Long-term change in the sensitivity of tree-ring growth to climate forcing in *Larix decidua*

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**Summary**

- Tree rings are widely used long-term proxy data which, if combined with long-term instrumental climate records, can provide excellent information on global climate variability. This research aimed to determine whether interannual climate–growth responses in Alpine treeline forests are stationary over time.
- We used tree-ring width chronologies of *Larix decidua* (European larch) from 17 sites and monthly temperatures and precipitation data for the period 1800–1999. Climate–growth relationships were assessed with correlation and response functions, and their stationarity and consistency over time were measured using moving correlation.
- Tree-ring chronologies showed similar interannual variations over the last two centuries, suggesting that the same climatic factors synchronously limited growth at most sites. The most sensitive variables showed significant transient responses varying within the time period, indicating a possible deviation from the uniformitarian principle applied to dendroclimatology.
- If these findings are confirmed in future studies on other species and in other regions, we suggest that time-dependent variables should be taken into account to avoid overestimation of treeline advance, future forest carbon storage in temperature-limited environments and inaccurate reconstruction of past climate variability.

**Key words:** climate–growth responses, dendroclimatology, *Larix decidua* (European larch), moving correlation function, tree ring, uniformitarian principle.


**Introduction**

One of the key questions concerning climate change is whether the temperature increase recorded over the last few decades is really unprecedented. In order to answer this question without bias, it is essential to place current global warming within the context of longer-term climate variability. The main drawback of this up-scaling process is the sparseness of instrumental climate records before the 20th century, requiring the use of ‘proxy’ indicators to estimate global climate variability during past centuries [see Bradley (1999) for a review; IPCC, 2001].

Tree rings are the most important and widely used sources of long-term proxy data. Their major strengths as climate change indicators are (i) their annual resolution, (ii) the existence of large geographic-scale patterns of synchronic interannual variability, (iii) the increasing availability of extensive networks of tree-ring chronologies, and (iv) the possibility of using simple linear models of climate–growth relationships that can be easily verified and calibrated (Hughes, 2002). Their weaknesses include: (i) an intrinsic sampling bias, given that tree-ring information is available only for terrestrial regions of the globe, (ii) the fact that methods used to extract growth signals from tree-ring series retain only certain wavelengths of climate variability (IPCC, 2001), (iii) the complexity of biological responses to climate forcing, and (iv) the presence of nonclimatic variability in the series attributable to intrinsic growth trends and other nonclimatic disturbances (Fritts, 1976).

Regardless of the biological nature of tree-ring information, James Hutton’s principle of uniformitarianism (Britannica
Concise Encyclopædia, 2005), a crucial keystone in any palaeoenvironmental study, is assumed to be true for tree-ring-based climate reconstructions. In dendroclimatological, this principle implies that tree-growth–climate relationships are stable over time so that we can reliably infer the nature of past climate from statistically derived tree-ring calibration in the recent past (Fritts, 1976). However, there have been several recent demonstrations of a change in the response of tree growth, and/or at least a reduction in tree sensitivity, to climate over the last 40 or 50 years. Briffa et al. (1998a, 1998b), Smith et al. (1999), Biondi (2000) and Solberg et al. (2002) found evidence that tree-ring widths and density variations have changed in their response to temperature in recent decades, possibly as a result of nonclimatic/human-induced factors. In contrast, Vaganov et al. (1999) and Wilmking et al. (2004) have presented evidence that such changes can be climatic and result from the delaying effects of increasing winter precipitation on the onset of the growing season or from recent climate warming. Many studies also focused on the fertilization effect of atmospheric CO₂ enrichment, although conclusions were not consistent. LaMarche et al. (1984), Graybill & Idso (1993), Nicolucci et al. (1995), Feng (1998) and Knapp et al. (2001) presented evidence of a probable CO₂ effect on tree growth, while Kienast & Luxmoore (1988), Graumlich (1991), D’Arrigo & Jacoby (1993) and Tognetti et al. (2000) found no such evidence. Other studies reported alternative causes for the late 20th century change in tree growth responses to climate: Barber et al. (2000) and Lloyd & Fastie (2002) found that temperature-induced drought stress could be an increasingly important limiting factor in the white spruce (Picea glauca) forest of Alaska, while Briffa et al. (2004) suggested the falling ozone concentration in the stratosphere as a possible nonclimatic factor influencing tree growth. In some cases, investigators found different anthropogenic forces acting on a local or regional scale; for example, Wilson & Elling (2004) reported evidence indicating that the anomalous trends observed in silver fir (Abies alba) data since the mid-1960s and the weakening of the climate signal in Norway spruce (Picea abies) data since the mid-1970s are likely to be predominantly related to local SO₂ emissions from power plants and refineries.

