005	326	15	29	265	0.713	0.165	0.947	0.90	0.41
<i>TTW</i>	A	2150	46.55	10.53	1636	2004	369	15	28	245	0.950	0.147	0.951	0.84	0.45
<i>FCN</i>	B	2250	46.41	10.46	1664	2004	341	15	28	217	1.106	0.165	0.949	0.74	0.44
<i>UPE</i>	B	2150	46.48	10.82	1751	2004	254	15	30	175	1.434	0.165	0.946	0.77	0.46
<i>TBN</i>	B	2100	46.54	10.52	1699	2004	306	15	28	203	1.070	0.153	0.939	0.86	0.42
<i>FLW</i>	C	2200	46.41	10.52	1685	2004	320	15	30	210	1.157	0.183	0.962	0.78	0.50
<i>ZFN</i>	C	2180	46.47	10.50	1756	2005	250	15	30	194	1.230	0.156	0.958	0.86	0.48
<i>FSN</i>	C	2170	46.42	10.55	1657	2004	348	15	29	232	0.949	0.163	0.945	0.89	0.43
<i>MGN</i>	C	2190	46.50	10.73	1760	2005	246	15	30	133	1.612	0.153	0.841	0.92	0.51
<i>MPN</i>	C	2110	46.49	10.70	1742	2005	264	15	28	166	1.314	0.150	0.930	0.80	0.46

The last letter of the site code indicates the site aspect. Italicized codes correspond to the sites selected to build the ‘SouthWest’ and ‘North’ composite chronologies
EPS expressed population signal, *AC* autocorrelation

^aThe values relate to the growth series

and over 60-year periods with the moving correlation functions (MCF) approach. In both the analyses, correlation coefficients were calculated with the bootstrapping method, with 1,000 iterations. With the MCF approach, correlation coefficients are calculated between tree-ring data and the climatic variables over fixed time periods (in our case 60 years) that are progressively shifted of 1 year starting from 1865. Since MCF were calculated on non-independent intervals, the significance of the correlation coefficients for the overlapping 60-year periods was assessed by means of the Bonferroni correction method. It is an adjustment made on confidence levels when multiple statistical tests are evaluated simultaneously (Snedecor and Cochran 1989).

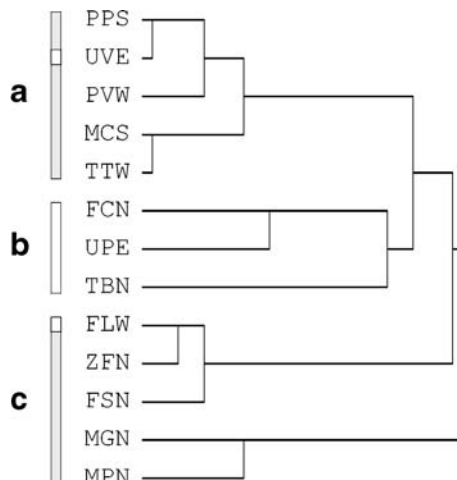
At the decadal scale, the 60-year period that we choose for the MCF analysis is the maximum time span for dividing 139 years of analysis in two not-overlapping equal periods (1865–1924, and 1944–2003). These two independent periods were later used to test if there were statistically significant differences in the correlation coefficient values computed at the beginning and at the end of the analysis.

3 Results

The cluster analysis of the 13 site chronologies produced a dendrogram with three main groups of site chronologies, mainly distinguished by site aspect (Fig. 2). According to this result, after excluding the UVE chronology (because from a E-facing site), four chronologies from S- and W-facing slopes (group A, in Fig. 2) were merged in the ‘SouthWest’ (SW) composite chronology as explained in the Methods. At the opposite side of the dendrogram (group C in Fig. 2), four chronologies, all from N-facing sites, were merged together in the ‘North’ (N) chronology and the FLW chronology excluded (because from a W-facing site).

