

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

Marco Carrer¹ and Carlo Urbinati²

¹Università degli Studi di Padova, Dip. TeSAF, Treeline Ecology Research Unit, Agripolis, I-35020 Legnaro (PD), Italy; ²Università Politecnica delle Marche, Dip. SAPROV, Forest Ecology and Management, Via Breccia Bianche, I-60131 Ancona, Italy

Summary

Author for correspondence:
Marco Carrer
Tel: +39 049 8272753
Fax: +39 049 8272686
Email: marco.carrer@unipd.it

Received: 17 October 2005
Accepted: 29 January 2006

- 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.

New Phytologist (2006) **170**: 861–872

© The Authors (2006). Journal compilation © *New Phytologist* (2006)
doi: 10.1111/j.1469-8137.2006.01703.x

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 dendroclimatology, 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), Nicolussi *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

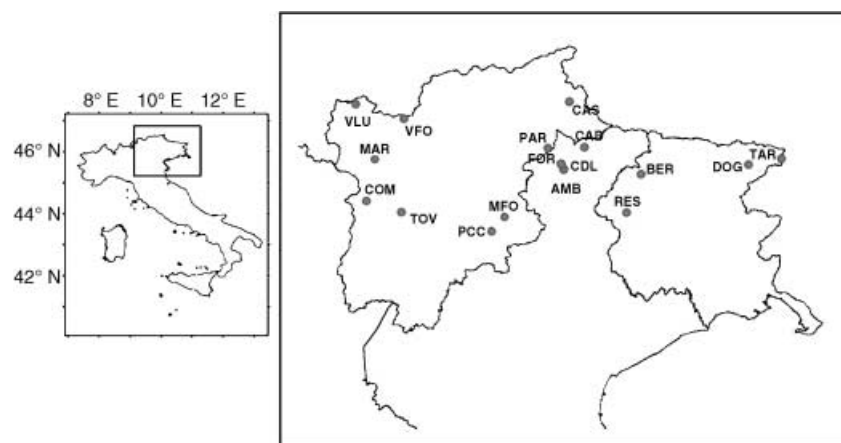


Fig. 1 Map of the area showing site locations.

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

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

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.

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) to estimate

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 Alps were quality-checked for potential bias, especially for the 19th century period, and then interpolated to a $1^\circ \times 1^\circ$ 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 (Ertl & 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 (r_{bt}) 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 r_{bt} 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 r_{bt} 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

Period	R^2	P	R calib.	SD calib.	R verif.	SD verif.
1800–1993	0.540	10.201	0.735	0.027	0.608	0.060
1800–1896	0.534	3.597	0.731	0.044	0.436	0.121
1897–1993	0.716	7.880	0.846	0.030	0.654	0.083

R^2 , 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.