The implications of these findings are important: long-term alteration of tree growth responses to climate forcing seems, at least to some extent, inconsistent with the underlying assumption of Hutton’s uniformitarianism and could significantly affect reconstruction of past climates and modelling of forest carbon uptake and biogeochemical cycles (Briffa et al., 1998a; Barber et al., 2000). Therefore, the occurrence and possible causes of changes in growth–climate relationships must be explored to assess the nature of these changes in detail.

However, regardless of the physical and/or physiological mechanism(s) inducing these changing responses, most of the existing research shares a common intrinsic bias, currently unresolved, as a result of the paucity of very long-term instrumental climate records: calibration and verification procedures in climate reconstruction were rarely applied before the 20th century and never before the mid-19th century. Most of the analyses were performed in the industrial era, when at least some of those physical and/or physiological factors were already in a nonstationary phase.

The availability of a very long-term climate record for the Alpine region provided an opportunity to better test the hypothesis that the effect of climate forcing on tree growth is changing. The study focuses on one of the highest-altitude and most climate-sensitive tree species of the Alps: Larix decidua. Our aim was to determine whether the year-to-year climate–growth responses are stationary over time and, accordingly, whether the uniformitarian principle is supported by the evidence. The temporal stability of climate–growth relationships is mainly assessed by means of correlation and moving correlation functions, and by splitting the climate record into two parts: before and after 1900.

Materials and Methods

Ring-width chronologies were developed for Larix decidua Mill. (European larch) trees at 17 sites located in high-altitude forest areas of the Eastern Italian Alps (Fig. 1). These are mainly open timberline forests at an altitude range of 1800–2200 m above sea level (asl), with a canopy density ranging between 5 and 20% and very low direct human-related disturbance (i.e. logging, livestock grazing, fire, etc.). Bedrocks and soils vary according to site, from dolomite and limestone bedrock with shallow rendzic leptosols, to volcanic and metamorphic silicates (such as granite, porphyry, gneiss and phyllite) with spodosols and podzols.

Following standard techniques (Phipps, 1985), two cores per tree were taken on the cross-slope sides of the trunk using increment borers at approx. 1.30 cm above ground level; core sample depth ranged from 13 (at site FRN) to 60 trees (at sites CDL and TOV) (Table 1). Individuals were randomly selected from among dominant or codominant trees free of structural damage.

In the laboratory, using a standard procedure (Stokes & Smiley, 1968), cores were glued onto grooved boards, and planed with progressively finer grade sandpaper to produce flat surfaces on which the ring boundaries were clearly defined under magnification and ring width measured to 1 µm precision. Dating and measurement errors were checked with the COFECHA computer program (Holmes, 1983).

Tree-ring growth chronologies were obtained from the cross-dated ring-width series using the program ARSTAN (Cook & Holmes, 1997). To remove the tree-ring trend in the series resulting from the tree circumference increasing with time, individual series were first standardized by fitting a negative exponential curve to measured data series and by dividing observed by expected values. These dimensionless indexes were then submitted to different standardization procedures, as follows. (i) To preserve common interdecadal and lower
frequency variations, we computed indexed site and regional mean chronologies adopting a robust estimation of the mean value function, which enhances the common signal, reducing the effect of outliers (Cook, 1985). The series were then smoothed with a low-pass filter (> 10 years) to assess the long-term (> 10 years) climate response of the species (Briffa et al., 1998b). (ii) To emphasize interannual higher frequency variations, a spline function with a 50% frequency response of 20 years was fitted to individual indexed series and the observed/expected ratio was computed again. Flexible cubic spline curves are very efficient at removing both the long-term trend and the effect of localized disturbance events, but at the risk of removing possible low-frequency climatic information (Cook & Peters, 1981; Cook et al., 1990). In some cases autoregressive modelling (Box & Jenkins, 1976) was used to remove a significant serial autocorrelation still retained after the spline indexing. A standard arithmetic mean function was used to produce a standardized growth curve for each tree, whereas a robust estimation of the mean value function was adopted for site and regional averaging.