All the 13 residual chronologies presented similar growth patterns (Fig. 3). They were built with trees that were on average older than 150 years (except for the MGN chronology), and up to 265 years old (MCS; Table 1). The time interval covered by

Fig. 2 Dendrogram resulting from the cluster analysis and the three main groups that we considered (*A*, *B* and *C*). The *grey bars* indicate the chronologies that were selected at the extremities of the dendrogram to build the ‘SouthWest’ (from group *A*) and ‘North’ (from group *C*) composite chronologies. *White bars* indicate the chronologies that were not included in the composite chronologies



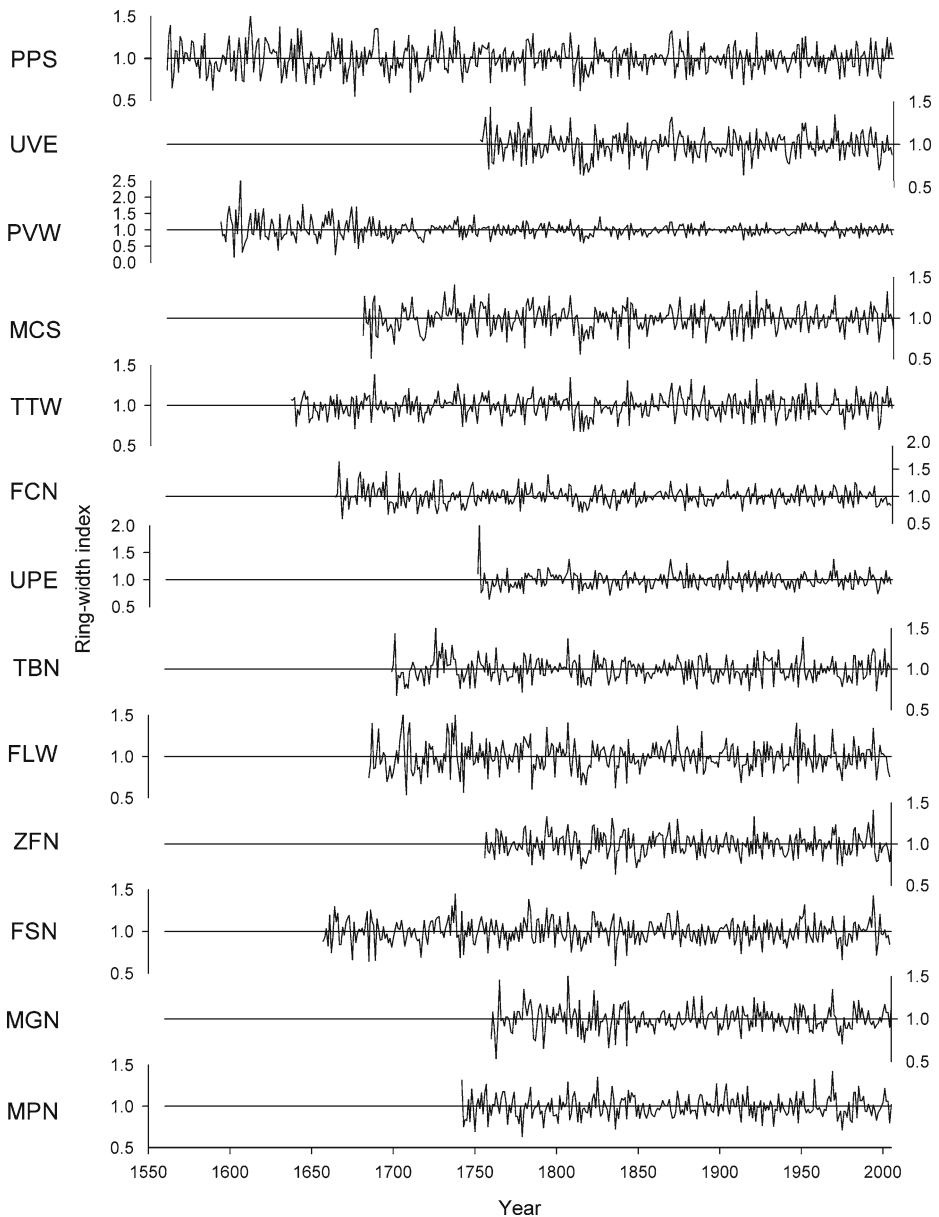
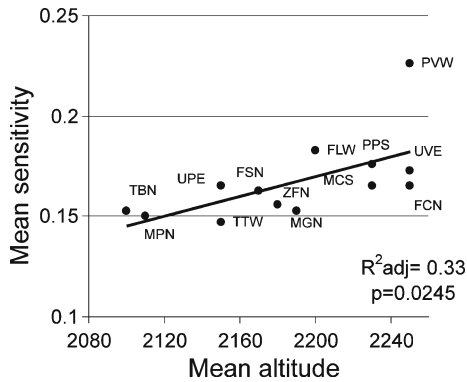


