

# Interannual growth response of Norway spruce to climate along an altitudinal gradient in the Tatra Mountains, Poland

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**Abstract** Ring-width chronologies of *Picea abies* (L.) Karst. from ten sites in the Tatra Mountains, Poland, were developed to explore growth/climate responses in stands along an altitudinal gradient ranging from 839 to 1468 m a.s.l. There were positive relationships between current-year radial growth and mean monthly temperatures in March, April, June and July, but with increasing elevation, the strength of this correlation declined for March–April and increased for June–July temperatures. The mean monthly temperature in

October of the previous year positively influenced radial growth of trees at all sites. Lower mean temperatures in January negatively affected growth of trees at the high-elevation sites. Trees at the low-elevation sites responded positively to a warm early spring, whereas trees at the high-elevation sites showed positive growth responses to higher summer temperatures. Growth of trees at the high-elevation sites was better explained by the temperature regime than was growth at the lower-elevation sites. Therefore, it is likely that these sites may be particularly sensitive to potential effects of temperature change.

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## Introduction

*Picea abies* is one of the most common and important forest trees in Europe. In central Europe, *Picea abies* is distributed predominantly in mountain habitats, but also occurs in lowland sites (Ellenberg 1996). There are several studies showing contrasting results for climate–growth relationships of *Picea abies* between low-elevation and high-elevation sites (Mäkinen et al. 2000, 2002a,b; Feliksik and Wilczyński 2004). For example, in mountainous regions in Europe, tree-ring growth at high-elevation sites was correlated with temperature, whereas growth at low-elevation sites was correlated with precipitation (Slåstad 1957; Dittmar and Elling 1999; Mäkinen et al. 2002b; Wilson et al. 2005a). In extreme environments, such as high-elevation sites of mountainous regions, climate is one of the main factors limiting tree growth (Fritts 1976).

Several studies reported recent increases in mean annual surface temperatures for Europe (Jones and Moberg 2003;

Luterbacher et al. 2004), especially at high elevations (Beniston et al. 1997). This may lead to changes in tree growth and forest productivity, and may be most significant at high latitudes and altitudes. Several studies reveal changes and shifts in the main climatic factors controlling tree growth in European high-elevation sites for the last several decades (Solberg et al. 2002; Wilson and Elling 2004; Buntgen et al. 2006). Temperature changes might also result in changes in the sensitivity of tree growth to climate variations. For example, Briffa et al. (1998) have found a reduced sensitivity of recent tree growth at high northern latitudes for the last several decades. Therefore, in the context of future climate change there is a need to understand the response of *Picea abies* to different growth conditions and the potential for contrasting population responses shaped, in part, by past climate selection along altitudinal and latitudinal clines.

Dendroclimatic studies of the growth/climate response of high-elevation conifers and subsequent reconstructions of past summer temperatures over a centuries to millennial timescale have been recently carried out in the European Alps (Buntgen et al. 2005; Frank and Esper 2005a,b). For example, Frank and Esper (2005a,b) developed a tree-ring data network of high-elevation sites in the European Alps and reconstructed regional temperatures. Wilson and Elling (2004) used tree-ring data to explore tree-growth/climate response of *Picea abies* and *Abies alba* in the lower Bavarian Forest region, Germany. Dendroclimatic reconstruction of spring–summer precipitation and summer temperature using tree-ring data has been carried out for Bavarian Forest region and Central Europe (Wilson et al. 2005a,b). Bednarz et al. (1999) carried out a dendrochronological analysis of *Picea abies* in the Babia Gora National Park in Poland. Bednarz (1984) compared dendroclimatological reconstructions of summer temperatures from the Alps and Tatra Mountains. Our study of growth–climate response of *Picea abies* in the Tatras could usefully contribute to the existing body of work in regional dendroclimatology.

The Tatras are the highest mountain range in the Carpathian arc. The high-elevation forests are unique and economically important to the region (Bytnerowicz et al.

2003). Given evidence of climate change (IPCC 2001) and its possible effect on European forests (Saxe et al. 2001) as well as the evidence of physiological and genetic differentiation between high-elevation and low-elevation populations in this region (Oleksyn et al. 1998), it is of interest to compare the long-term growth/climate response of *Picea abies* trees growing in different elevations. We studied long-term chronologies from ten sites at varying elevations in the Tatras, ranging from about 800 to 1500 m, to specifically address the altitudinal effects on tree growth, the role of temperature and precipitation in tree-ring formation, and the potential effect of future climate change on growth of *Picea abies*.