Several descriptive statistics, commonly adopted in dendrochronology, were used to compare the site chronologies. These statistics included the mean sensitivity (MS) and standard deviation (SD) to assess the high-frequency variations (Fritts, 1976), the first-order serial autocorrelation (AC) to detect eventual persistence retained after the standardization, the mean correlation between trees ($r_{bt}$) and the variance explained by the first principal component (PC1). See Fig. 1 for site locations.

### Table 1 Site description and descriptive statistics for larch (Larix decidua) tree-ring chronologies

<table>
<thead>
<tr>
<th>Site code</th>
<th>Latitude (°N)</th>
<th>Longitude (°E)</th>
<th>Altitude (m)</th>
<th>No. of trees</th>
<th>Chronology time-span (years)</th>
<th>Mean tree age (years)</th>
<th>MS</th>
<th>AC</th>
<th>$r_{bt}$</th>
<th>PC1</th>
</tr>
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<tbody>
<tr>
<td>TAR</td>
<td>46.47</td>
<td>13.69</td>
<td>1700</td>
<td>17</td>
<td>1594–1999 (406)</td>
<td>250</td>
<td>0.27</td>
<td>0.22</td>
<td>0.48</td>
<td>51</td>
</tr>
<tr>
<td>DOG</td>
<td>46.45</td>
<td>13.45</td>
<td>1600</td>
<td>18</td>
<td>1645–1999 (355)</td>
<td>217</td>
<td>0.27</td>
<td>0.09</td>
<td>0.46</td>
<td>49</td>
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<tr>
<td>BER</td>
<td>46.43</td>
<td>12.67</td>
<td>1850</td>
<td>18</td>
<td>1685–1999 (315)</td>
<td>216</td>
<td>0.38</td>
<td>0.21</td>
<td>0.50</td>
<td>54</td>
</tr>
<tr>
<td>RES</td>
<td>46.24</td>
<td>12.55</td>
<td>1750</td>
<td>16</td>
<td>1698–1999 (302)</td>
<td>174</td>
<td>0.27</td>
<td>0.11</td>
<td>0.29</td>
<td>37</td>
</tr>
<tr>
<td>CAD</td>
<td>46.58</td>
<td>12.27</td>
<td>2000</td>
<td>17</td>
<td>1463–1998 (536)</td>
<td>335</td>
<td>0.32</td>
<td>0.13</td>
<td>0.62</td>
<td>63</td>
</tr>
<tr>
<td>PAR</td>
<td>46.58</td>
<td>12.26</td>
<td>2050</td>
<td>18</td>
<td>1695–1998 (304)</td>
<td>243</td>
<td>0.28</td>
<td>0.06</td>
<td>0.59</td>
<td>61</td>
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<tr>
<td>CAS</td>
<td>46.81</td>
<td>12.17</td>
<td>2100</td>
<td>15</td>
<td>1414–1999 (586)</td>
<td>316</td>
<td>0.34</td>
<td>0.02</td>
<td>0.58</td>
<td>60</td>
</tr>
<tr>
<td>AMB</td>
<td>46.47</td>
<td>12.11</td>
<td>2150</td>
<td>43</td>
<td>1525–1997 (423)</td>
<td>250</td>
<td>0.31</td>
<td>0.04</td>
<td>0.62</td>
<td>63</td>
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<tr>
<td>CDL</td>
<td>46.49</td>
<td>12.10</td>
<td>2100</td>
<td>60</td>
<td>1515–1994 (480)</td>
<td>284</td>
<td>0.39</td>
<td>0.00</td>
<td>0.67</td>
<td>67</td>
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<tr>
<td>FOR</td>
<td>46.50</td>
<td>12.09</td>
<td>2150</td>
<td>13</td>
<td>1717–1995 (279)</td>
<td>216</td>
<td>0.31</td>
<td>−0.01</td>
<td>0.59</td>
<td>63</td>
</tr>
<tr>
<td>MFO</td>
<td>46.24</td>
<td>11.67</td>
<td>2100</td>
<td>15</td>
<td>1681–1998 (318)</td>
<td>221</td>
<td>0.37</td>
<td>0.15</td>
<td>0.60</td>
<td>62</td>
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<tr>
<td>PCC</td>
<td>46.17</td>
<td>11.57</td>
<td>2050</td>
<td>15</td>
<td>1468–1999 (532)</td>
<td>257</td>
<td>0.32</td>
<td>0.11</td>
<td>0.54</td>
<td>57</td>
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<tr>
<td>TOV</td>
<td>46.13</td>
<td>10.55</td>
<td>2030</td>
<td>60</td>
<td>1266–2002 (737)</td>
<td>352</td>
<td>0.37</td>
<td>−0.01</td>
<td>0.56</td>
<td>58</td>
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<tr>
<td>VFO</td>
<td>46.75</td>
<td>10.96</td>
<td>2100</td>
<td>17</td>
<td>1528–1999 (472)</td>
<td>335</td>
<td>0.29</td>
<td>0.22</td>
<td>0.56</td>
<td>58</td>
</tr>
<tr>
<td>MAR</td>
<td>46.55</td>
<td>10.74</td>
<td>2200</td>
<td>14</td>
<td>1525–1999 (475)</td>
<td>393</td>
<td>0.37</td>
<td>−0.01</td>
<td>0.68</td>
<td>69</td>
</tr>
<tr>
<td>COM</td>
<td>46.34</td>
<td>10.67</td>
<td>2200</td>
<td>17</td>
<td>1438–1999 (562)</td>
<td>483</td>
<td>0.32</td>
<td>0.05</td>
<td>0.58</td>
<td>60</td>
</tr>
<tr>
<td>VLU</td>
<td>46.83</td>
<td>10.61</td>
<td>1900</td>
<td>14</td>
<td>1498–1999 (503)</td>
<td>375</td>
<td>0.27</td>
<td>0.35</td>
<td>0.68</td>
<td>70</td>
</tr>
<tr>
<td>Mean</td>
<td>46.47</td>
<td>11.89</td>
<td>2000</td>
<td>370</td>
<td>1266–2002 (737)</td>
<td>279</td>
<td>0.26</td>
<td>0.03</td>
<td>0.50</td>
<td>70</td>
</tr>
</tbody>
</table>