Fig. 3 The 13 residual chronologies of *Pinus cembra* used in the present study and ordered according to the patterns emerged from the cluster analysis

all the chronologies was over 250 years (except for the MGN chronology), and up to 445 years (PPS). Year to year variations expressed by mean sensitivity ranged between 0.147 and 0.226, and generally showed greater values at high-altitude sites, the regression of mean sensitivity on mean altitude being statistically significant (Fig. 4). Expressed population signal statistics (EPS; Wigley et al. 1984), a measure of

Fig. 4 Mean sensitivity of the residual chronologies expressed as a function of altitude. Regression is significant at the 95% level



the chronologies’ signal strength related to mean interseries correlation (R_{bar}) and the series replication, show a mean value of 0.94.

Testing the differences between groups, sites of group A presented a slightly higher mean altitude (+52 m; $P = 0.044$) and also slightly older trees (+33 years) than group C (Table 2). Considering the two subgroups of S-W- and N-facing sites, differences in altitude were not statistically significant for mean altitude, but were significant for mean age (+55 years; $P = 0.046$). However no significant differences between chronologies both of A and C groups, and SW and N subgroups, were found in mean sensitivity and EPS (Table 2). Also for first-order autocorrelation, and variance in the first principal component, no significant differences were found (data not shown). Site aspect appears to be the main factor that better distinguish the two groups of chronologies at the extremities of the dendrogram (Fig. 2).

Climatic analysis over the whole period revealed a strong positive influence of summer temperatures on tree-ring growth, with both the whole summer (JJA) and

Table 2 Test of the differences between groups of chronologies for some of the characteristics reported in Table 1

	<i>N</i>	Mean altitude (m)	<i>SD</i>	Mean tree age (yr)	<i>SD</i>	Mean sensitivity	<i>SD</i>	Mean EPS	<i>SD</i>
Complete groups from cluster analysis									
Group A	5	2222	37.1	220	37.7	0.177	0.026	0.938	0.013
Group B	3	2167	62.4	198	17.5	0.161	0.006	0.945	0.004
Group C	5	2170	31.6	187	34.5	0.161	0.012	0.927	0.045
Difference A–C		52		33		0.016		0.011	
<i>P</i>		0.044 ^a		0.189		0.239		0.624	
Composite-chronology groups									
‘SouthWest’ (SW)	4	2215	38.4	236	23.3	0.179	0.029	0.941	0.013
‘North’ (N)	4	2163	31.1	181	36.4	0.156	0.005	0.919	0.046
Difference SW–N		52		55		0.023		0.022	
<i>P</i>		0.078		0.046 ^a		0.172		0.387	

Significant levels were adjusted according to the Bonferroni correction

^aStatistical significance level = 95%

N number of chronologies, *SD* standard deviation, *EPS* expressed population signal

July temperatures showing the strongest correlation coefficient (CC) values (Fig. 5). In general, trees appear to be more sensitive to the current-year temperatures than to precipitation. However, we found a positive influence of previous-year autumn precipitation on tree-growth, especially for the SW chronology.

MCF analysis revealed that growth-climate relationships significantly changed over time both for temperature (Fig. 6) and precipitation (Fig. 7), with almost synchronous variations in the CC values. Significant differences in CC values were noticed. We found a long-term decrease in the CC values for summer temperature for ‘All’ and SW chronologies (Fig. 6). A strong and significant ($P < 0.001$) variation in the CC was found for the SW chronology, with CC being non-significant in the most recent periods of analysis. On the contrary, the CC values of N chronology were almost stable over time and the differences between the first and last period of analysis were not significant ($P = 0.841$). Comparing the CC values between SW and N chronologies in the first and in the last 60 years of analysis, we found more statistically significant ($P < 0.001$) differences in the first 60 years of analysis than in the last ($P = 0.02$).

The monthly analysis of long-term changes in the temperature-growth relationships revealed significant non-stationary responses especially for late spring (May) and early summer temperature (June; Fig. 6). In particular, for June temperature both SW and N chronologies revealed a strong negative trend in CC values, with significant ($P < 0.001$) changes over time for the SW chronology. In the first 60-year period of analysis we found significant ($P < 0.001$) differences in CC values between SW and N chronologies, whereas in the more recent 60-year period CC values tend to coincide. Stronger CC values were found for July temperature over time. Especially the N chronology showed a significant ($P < 0.001$) increase in CC values, whereas SW chronology showed more stationary values. Differences in CC values between SW and N chronologies were significant ($P < 0.001$) in the last 60-year period of analysis.