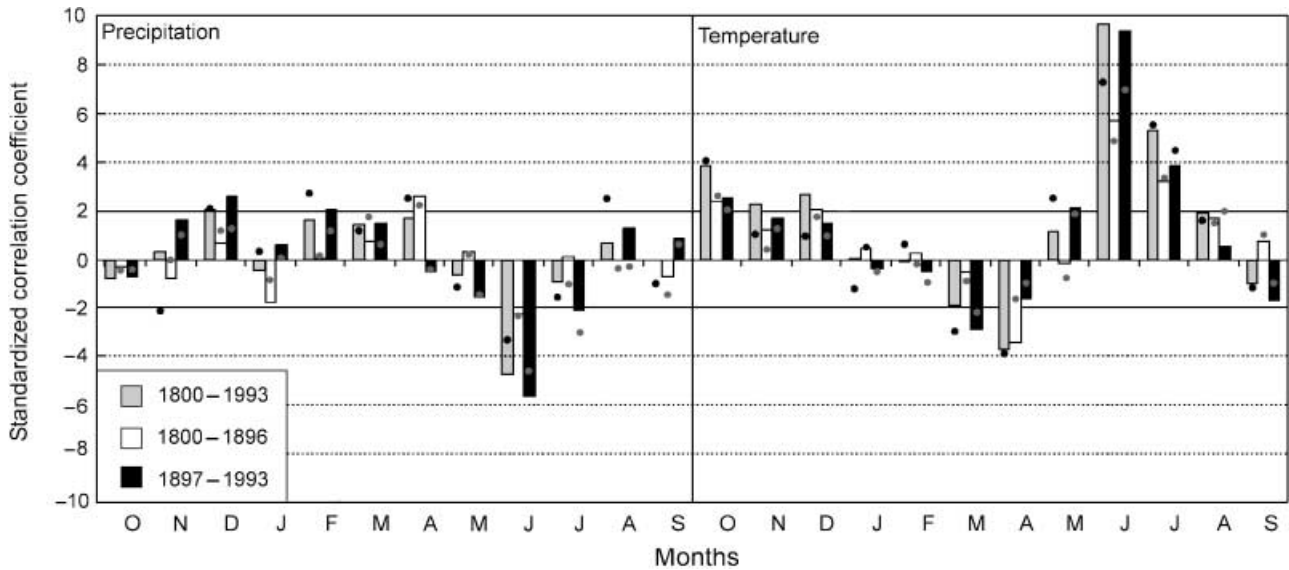


Fig. 2 Correlation functions for the entire time interval and the two subperiods. Grey dots are the correlation function (CF) results for the two subperiods using the low-pass filtered chronology. Black dots are the corresponding response function results for 1800–1993. Standardized coefficients were obtained by dividing the mean correlation (for CF) or partial regression coefficients (for response function) by their standard deviations after the bootstrap replications. They express the significance of monthly parameters. Values greater than |2| are significant at $P < 0.05$.

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

	Month											
	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep
Precipitation												
Mean difference	0.23	-1.42	-1.26	-1.41	-1.06	-0.02	2.13	1.60	2.47	1.86	-0.88	-1.57
<i>t</i> -value	3.5	-19.3	-18.0	-19.3	-14.4	-0.2	22.5	25.5	29.2	22.6	-10.7	-25.3
<i>N</i> 1800–1896	0	14	17	29	12	39	121	12	80	9	3	4
<i>N</i> 1897–1993	5	25	118	4	45	17	4	28	207	90	19	12
Temperature												
Mean difference	-0.10	-0.31	0.60	0.31	0.37	1.63	-0.78	-1.74	-1.38	-0.38	0.96	1.64
<i>t</i> -value	-1.4	-4.8	8.7	4.7	4.5	23.0	-9.0	-28.0	-11.9	-4.6	13.1	26.8
<i>N</i> 1800–1896	89	27	76	6	5	8	146	3	203	153	59	1
<i>N</i> 1897–1993	95	35	18	2	10	127	64	60	214	180	8	38

'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.

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:

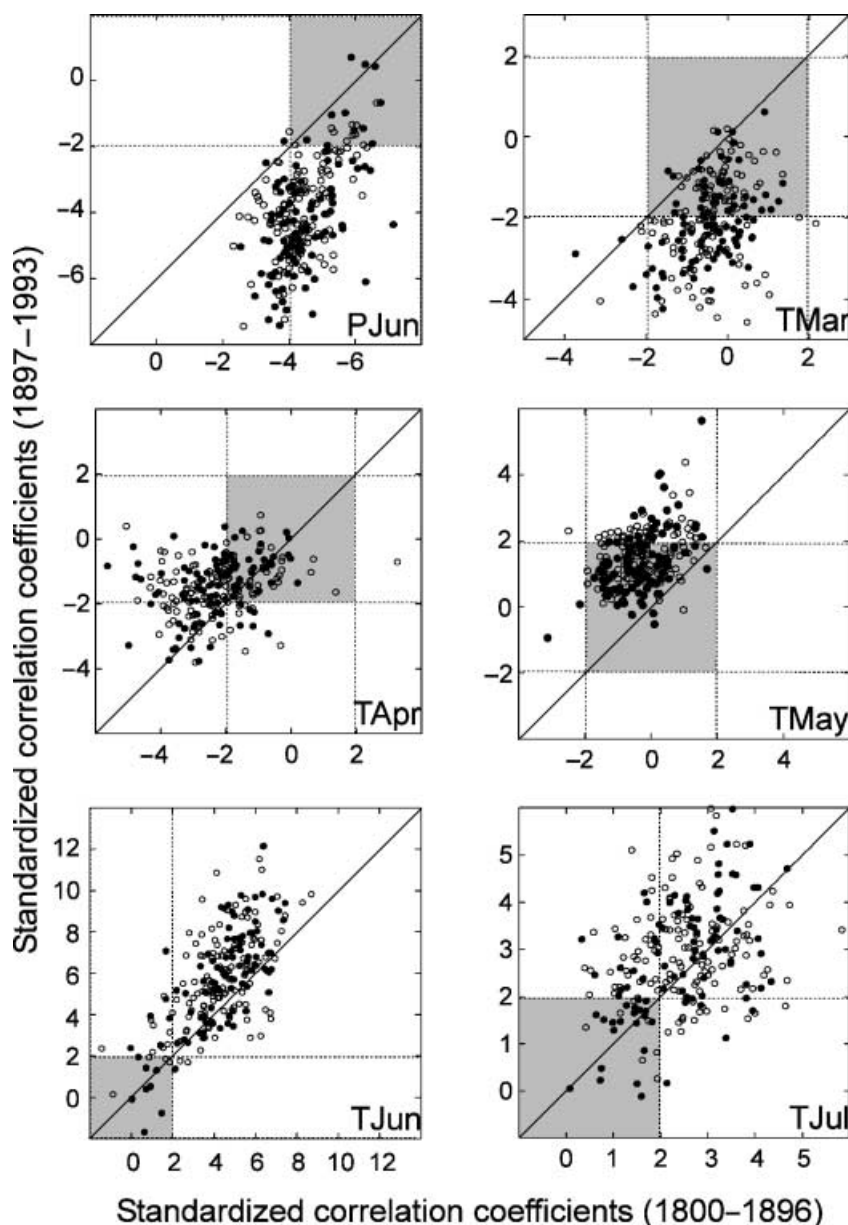


Fig. 3 Single tree standardized correlation values for selected climate variables for the 1800–1896 (on the x-axis) and 1897–1993 periods. P = precipitation, T = temperature. Black and open dots are, respectively, larch (*Larix decidua*) trees older ($n = 100$) or younger ($n = 129$) than 230 years in the year 1800. Dotted lines indicate significance levels ($P < 0.05$) while the diagonal lines represent a perfect stationary response. Trees inside the shaded box have nonsignificant values for both subperiods. Note the different axis scales for each variable.