Chronology statistics include mean sensitivity (MS), first-order serial autocorrelation (AC), mean interseries correlation ($r_{bt}$) and the variance explained by the first principal component (PC1). For the mean chronology, PC1 was calculated using the 17 mean site chronologies. Bold font indicates significant AC values removed by the autoregressive model. See Fig. 1 for site locations.
the amount of year-to-year growth variations shared among trees of the same chronology.

We used standard correlation function (CF) analysis to assess climate–growth relationships (Fritts, 1976) and moving CF to test their stationarity and consistency through time with the computer program DENDROCLIM2002 (Biondi & Waikul, 2004). We adopted a 100-year interval, which was progressively slid across time, to compute the correlation coefficients (Biondi, 1997, 2000), split the climate record into two subperiods (1800–1896 and 1897–1993), and computed CFS for the mean chronologies and for each single tree. The statistical significance and stability of the CFS and moving CFS were evaluated with a bootstrap procedure with 1000 replications. Each correlation coefficient was deemed significant if the mean value was at least twice the standard deviation of its 1000 replications (Guiot, 1991). To assess any intercollinearity present in the CF parameters, we performed response function analysis, using the same climatic variables and significance criteria. Response function is a multiple regression technique where the independent variables are transformed into a smaller number of uncorrelated variables defined as principal components (Fritts, 1976; Briffa & Cook, 1990). For moving CF, the Benjamini & Hochberg (1995) false discovery rate approach was applied for multiple test correction of the significance levels.

Mean monthly temperatures and total monthly precipitation data for the period 1800–1999 were retrieved from the ALP-IMP dataset (2004). In this dataset, records from 192 precipitation and 131 temperature stations throughout the ALP-IMP dataset (2004). We adopted a 100-year interval, which was progressively slid across time, to compute the correlation coefficients (Biondi, 1997, 2000), split the climate record into two subperiods (1800–1896 and 1897–1993), and computed CFS for the mean chronologies and for each single tree. The statistical significance and stability of the CFS and moving CFS were evaluated with a bootstrap procedure with 1000 replications. Each correlation coefficient was deemed significant if the mean value was at least twice the standard deviation of its 1000 replications (Guiot, 1991). To assess any intercollinearity present in the CF parameters, we performed response function analysis, using the same climatic variables and significance criteria. Response function is a multiple regression technique where the independent variables are transformed into a smaller number of uncorrelated variables defined as principal components (Fritts, 1976; Briffa & Cook, 1990). For moving CF, the Benjamini & Hochberg (1995) false discovery rate approach was applied for multiple test correction of the significance levels.