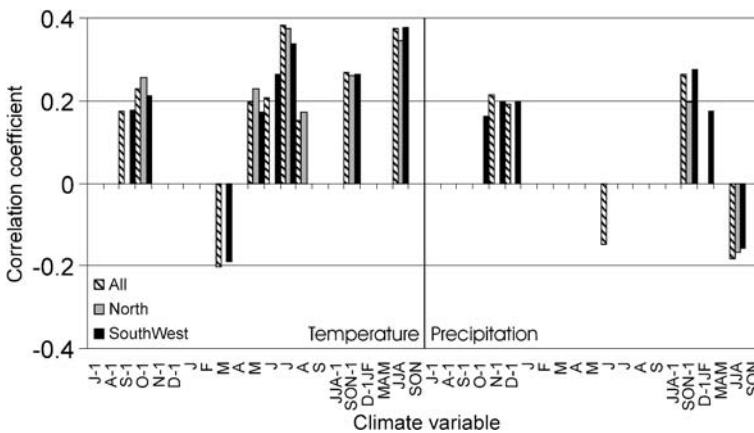


Fig. 5 Correlation coefficient computed between the three composite chronologies and all the considered seasonal and monthly variables during the period 1865–2003. Correlation significance was assessed by means of the 95th percentile range and only significant correlation values are showed