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

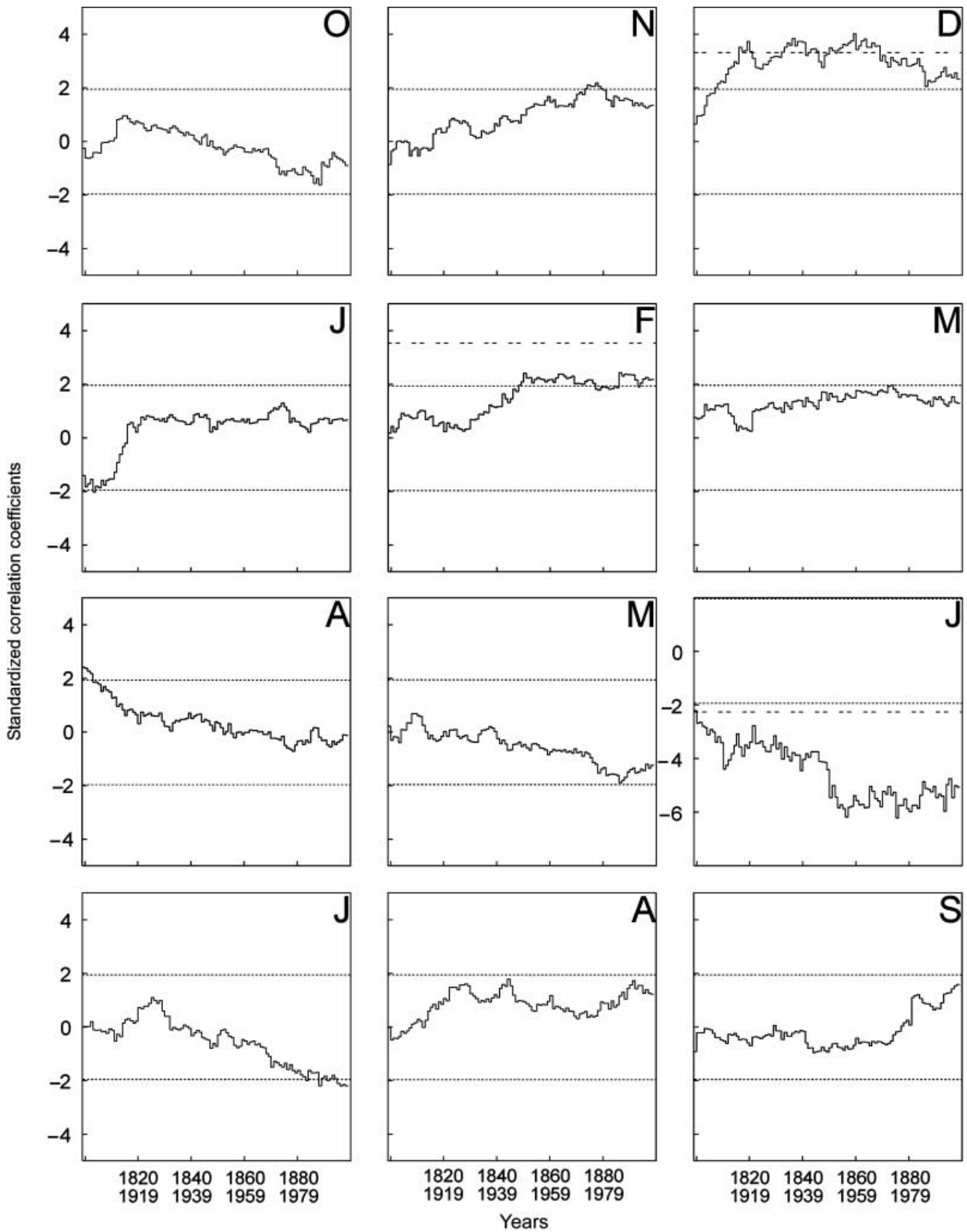


Fig. 4 Course of monthly precipitation effect on tree-ring growth of larch (*Larix decidua*) during the period 1800–1999, using moving correlation function with a 100-year time window. Dotted and dashed horizontal lines indicate normal (i.e. the standard approach considering each single test independent) and false discovery rate adjusted significance levels ($P < 0.05$), respectively. Note the different scale for June.