The objectives of the study were to (1) develop long-term dendrochronological series; (2) compare the variation in radial growth of *Picea abies* among sites of contrasting altitude in a mountainous region of the Tatras; and (3) identify the climatic factors affecting variation in tree-ring growth and whether these factors or growth responses differ with altitude.

## Materials and method

### Study area

The study area is located in the Tatra Mountains, Poland (49° 12'–49° 19'N, 19° 52'–20° 06'E). The Tatra Mountains, with a typical alpine landscape and altitudes exceeding 2600 m a.s.l., are the highest and most rugged range of the Carpathians. Climatic characteristics of the Tatra Mountains region were described by Koncek (1974) and Niedzwiedz (1992). Thermic conditions in mountains areas depend mainly on altitude and to a lesser degree on slope, aspect, and the mountain mass effect (Hess 1965). Mean annual temperature data for the study sites in the Tatras were calculated as described below and presented in Table 1. The study sites lie on two vertical climatic belts, cool and moderately cool. The lower-elevation sites (below 1000 m) coincide closely with the upper limit of agriculture and mixed forests and

**Table 1** Regional climate stations for which mean monthly temperature data were used<sup>a</sup> to model mean monthly temperatures for each of ten study sites in the Tatra Mountains, Poland

Distance from Poprad (km)	Site	Climate record (years)	Latitude (°N)	Longitude (°E)	Altitude (m) above sea level
0	Poprad	1951–1991	49.07	20.25	722
15	Lomnický štít	1941–1989	49.20	20.22	2635
27	Kasprowy Wierch	1951–1989	49.23	19.98	1458
34	Zakopane	1951–1989	49.30	19.95	964
48	Chopok	1956–1989	48.98	19.60	1054
66	Krynica	1941–1960	49.40	21.00	651
69	Nowy Sącz	1954–1989	49.62	20.70	311
93	Sliac	1951–1991	48.65	19.15	406
117	Kraków	1951–1980	50.08	19.80	262

<sup>a</sup>Data obtained from the U.S. National Oceanic and Atmospheric Administration (NOAA) website (<ftp://ftp.ncdc.noaa.gov/>).

**Table 2** Site descriptions and associated climatic parameters for each sampling location of *Picea abies* from ten sites in the Tatra Mountains, Poland (49° 12'–49° 19'N, 19° 52'–20° 06'E)

Altitude (m)	Transect and location	Annual temperature (°C)	Annual precipitation (mm) (Oleksyn et al. 1998)	Exposure			Plant association
				Aspect	Slope (°)	Type of soil	
839	Dolina Rybiego Potoku	5.2	1125	NW	3	Warp soil	<i>Abieti-Piceetum</i>
981	Dolina Mietusia	4.4	1243	W	33	Brown soil	<i>Abieti-Piceetum</i>
1001	Dolina Kondratowa	4.3	1263	NNW	5	Podzol	<i>Abieti-Piceetum</i>
1009	Dolina Mietusia	4.3	1383	WSW	5	Warp soil	<i>Abieti-Piceetum</i>
1091	Dolina Rybiego Potoku	3.9	1342	N	5	Brown soil	<i>Abieti-Piceetum</i>
1180	Dolina Kondratowa	3.4	1410	N	36	Podzol	<i>Abieti-Piceetum</i>
1202	Dolina Mietusia	3.3	1434	NNW	5	Rendzina	<i>Plagiothecio-Piceetum (Piceetum tatricum)</i>
1433	Dolina Kondratowa	2.2	1625	NNW	28	Podzol	<i>Plagiothecio-Piceetum (Piceetum tatricum)</i>
1461	Dolina Rybiego Potoku	2.0	1668	SW	33	Rendzina	<i>Plagiothecio-Piceetum (Piceetum tatricum)</i>
1468	Dolina Mietusia	2.0	1652	NW	35	Podzol	<i>Plagiothecio-Piceetum (Cembro-Piceetum)</i>

Sites are ordered by altitude.