Mean monthly temperatures and total monthly precipitation data for the period 1800–1999 were retrieved from the ALP-IMP dataset (2004). In this dataset, records from 192 precipitation and 131 temperature stations throughout the Alps were quality-checked for potential bias, especially for the 19th century period, and then interpolated to a 1° × 1° longitude–latitude grid (Böhm et al., 2001; Auer et al., 2005). CFS were computed using 24 independent variables (12 1-month time series each of temperature and precipitation) sequenced according to a ‘biological’ year frequently adopted for Alpine species studies (Ettl & Peterson, 1995; Nola, 1996; Carrer & Urbinati, 2004), ranging from October of the year before growth (t − 1) to September of the year of growth (t).

Results

Descriptive statistics for chronology

Table 1 lists the locations and altitudes of the 17 sample sites and the descriptive statistics for the corresponding tree-ring site chronologies. The four easternmost sites (TAR, DOG, BER and RES) are at lower altitude, because of the reduced height of the timberline and mountain ranges in that sector of the Alps. Tree-ring series were obtained from mature larch trees, with site mean tree ages (at coring height) of 174–483 years. The time-span for each chronology ranged from 279 years (FOR) to 737 years (TOV), with an overall mean tree age of 279 years. Mean sensitivity and first-order serial autocorrelation were 0.32 ± 0.04 and 0.10 ± 0.10 (mean ± 1 SD), respectively.

Five sites exhibited significant serial autocorrelation in their mean chronologies (bold font in Table 1), which was mostly removed after autoregressive modelling of the single tree series. Two useful parameters for evaluating the quality of a chronology are the mean interseries correlation (r0), and the percentage of common variance among trees included in the chronology (PC1): their values were 0.56 ± 0.09 and 59 ± 8, respectively. Neither of these statistics displayed a clear trend with respect to altitude or latitude. However, the four easternmost sites had lower r0 and PC1 statistics.

Considering the high correlation among the different site chronologies (values of median correlations, 5th and 95th percentiles were 0.69, 0.39 and 0.87, respectively, for the 1800–1994 period), we computed a regional chronology used for most of the climate–tree-growth analysis. Statistics for the regional mean chronology were consistent with the single site values, and the relatively high values of r0 and PC1 indicated a high common variance of tree growth patterns (and probably also tree growth responses to climatic variability) between sites.

Climatic influences on tree growth

The CF profiles of larch (Fig. 2) show that (i) the influence of climate on growth is mainly attributable to temperature and is concentrated in a 5–month period from March to July; (ii) June temperature and precipitation are probably the best predictors of larch growth throughout the investigated region; (iii) intercorrelation bias between climate series appears to be negligible as the response function profile for the 1800–1993 period was essentially similar to that of CF.

The splitting of the record into two subperiods produced similar CF profiles but also some relevant differences (Fig. 2; Table 2): (i) tree-ring growth appeared to be closely correlated with climatic variables, especially with June and, to a lesser extent, July precipitation and temperature; (ii) a shift between the first and second periods occurred at the onset of the negative and positive responses to temperature in March and May, respectively; (iii) very similar CF profiles between high- and low-frequency responses were obtained.

Table 2 Statistics of the response functions computed with the high-frequency chronologies for the entire time interval and each subperiod

<table>
<thead>
<tr>
<th>Period</th>
<th>R²</th>
<th>P</th>
<th>R calib. SD</th>
<th>calib.</th>
<th>R verif. SD</th>
<th>verif.</th>
</tr>
</thead>
<tbody>
<tr>
<td>1800–1993</td>
<td>0.540</td>
<td>0.020</td>
<td>0.735</td>
<td>0.027</td>
<td>0.608</td>
<td>0.060</td>
</tr>
<tr>
<td>1800–1896</td>
<td>0.534</td>
<td>0.044</td>
<td>0.731</td>
<td>0.040</td>
<td>0.436</td>
<td>0.121</td>
</tr>
<tr>
<td>1897–1993</td>
<td>0.716</td>
<td>0.030</td>
<td>0.846</td>
<td>0.065</td>
<td>0.083</td>
<td></td>
</tr>
</tbody>
</table>