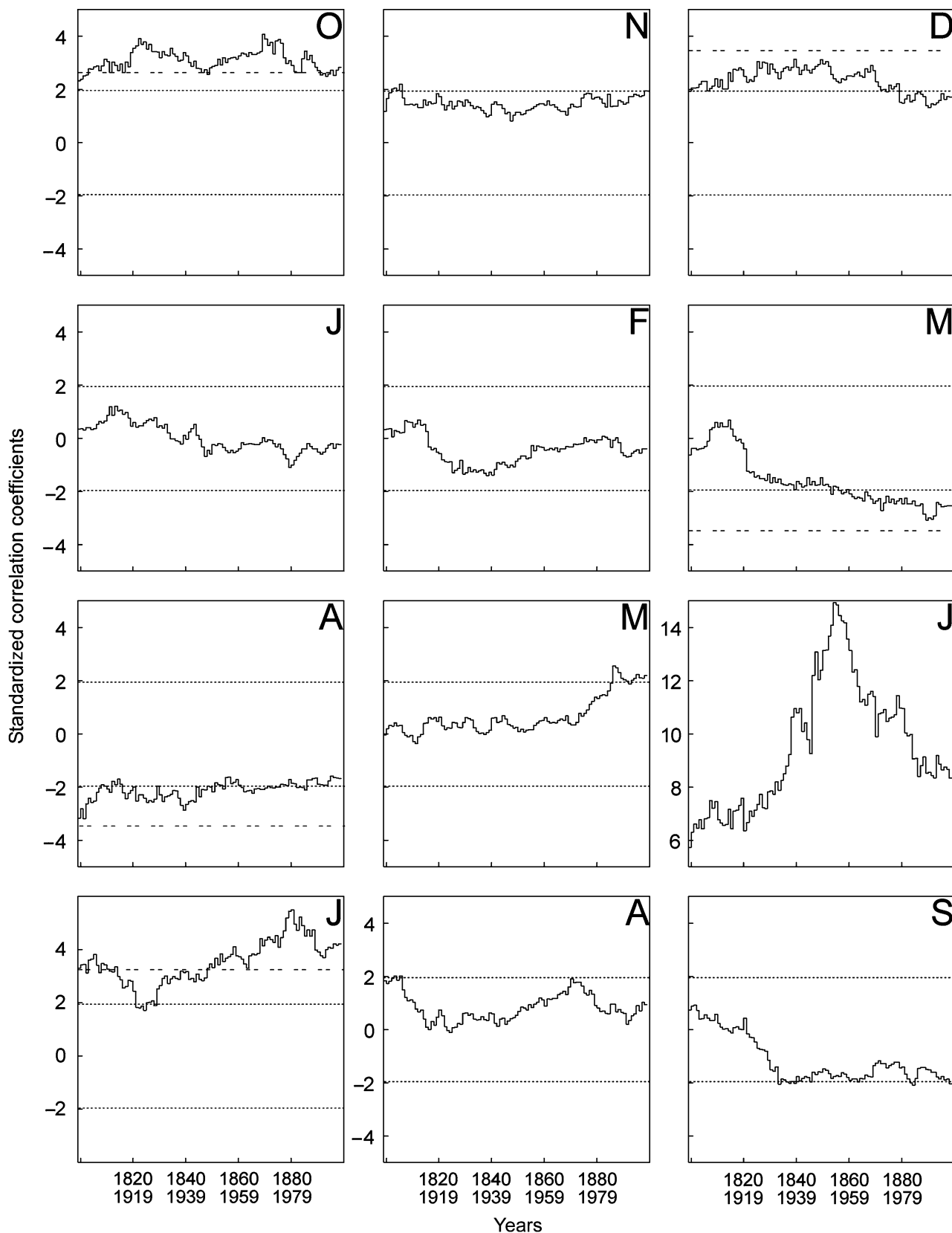


Fig. 5 Course of monthly temperature effect on tree-ring growth of larch (*Larix decidua*) during the period 1800–1999, using moving correlation function with a 100-year time window. See Fig. 3 for further explanation. Note the different scales for June and July.

chronologies showed similar annual growth variations over the past two centuries, as indicated by the high values of r_{bt} 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.

Acknowledgements

This research was funded by the European Union project 'Sensitivity of tree growth to climate change and growth modelling from past to future' (FORMAT; EU-ENV4-CT97-0641) and by the Trento Autonomous Province project 'Study on the non-reddening of lake Tovel' (SALTO; 2001–2004). We thank Reinhard Böhm for kindly providing meteorological data from the ALP-IMP project (EU, EVK2-CT-2002-00148), and Ruggero Dal Cin, Paola Mottes and Cristiano Pastorello for assistance with sampling and measuring.