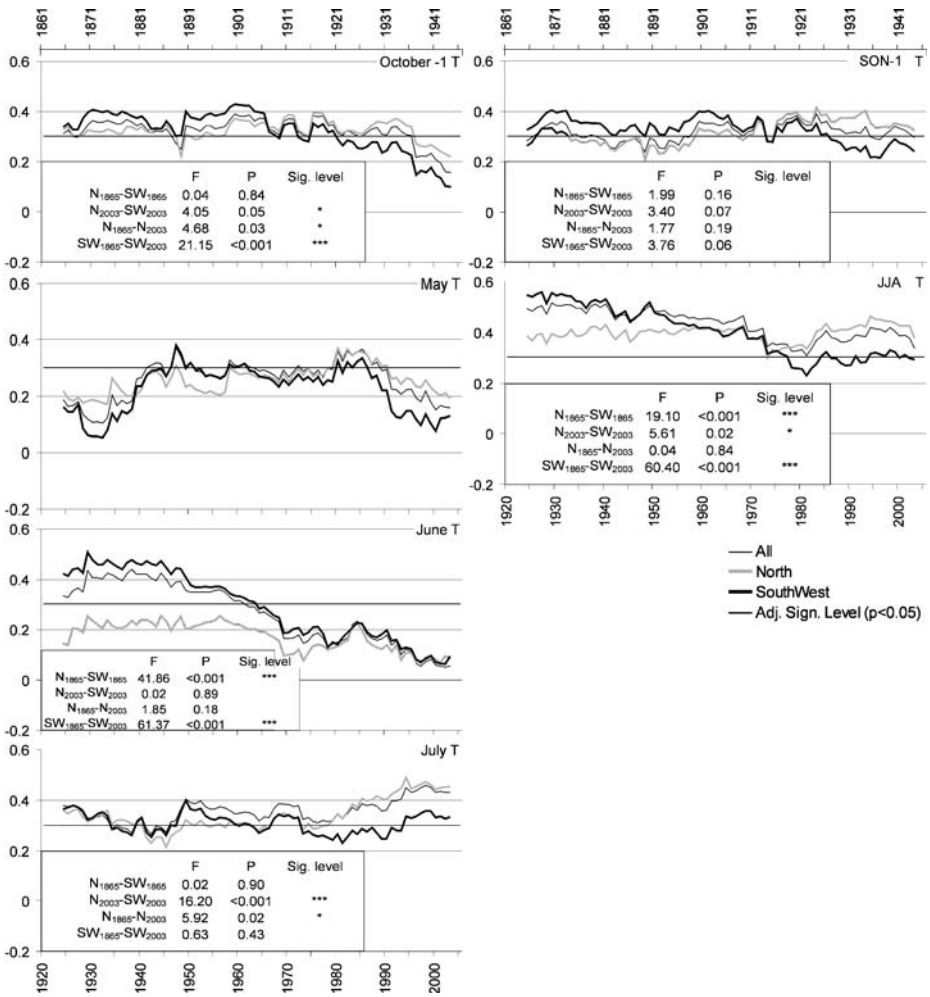


Fig. 6 MCF computed between the composite chronologies and the seasonal and monthly temperature variables for the most important months during the period 1865–2003. Horizontal lines indicate the adjusted significance limits ($p < 0.05$), according to the Bonferroni correction. The variables presenting at least 15 significant CC were considered as more important for tree growth. The boxes in the graphs report the results of t -tests performed on CC values of SW and N chronologies for the same 60-year period (1865–1924 named ‘1865’, and 1944–2003 named ‘2003’), and on CC values of the same chronology for the first (‘1865’), and last (‘2003’) 60-year periods of analysis

We also found changes in climate-growth relationships over time for previous-year Autumn and Winter precipitation (Fig. 7). Stronger changes were noticed especially with Autumn⁻¹ precipitation with SW chronology showing the strongest and more significant ($P < 0.001$) variation over time, with decreasing CC values. On the contrary, N chronology revealed almost no significant CC. Both SW and N chronologies showed an increasing negative trend towards negative CC values for June precipitation, but a significant influence on tree growth appear to be limited only to the central period of analysis.

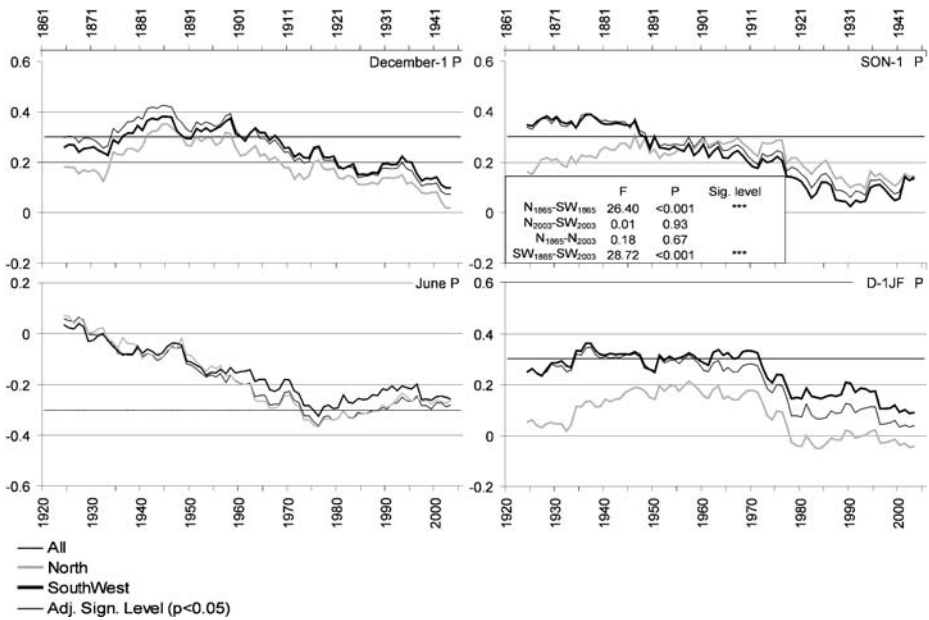


Fig. 7 MCF computed between the composite chronologies and the seasonal and monthly precipitation variables for the most important months during the period 1865–2003. Horizontal lines indicate the adjusted significance limits ($p < 0.05$), according to the Bonferroni correction. The variables presenting at least 15 significant CC were considered as more important for tree growth. The boxes indicate t -tests results as in Fig. 6

To highlight long-term trends in temperature and precipitation of summer months (J, J, and A) we smoothed the anomaly series of the HISTALP data set for our study area with a 3-year running mean filter. A general linear trend towards higher temperature values is visible for these 3 months especially since the 1980s and the trends on the whole period result highly significant for June and August temperature (Fig. 8a). August presents the strongest trend (of nearly 2°C since 1865), whereas July presents the weakest trend (of about 1°C). A higher variability is noticed for precipitation, and the stronger trend is presented by August (with about 10% higher precipitation since 1865), but trends on the whole period are always not significant (Fig. 8b).