R², coefficient of determination; P, significance of the model (< 0.05 for values > 1.96); R, mean multiple correlation coefficient of the 1000 bootstrap replications, for the calibration (calib.) and verification (verif.) periods, respectively; SD, standard deviation of the multiple correlation coefficient.
The consistency of these split CFs can be appreciated by considering the single tree responses. Table 3 shows that the differences between the responses of the two subperiods, 1800–1896 and 1897–1993, were highly significant, with only two exceptions (March precipitation and October temperature). In a previous study in the Alpine area on larch and cembran pine (Pinus cembra), we found that the older the trees were, the higher the climate signal retained in tree-ring width and the higher the percentage of trees with significant responses, but also that the effect of age on climate sensitivity is likely to be nonmonotonic (Carrer & Urbinati, 2004). In larch, the overall climate response changed with age according to a twofold pattern: increasing for trees younger than 200 years and mainly constant for older trees. Considering the very long time-span of the climate record and the age structure of this study, we performed an additional analysis by plotting the single tree-ring responses, stratified by age, for March–July temperatures and for June precipitation (Fig. 3). Trees younger or older than 230 years at the beginning of the 19th century showed similar and homogenous distributions. A t-test computed for each month and for both subperiods between the two age groups confirmed the absence of a possible age-related bias.

Table 3 Statistical and numerical comparisons of the climate responses between the two subperiods

<table>
<thead>
<tr>
<th>Month</th>
<th>Oct</th>
<th>Nov</th>
<th>Dec</th>
<th>Jan</th>
<th>Feb</th>
<th>Mar</th>
<th>Apr</th>
<th>May</th>
<th>Jun</th>
<th>Jul</th>
<th>Aug</th>
<th>Sep</th>
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<tbody>
<tr>
<td>Precipitation</td>
<td></td>
<td></td>
<td></td>
<td></td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean difference</td>
<td>0.23</td>
<td>−1.42</td>
<td>−1.26</td>
<td>−1.41</td>
<td>−1.06</td>
<td>−0.02</td>
<td>2.13</td>
<td>1.60</td>
<td>2.47</td>
<td>1.86</td>
<td>−0.88</td>
<td>−1.57</td>
</tr>
<tr>
<td>t-value</td>
<td>3.5</td>
<td>−19.3</td>
<td>−18.0</td>
<td>−19.3</td>
<td>−14.4</td>
<td>−0.2</td>
<td>22.5</td>
<td>25.5</td>
<td>29.2</td>
<td>22.6</td>
<td>−10.7</td>
<td>−25.3</td>
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<td>N 1800–1896</td>
<td>0</td>
<td>14</td>
<td>17</td>
<td>29</td>
<td>12</td>
<td>39</td>
<td>121</td>
<td>12</td>
<td>80</td>
<td>9</td>
<td>3</td>
<td>4</td>
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<tr>
<td>N 1897–1993</td>
<td>5</td>
<td>25</td>
<td>118</td>
<td>4</td>
<td>45</td>
<td>17</td>
<td>4</td>
<td>28</td>
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<tr>
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<td>−0.31</td>
<td>0.60</td>
<td>0.31</td>
<td>0.37</td>
<td>1.63</td>
<td>−0.78</td>
<td>−1.74</td>
<td>−1.38</td>
<td>−0.38</td>
<td>0.96</td>
<td>1.64</td>
</tr>
<tr>
<td>t-value</td>
<td>−1.4</td>
<td>−4.8</td>
<td>8.7</td>
<td>4.7</td>
<td>4.5</td>
<td>23.0</td>
<td>−9.0</td>
<td>−28.0</td>
<td>−11.9</td>
<td>−4.6</td>
<td>13.1</td>
<td>26.8</td>
</tr>
<tr>
<td>N 1800–1896</td>
<td>89</td>
<td>27</td>
<td>76</td>
<td>6</td>
<td>5</td>
<td>8</td>
<td>146</td>
<td>3</td>
<td>203</td>
<td>153</td>
<td>59</td>
<td>1</td>
</tr>
<tr>
<td>N 1897–1993</td>
<td>95</td>
<td>35</td>
<td>18</td>
<td>2</td>
<td>10</td>
<td>127</td>
<td>64</td>
<td>60</td>
<td>214</td>
<td>180</td>
<td>8</td>
<td>38</td>
</tr>
</tbody>
</table>