References

- ALP-IMP. 2004. Multi-centennial climate variability in the Alps based on instrumental data, model simulation and proxy data. <http://www.zamg.ac.at/alp-imp/main.htm> (accessed 16 October 2005).
- Auer I, Böhm R, Jurkovic A, Orlik A, Potzmann R, Schoner W, Ungersböck M, Brunetti M, Nanni T, Maugeri M, Briffa K, Jones P, Efthymiadis D, Mestre O, Moisselin JM, Begert M, Brazdil R, Bochnicek O, Cegnar T, Gajic Capkaj M, Zaninovic K, Majstorovic Z, Szalai S, Szentimrey T, Mercalli L. 2005. A new instrumental precipitation dataset for the greater alpine region for the period 1800–2002. *International Journal of Climatology* 25: 139–166.
- Barber VA, Juday GP, Finney BP. 2000. Reduced growth of Alaskan white spruce in the twentieth century from temperature-induced drought stress. *Nature* 405: 668–673.
- Benjamini Y, Hochberg Y. 1995. Controlling the false discovery rate – a practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society Series B, Methodology* 57: 289–300.
- Bernoulli M, Körner C. 1999. Dry matter allocation in treeline trees. *Phyton Annales Rei Botanicae* 39: 7–11.
- Biondi F. 1997. Evolutionary and moving response functions in dendroclimatology. *Dendrochronologia* 15: 139–150.
- Biondi F. 2000. Are climate–tree growth relationships changing in North-Central Idaho, USA? *Arctic, Antarctic and Alpine Research* 32: 111–116.
- Biondi F, Waikul K. 2004. DENDROCLIM2002: a C++ program for statistical calibration of climate signals in tree-ring chronologies. *Computers and Geosciences* 30: 303–311.
- Böhm R, Auer I, Brunetti M, Maugeri M, Nanni T, Schoner W. 2001. Regional temperature variability in the European Alps: 1760–1998 from homogenized instrumental time series. *International Journal of Climatology* 21: 1779–1801.
- Box GEP, Jenkins GM. 1976. *Time series analysis: forecasting and control*. San Francisco, CA, USA: Holden Day.
- Bradley RS. 1999. *Paleoclimatology: reconstructing climates of the Quaternary*. Harcourt, San Diego, CA, USA: Academic Press.
- Briffa KR, Cook ER. 1990. Methods of response function analysis. In: Cook ER, Kairiukstis LA, eds. *Methods of dendrochronology; applications in the environmental sciences*. Dordrecht, the Netherlands: Kluwer Academic Publishers, 240–247.
- Briffa KR, Osborn TJ, Schweingruber FH. 2004. Large-scale temperature inferences from tree rings: a review. *Global and Planetary Change* 40: 11–26.
- Briffa KR, Schweingruber FH, Jones PD, Osborn TJ, Harris IC, Shiyatov SG, Vaganov EA, Grudd H, Cowie J. 1998a. Trees tell of past climates: But are they speaking less clearly today? *Philosophical Transactions of the Royal Society of London Series B, Biological Sciences* 353: 65–73.
- Briffa KR, Schweingruber FH, Jones PD, Osborn TJ, Shiyatov SG, Vaganov EA. 1998b. Reduced sensitivity of recent tree-growth to temperature at high northern latitudes. *Nature* 391: 678–682.
- Britannica Concise Encyclopædia. 2005. 'Uniformitarianism'. In: *Encyclopædia Britannica, Premium Service*. <http://www.britannica.com/ebc/article-9381521> (accessed 6 October 2005).
- Carrer M, Urbinati C. 2001. Assessing climate–growth relationships: a comparative study between linear and non-linear methods. *Dendrochronologia* 19: 57–65.
- Carrer M, Urbinati C. 2004. Age-dependent tree-ring growth responses to climate in *Larix decidua* and *Pinus cembra*. *Ecology* 85: 730–740.
- Cook ER. 1985. A time series approach to tree-ring standardization. PhD thesis, University of Arizona, Tucson, AZ, USA.
- Cook ER, Briffa K, Shiyatov S, Mazepa V. 1990. Tree-ring standardization and growth-trend estimation. In: Cook ER, Kairiukstis LA, eds. *Methods of dendrochronology; applications in the environmental sciences*. Dordrecht, the Netherlands: Kluwer Academic Publishers, 104–123.
- Cook ER, Holmes RL. 1997. ARSTAN: chronology development. In: Grissino Mayer HD, ed. *The International Tree-Ring Data Bank Program Library, version 21, user's manual*. Tucson, AZ, USA: University of Arizona Laboratory of Tree-Ring Research, 75–92.
- Cook ER, Peters K. 1981. The smoothing spline: a new approach to standardizing forest interior tree-ring width series for dendroclimatic studies. *Tree Ring Bulletin* 41: 45–53.
- D'Arrigo RD, Jacoby GC. 1993. Tree growth–climate relationships at the northern boreal forest tree line of North America: evaluation of potential response to increasing carbon dioxide. *Global Biogeochemical Cycles* 7: 525–535.
- Ettl GJ, Peterson DL. 1995. Extreme climate and variation in tree growth: individualistic response in subalpine fir (*Abies lasiocarpa*). *Global Change Biology* 1: 231–241.