We also checked how trees from the dendroclimatic network responded to the extreme climatic event that happened during summer 2003, when very high temperatures were recorded because of a heat wave settled over Europe and the Alps (Rebetez 2004; Beniston 2004). In our study area higher temperatures were recorded for June and August, whereas July temperature were not exceptional. Analysis of the ring-width chronologies revealed no particular growth release in summer-temperature sensitive trees in 2003. Trees did not linearly respond to higher temperatures as underlined by a ring-width index that resulted in the mean (Fig. 9). However, trees from S- and W-facing sites formed a slightly wider ring, but the 2003 ring width was not significantly different from the one of N-facing sites.

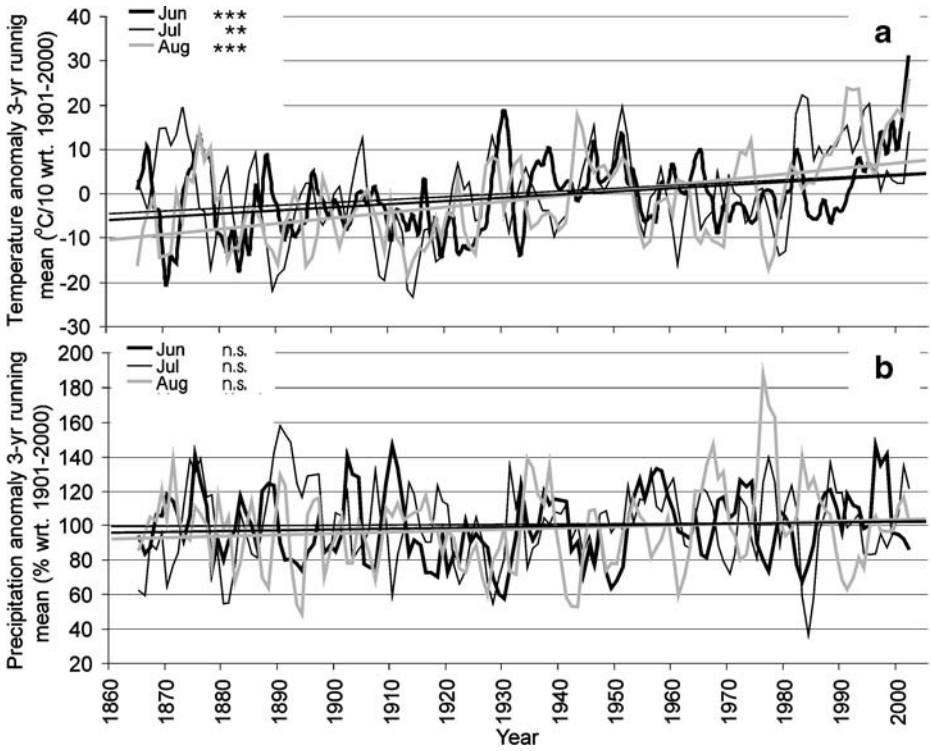
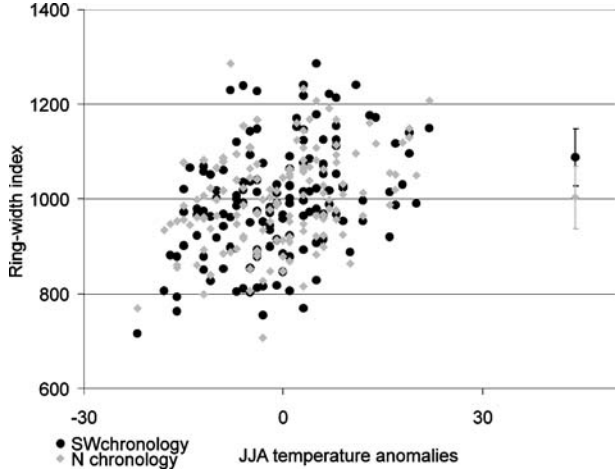


Fig. 8 Three-year running mean for temperature and precipitation anomalies calculated between 1865 and 2003. Temperature (a) are expressed as 0.1° with respect to the twentieth century mean (1901–2000) and precipitation (b) as percentages of the twentieth century mean (HISTALP data, Auer et al. 2007). In both graphs, *straight lines* represent the linear trends in the instrumental data; *asterisks* indicate the statistical significance level of the trend: *** $p < 0.001$; ** $p < 0.01$; n.s., not significant