'Mean difference' refers to the standardized correlation values; N 1800–1896 and N 1897–1993 are the number of trees with a significant correlation for the corresponding month in the two subperiods. Bold values indicate a nonsignificant difference, evaluated by t-test, between the two subperiods [degrees of freedom (d.f.) = 456]. Italic values indicate a significant (P < 0.05; d.f. = 229) difference, evaluated by t-test, between age groups (younger and older than 230 years) within each subperiod.
only nine of 48 variables retained a significant difference and all of these were limited to a time period apparently not significantly involved in tree growth.

Time dependence of tree responses to climate
Moving CFs confirmed the results obtained, but they also provided a dynamic perspective on the evolution of the tree responses to climate (Figs 4, 5). Some nonsignificant variables (e.g. March Precipitation, November temperature) have a stationary response over time. In contrast, the most climate-sensitive variables, such as June temperature and precipitation, produced significant transient responses, which varied markedly within the 200-year period. It is also clear that there were both regular trends and step-wise shifts in the variability of the climate responses. For instance, tree-ring growth sensitivity to temperature exhibited opposite but regular trends towards more (March) and less (April) significant values, respectively, whereas it increased abruptly for May temperature from 1870–1970 and for June precipitation from 1850–1950. June temperature was the key variable for larch tree growth in this area, producing highly significant correlation values for the whole time-span, but also the greatest variability over time.

Discussion
Regardless of site features, the variability of larch in the study area and, to a lesser extent, local climate conditions, tree-ring
Fig. 4 Course of monthly precipitation effect on tree-ring growth of larch (Larix decidua) during the period 1800–1999, using moving correlation function with a 100-year time window. Dotted and dashed horizontal lines indicate normal (i.e. the standard approach considering each single test independent) and false discovery rate adjusted significance levels ($P < 0.05$), respectively. Note the different scale for June.
Fig. 5 Course of monthly temperature effect on tree-ring growth of larch (Larix decidua) during the period 1800–1999, using moving correlation function with a 100-year time window. See Fig. 3 for further explanation. Note the different scales for June and July.
chronologies showed similar annual growth variations over the past two centuries, as indicated by the high values of \( r_m \) and PC1 computed for the mean series. Similar growth patterns suggest that the same climatic factors limit growth at most sites and that the magnitude of growth limitation is influenced synchronously by regional climatic variability (Peterson et al., 2002). Climatological studies have confirmed that all our sampling sites are located in the same homogeneous climatic subregion (Böhm et al., 2001), whereas the differences in altitude and in some chronology statistics for the easternmost sites (near the Slovenian border) can be attributed to the lower mass effect of the mountains and to the more pronounced oceanic climate resulting from the Adriatic Sea being closer.

As expected, in high-altitude forests, temperature is the most important climatic factor influencing radial growth, but with opposite effects within a 5-month interval, just before and during the growing season. CF profiles were generally similar and are apparently in agreement with the uniformitarian principle; however, the significant differences observed for the two subperiods are not consistent with this principle. The increased closeness of the climate–growth relationship in the last century, observed in both the high- and low-frequency profiles, contrasts with the hemisphere-wide decrease in the sensitivity of northern tree growth to summer temperature in recent decades (Briffa et al., 1998b), but is consistent with the findings for white spruce in Alaska (Wilmking et al., 2004). Possible explanations for these differences include: (i) the different climate datasets used (Climate Research Unit (CRU), University of East Anglia and ALP-IMP) and, in particular, limitations in describing regional- and local-scale climate variability in the work of Briffa and colleagues (Jones, 1994; Jones & Moberg, 2003); (ii) the wider temporal perspective provided by these exceptionally long-term climate series; (iii) the exclusion of contrasting behaviour of other tree species, as this study is limited to larch on the regional scale.

With regard to the first point, comparing data for common areas, the differences between the two datasets are 'astonishingly high and systematic with no summer warming at all in the CRU dataset', whereas the ALP-IMP series has a 0.5 K per 100 year warming trend in summer which doubles for winter temperature (0.6–0.7 K compared with 1.1–1.3 K) (Böhm et al., 2001).