- Feng X. 1998. Long-term c/c_a response of trees in western North America to atmospheric CO_2 concentration derived from carbon isotope chronologies. *Oecologia* 117: 19–25.
- Fritts HC. 1976. *Tree ring and climate*. London, UK: Academic Press.
- Grace J, Berninger F, Nagy L. 2002. Impacts of climate change on the tree line. *Annals of Botany* 90: 537–544.
- Graumlich LJ. 1991. Subalpine tree growth, climate, and increasing CO_2 : an assessment of recent growth trends. *Ecology* 72: 1–11.
- Graybill DA, Idso SB. 1993. Detecting the aerial fertilization effect of atmospheric CO_2 'SUB 2' enrichment in tree-ring chronologies. *Global Biogeochemical Cycles* 7: 81–95.
- Guiot J. 1991. The bootstrapped response function. *Tree Ring Bulletin* 51: 39–41.
- Hoch G, Körner C. 2003. The carbon charging of pines at the climatic treeline: a global comparison. *Oecologia* 135: 10–21.
- Holmes RL. 1983. Computer-assisted quality control in tree-ring dating and measurement. *Tree Ring Bulletin* 43: 69–78.
- Hughes MK. 2002. Dendrochronology in climatology – the state of the art. *Dendrochronologia* 20: 95–116.
- Idso KE, Idso SB. 1994. Plant responses to atmospheric CO_2 enrichment in the face of environmental constraints: a review of the past 10 years' research. *Agricultural and Forest Meteorology* 69: 153–203.
- IPCC. 2001. *Climate change 2001: the scientific basis. Contribution of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge, UK and New York, NY, USA: Cambridge University Press.
- Jones PD. 1994. Hemispheric surface air temperature variations: a reanalysis and an update to 1993. *Journal of Climate* 7: 1794–1802.
- Jones PD, Moberg A. 2003. Hemispheric and large-scale surface air temperature variations: An extensive revision and an update to 2001. *Journal of Climate* 16: 206–223.
- Keeling CD, Chin JFS, Whorf TP. 1996. Increased activity of northern vegetation inferred from atmospheric CO_2 measurements. *Nature* 382: 146–149.
- Kienast F, Luxmoore RJ. 1988. Tree-ring analysis and conifer growth responses to increased atmospheric CO_2 levels. *Oecologia* 76: 487–495.
- Knapp PA, Soule PT, Grissino Mayer HD. 2001. Detecting potential regional effects of increased atmospheric CO_2 on growth rates of western juniper. *Global Change Biology* 7: 903–917.
- Körner C. 2003. Carbon limitation in trees. *Journal of Ecology* 91: 4–17.
- LaMarche VC, Graybill DA Jr, Fritts HC, Rose MR. 1984. Increasing atmospheric carbon dioxide: tree ring evidence for growth enhancement in natural vegetation. *Science* 225: 1019–1021.
- Lloyd AH, Fastie CL. 2002. Spatial and temporal variability in the growth and climate response of treeline trees in Alaska. *Climatic Change* 52: 481–509.
- Nadelhoffer KJ, Emmett BA, Gundersen P, Kjonaas OJ, Koopmans CJ, Schleppi P, Tietema A, Wright RF. 1999. Nitrogen deposition makes a minor contribution to carbon sequestration in temperate forests. *Nature* 398: 145–148.
- Nicolussi K, Bortenschlager S, Korner C. 1995. Increase in tree-ring width in subalpine *Pinus cembra* from the central Alps that may be CO_2 -related. *Trees: Structure and Function* 9: 181–189.
- Nola P. 1996. Climatic signal in earlywood and latewood of deciduous oaks from northern Italy. In: Dean JS, Meko DM, Swetnam TW, eds. *Tree rings, environment and humanity. Proceedings of the International Conference, Tucson, Arizona, 17–21 May 1994*. Tucson, AZ, USA: Radiocarbon, 249–258.