Fig. 9 Scatter plot of SW and N chronologies versus summer temperature (JJA) record over the period 1865–2003. For the ring-width of year 2003 the *vertical bars* indicate one standard deviation from the mean value



4 Discussion

The three composite chronologies that were analysed (SW, N and 'All') showed synchronous variations in CC values to seasonal and monthly climate variables over the period we studied (1865–2003) for which instrumental data were available. However, sensitivity of trees to climate of important months for tree growth significantly varied over time according to the different site aspect. As reported, the SW chronology was built with trees that are about 50 years older and grow at slightly higher altitudes than the trees of the N chronology, but no significant differences were noticed between groups when checking the chronology characteristics.

We found that N-facing sites present a higher sensitivity to July temperatures, especially since 1911–1970. S- and W-facing sites, instead, showed no changes in sensitivity through time for July, with values of CC close to the 95% significance level. At the moment we cannot explain why our tree-ring chronologies show higher sensitivity to July temperatures in the recent years. What is clear from our results is that some climatic factor related to slope aspect (e.g. temperature regime, snow-cover persistence or growing season length) play a key role in limiting pine tree-ring growth at high altitudes, especially in N-facing sites.

Relationships with temperature of early growing season months (May and June), suggest that June temperatures are now over a threshold and no longer limit growth as they did in earlier decades. Stronger changes are involving especially the S- and W-facing sites that in the past were more limited by June temperature. Furthermore, we hypothesize that trees on N-facing slopes are generally less adapted to warmer conditions at the beginning of the growing season (June) and therefore respond less to increasing temperature than trees on S- and W-facing slopes sites.

However, the influence of slope aspect on stone pine tree-ring growth was discussed by several authors as Oberhuber and Kofler (2003), who reported the strongest growth responses to recent climate warming in high-altitude stands on N-facing slopes. According to them, cool-moist sites are primarily affected by general climatic trends that induce faster snow-melting and longer growing seasons. Peterson and Peterson (1994) and Villalba et al. (1997) also reported the strongest responses to climate warming on N-facing sites, and attributed this to a faster snow-melting or longer growing seasons.

On the other hand, our high-altitude tree-ring network showed a general decreasing sensitivity to summer season temperature records too. The generally divergent trend in correlations with summer season temperatures at our sites mainly affects S- and W-facing sites and may probably be mainly explained by the decreasing sensitivity of tree growth to June temperatures. On the contrary, trees from N-facing sites show quite stable relationships with summer temperature over time, even if for these sites sensitivity to July temperatures is increasing in the recent years. A decreasing sensitivity to summer temperatures has been reported at many high latitude and altitude sites and appears to be a general trend affecting tree-ring growth on a global scale (Jacoby and D'Arrigo 1995; Briffa et al. 1998; Wilson and Luckman 2003; Frank and Esper 2005; Büntgen et al. 2006; Carrer and Urbinati 2006). In particular, Carrer et al. (2007) performing a MCF analysis with monthly variable also found an increasing sensitivity to July temperatures for a high-altitude (1,900–2,300 m a.s.l.) *Pinus cembra* tree-ring network from the Eastern Alps, which partially overlap our network. They also found much lower correlation and no

correlation with July temperature for another two networks of the same species from the Western Alps. However, their study was performed at the regional scale and no specific information on different altitudes or different site aspect between the three networks was reported.

In a geographically close high-altitude tree-ring network for European larch (*Larix decidua* Mill.), a decreasing trend of CC values has been reported for June temperatures for the recent years, as well as a strong increasing negative correlation over time between tree-ring growth and June precipitation (Carrer and Urbinati 2006). Büntgen et al. (2006) reported a loss in sensitivity for all summer months since the mid months since the mid nineteenth century for a Norway spruce tree-ring network in the Swiss Alps, but no significant correlation with June precipitation was found.