With regard to the second point, the warmer temperatures of the 20th century compared with those of the 19th century seemed to trigger not only a shift of the temperature-sensitive period in larch but also a moderate lengthening of the growing season, expressed as increasing correlation coefficients for July precipitation and temperature. Several studies concluded that one of the main effects of global warming would be a prolonging of the growing season, particularly in temperature-limited environments such as high-altitude and/or boreal forests (Keeling et al., 1996; Saxe et al., 2001; Grace et al., 2002).

The increased sensitivity to climate observed for the last century in Eastern Alpine larch appears to provide a very consistent signal of the climatic homogeneity of the region, on population, individual and time-domain scales (Table 2). The risk of an age-related effect, enhanced by the long-term climate record, could be excluded as young and old trees had similar responses to most of the climate variables (Table 3) and especially to the most significant ones (Fig. 3).

Moving correlation functions permit the dynamics of this strengthened signal to be assessed in detail. There seemed to be a general stationary response to climate for most of the variables affecting tree growth less significantly, but a major time-dependent change for the ‘key’ month of June. Larch seems to calibrate most of its climate sensitivity according to the mean values of June temperature (Fig. 5). The particular bell-course of the growth–June temperature correlation could introduce a significant and paradoxical bias in time-dependent growth–climate-related models. In climate reconstruction, for instance, an over- or underestimation of the reconstructed temperature means could occur depending on the time period selected in contrast to the uniformitarian principle.

The step-wise increase of growth sensitivity in certain months (e.g. June precipitation or May temperature) may suggest the presence of underlying threshold-controlled mechanisms. Some threshold effects were detected in high-altitude species using nonlinear models (Carrer & Urbinati, 2001) or in boreal areas (Wilmking et al., 2004), but additional work is needed, especially at the ecophysiological level, to elucidate such complex feedback mechanisms. More research is also required to establish whether trees have previously reached these thresholds as, if they are related to some unprecedented environmental conditions that could affect tree growth (e.g. atmospheric CO₂ level, anthropogenic nitrogen deposition or ozone concentration in the stratosphere), the retrodiction or prediction potential of any growth-related model would be further reduced.

At this stage we are unable to link the cause of these fluctuating responses to a specific factor, as there are many interacting factors with potentially strong effects on tree growth. Nonetheless, we can form some hypotheses. (i) The 30% rise in atmospheric carbon dioxide concentration since the mid-1800s appears to play a minor role: several investigators have asserted that high-altitude and treeline trees are unlikely to respond appreciably to elevated CO₂, simply because they are not photosynthesis-limited (Bernoulli & Körner, 1999; Hoch & Körner, 2003; Körner, 2003). Moreover, the effects of elevated CO₂ concentration should be more evident in a precipitation-limited environment through the amelioration of water stress during drought periods, thanks to increased water-use efficiency (Idso & Idso, 1994; Woodward, 2002). This does not occur at our sites, where precipitation is not limiting. (ii) Nitrogen deposition increased significantly during the last century and should induce positive feedback in mountain ecosystems, which are often nutrient-limited; however, there is no consensus on whether this has a major or a negligible effect on tree growth responses (Spiecker et al.,...
1996; Nadelhoffer et al., 1999). (iii) Climate, especially temperature, seems to fit the transient responses of larch better: for instance, the strong ‘fingerprint’ of June temperature is not related to the trends of increasing nitrogen and/or CO₂ supply.

Conclusions
This study has documented the nonstationary nature of the responses of tree-ring growth to climate variation and their increase for highly significant variables. This would imply a possible deviation from the uniformitarian principle applied to climate–growth relationships. All the forcing factors (i.e. temperature, precipitation, atmospheric CO₂ concentration and nitrogen deposition) capable of driving this change covary, making it very difficult to discriminate their individual impacts and to make definite inferences. However, the particular course of some transient responses suggests that temperature is still the major driving force for climate–growth relationships in this area of the Alps.

These results are geographically limited and species-specific but, if they are replicated in future studies on different species and in different regions, we suggest that time-dependent variables should be taken into account to avoid (i) overestimation of treeline advance, carbon uptake and future forest carbon storage in temperature-limited environments and (ii) inaccurate reconstruction of past climate variability.

Further work, taking advantage of the rich source of information represented by tree rings, is required to explore the detailed nature of this bias in the uniformitarian principle with regard to species, region and time dependence.

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