- Peterson DW, Peterson DL, Ettl GJ. 2002. Growth responses of subalpine fir to climatic variability in the Pacific Northwest. *Canadian Journal of Forest Research* 32: 1503–1517.
- Phipps RL. 1985. Collecting, preparing, cross-dating and measuring tree increment cores. *US Geological Survey Water Resource Investigations Report* 85–4148.
- Saxe H, Cannell MGR, Johnsen B, Ryan MG, Vourlitis G. 2001. Tree and forest functioning in response to global warming. *New Phytologist* 149: 369–399.
- Smith KT, Cufar K, Levanić T. 1999. Temporal stability and dendroclimatology in silver fir and red spruce. *Phyton Annales Rei Botanicae* 39: 117–122.
- Solberg BO, Hofgaard A, Hytteborn H. 2002. Shifts in radial growth responses of coastal *Picea abies* induced by climatic change during the 20th century, central Norway. *Ecoscience* 9: 79–88.
- Spiecker H, Mielikäinen K, Köhl M, Skovsgaard JP (eds). 1996. *Growth trends in European forests*. New York, NY, USA: Springer.
- Stokes MA, Smiley TL. 1968. *Introduction to tree-ring dating*. Chicago, IL, USA: University of Chicago Press.
- Tognetti R, Cherubini P, Innes JL. 2000. Comparative stem-growth rates of Mediterranean trees under background and naturally enhanced ambient CO_2 concentrations. *New Phytologist* 146: 59–74.
- Vaganov EA, Hughes MK, Kirdyanov AV, Schweingruber FH, Silkin PP. 1999. Influence of snowfall and melt timing on tree growth in subarctic Eurasia. *Nature* 400: 149–151.
- Wilmking M, Juday GP, Barber VA, Zald HSJ. 2004. Recent climate warming forces contrasting growth responses of white spruce at treeline in Alaska through temperature thresholds. *Global Change Biology* 10: 1724–1736.
- Wilson R, Elling W. 2004. Temporal instability in tree-growth/climate response in the Lower Bavarian Forest region: implications for dendroclimatic reconstruction. *Trees: Structure and Function* 18: 19–28.
- Woodward FI. 2002. Potential impacts of global elevated CO_2 concentrations on plants. *Current Opinion in Plant Biology* 5: 207–211.



About *New Phytologist*

- *New Phytologist* is owned by a non-profit-making **charitable trust** dedicated to the promotion of plant science, facilitating projects from symposia to open access for our Tansley reviews. Complete information is available at www.newphytologist.org.
- Regular papers, Letters, Research reviews, Rapid reports and both Modelling/Theory and Methods papers are encouraged. We are committed to rapid processing, from online submission through to publication 'as-ready' via *OnlineEarly* – the 2004 average submission to decision time was just 30 days. Online-only colour is **free**, and essential print colour costs will be met if necessary. We also provide 25 offprints as well as a PDF for each article.
- For online summaries and ToC alerts, go to the website and click on 'Journal online'. You can take out a **personal subscription** to the journal for a fraction of the institutional price. Rates start at £109 in Europe/\$202 in the USA & Canada for the online edition (click on 'Subscribe' at the website).
- If you have any questions, do get in touch with Central Office (newphytol@lancaster.ac.uk; tel +44 1524 594691) or, for a local contact in North America, the US Office (newphytol@ornl.gov; tel +1 865 576 5261).