Various factors may induce the divergence between tree-ring growth and temperature records. The rise in atmospheric concentration of CO₂, however, does not seem to play a role because, at the tree-line, tree growth is not limited by photosynthesis (e.g. Körner 2003). Drought stress does not seem to play a role either, at least not at our high-altitude sites where the summer months are mostly rainy. We also noticed a slight increasing trend of August precipitation. Lack of water is not, therefore, limiting growth and this stress should not be driving the increasing loss in sensitivity to summer temperatures. However, according to Büntgen et al. (2006), a temperature-induced drought stress may, if it is above some threshold value, break down the idealized “linear” growth-climate relationships. D’Arrigo et al. (2004) reported a negative effect on tree-growth of summer temperatures over a threshold optimum in combination with increasing soil-moisture stress towards the end of the growing season. The combined effect of these two factors seems to explain the recent decline in temperature sensitivity.

With increasing global temperatures, threshold temperatures are expected to be more frequently exceeded in the future and to affect tree-growth when extreme episodic events occur. But these events are unlikely to be responsible for a gradual loss in trees’ sensitivity to temperatures, apparent globally at high latitudes and altitudes. Pollution and atmospheric deposition could also play a role in the ‘divergence problem’, since they also can affect tree-ring growth (e.g. Wilson and Elling 2004; Pärn 2003). Their effects on tree growth, however, do not seem sufficient to explain the observed change in climate sensitivity (e.g. Nadelhoffer et al. 1999).

Summer 2003 was the warmest Europe had experienced during the previous 500 years (Luterbacher et al. 2004). This caused a reduction in primary productivity (Ciais et al. 2005) and induced various responses in vegetation at different altitudes, as a survey using a remote sensing revealed (Jolly et al. 2005). Jolly et al. (2005) observed a longer growing season at higher altitudes (from +2% to +12% longer season from >1,400 to 2,800 m) and reported a radial-growth enhancement from a sample of broadleaf and conifer species in the Swiss Alps at 1,400–2100 m. At our sites, temperatures were especially high in June and August 2003, whereas in July they were close to the mean (Fig. 8). We found that pine trees at our network (2100–2250 m) did not respond to the warmer and longer growing season by forming wider rings: summer 2003 can be therefore seen as strong divergence “event” between the summer temperature records and tree-ring growth. Since this kind of climatic extremes will likely become more frequent in a warmer atmosphere, we think that in the future, ring-width chronologies from high-altitude temperature-limited environments will diverge even more markedly from summer temperature

records. Our results suggest that carbon storage of pine trees at high altitudes may not be effective above a particular temperature threshold. According to Carrer et al. (1998), subalpine pine trees seem unable to fully benefit from warm and sunny days already at temperatures above $\sim 13^{\circ}\text{C}$.

5 Conclusions

Our high-altitude tree-ring network indicates that changes in climate sensitivity took place over the last 139 years (period covered by our analysis) according to site aspect. Global climatic factors seem to play an important role, since the phenomenon of a divergence between tree growth and temperature records has been affecting tree rings at many sites worldwide. However we found that slope aspect may play an important role in modulating the sensitivity changes over time, probably because trees are exposed to different temperature regimes. Trees from S- and W- facing sites show a strong increasing divergence from summer temperature record (and with May and June), whereas trees from N-facing sites show stationary relationships with summer temperature, but increasing sensitivity to July temperature.

Our pine trees from the high-altitude network did not respond linearly to the 2003 heat wave event and did not form exceptionally wide rings: the resulting ring width was close to the mean. Extremely warm climatic conditions during the growing season, like those during summer 2003 will likely increase the divergence between ring-width data and temperature records since extreme temperature events will likely become more frequent in Europe (Beniston 2004), and trees appeared not able to record this climatic information in their radial growth. Ring-width chronologies do not seem able to record information about extreme warm events, probably because of threshold temperatures that limit growth processes.

Our results point to the need to test growth-climate relationships over time to detect possible trends in climate sensitivity. This should be done before choosing the period for calibrating the models for tree-ring based reconstructions since wide variation in climate sensitivity over time could lead to over- or underestimations of past temperatures. Our findings also showed that slope aspect plays an important role in influencing tree sensitivity to climate, which means that site ecology could also affect dendroclimatic reconstructions.

Local meteorological factors are highly variable in high mountains, and there are also species-specific responses to climatic and microsite ecological conditions, e.g. those related to slope aspect: responses to climate change are species specific (Huntley 1991) and depend also on site characteristics. Nevertheless, it is likely that temperature-induced drought stress can explain episodic strong growth reductions, but cannot fully explain the general trends towards increasing divergence between tree-ring growth and the temperature records. Physiological responses to co-varying environmental variables may help in solving the problem about divergence with temperature records.

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