the high-elevation sites (above 1000 m) coincide with the upper timberline. The number of freezing days with temperatures below 0°C throughout the day increases by about 5 days per 100 m of elevation (Niedzwiedz 1992). Among sites, the number of freezing days ranges from about 45 in the lower to 90 in the higher elevations. There are about 5 or 6 days when the temperature maxima remains below –10°C at 900–1000 m and about 10 days near the upper timberline (1500–1550 m). Mountains in the temperate climatic zone receive large amounts of precipitation. The average annual totals in the Tatras vary from 1100 to 1900 mm. Mean annual precipitation for the study sites ranges between 1125 and 1668 mm (Table 2). Maximum monthly precipitation occurs in summer, mainly in June and July. The ratio of winter (December–February) to summer (June–August) precipitation increases with altitude from 0.31 at the Zakopane climatic station (844 m), 0.5 at 1600 m, to more than 0.6 at the summits (Kasprowy Wierch 0.69, Lomnický Stit 0.75).

### Study material

In fall of 1994 tree-ring cores of *Picea abies* were collected from ten different elevations ranging from 839 to 1468 m a.s.l. in the Tatra Mountains (Table 2). A map of the location of the ten study sites in the Tatra Mountains is provided by Oleksyn et al. (1998). Each selected site had mature or old-growth closed-canopy stands. The stands were all more

than 80 years old (Table 3) and of probable natural origin, especially those at higher elevations. A common garden study of seed sources from the same stands revealed genetic differences that supported a close agreement between adaptive traits and the altitudinal conditions of their origin (Oleksyn et al. 1998). As typical for the region, the soils differed among the sites decreasing in depth and increasing in organic matter content with increasing altitude and above 1200 m were predominately organic soils (Oleksyn et al., unpublished data). For each population, about 20 cores were sampled from canopy-dominant individuals using an increment borer. For each tree, one core was taken from one radius. Cores were taken at approximately 130 cm above ground. This height above the base represents a loss of at least 10-year growth in relation to the total tree age (Szymanski and Modrzynski 1973; Fritts 1976). Therefore, the age of each tree was calculated as the number of tree rings plus 10 years.

### Chronology development

The total ring-widths, earlywood, latewood widths and latewood percentage were measured with the WinDENDRO image-analysis system (Regent Instruments, Inc., Quebec City, Quebec, Canada), based on digitally scanned images (1200 dpi resolution) of mounted and sanded tree-ring cores. The measured tree-ring series were cross-dated and quality-

**Table 3** Statistical characteristics of *Picea abies* tree-ring chronologies from ten sites in the Tatra Mountains, Poland (49°12'–49°19'N, 19°52'–20°06'E)

Altitude (m)	Transect and location	Number of series	Full period covered (years)	Period covered after truncation (at <5 series)	Median segment length (years)	Mean tree-ring-width (mm)	Mean RBAR	Mean sensitivity	First-order autocorrelation
839	Dolina Rybiego Potoku	12	1907–1993	1916–1993	70	1.875	0.346	0.153	0.694
981	Dolina Mietusia	15	1890–1993	1902–1993	86	1.761	0.367	0.168	0.577
1001	Dolina Kondratowa	16	1856–1993	1865–1993	122	1.692	0.298	0.150	0.412
1009	Dolina Mietusia	13	1908–1993	1913–1993	80	2.126	0.342	0.156	0.454
1091	Dolina Rybiego Potoku	14	1872–1993	1878–1993	113	1.804	0.391	0.170	0.426
1180	Dolina Kondratowa	18	1912–1993	1912–1993	81	2.058	0.326	0.154	0.170
1202	Dolina Mietusia	12	1791–1993	1827–1993	155	1.367	0.335	0.154	0.625
1433	Dolina Kondratowa	18	1871–1993	1892–1993	94	1.564	0.380	0.175	0.442
1461	Dolina Rybiego Potoku	17	1764–1993	1805–1993	125	1.147	0.390	0.173	0.698
1468	Dolina Mietusia	16	1840–1993	1879–1993	108	1.567	0.415	0.144	0.593
	Average for all sites	15	1861–1993	1879–1993	103.4	1.696	0.359	0.160	0.494

Sites are ordered by altitude. RBAR: average correlation between all series.

checked with the COFECHA software (Holmes 1983). The cores of poor quality (e.g., fragmented, rotted, not cross-datable) were excluded from further analysis. The tree-ring *Picea abies* chronology for Swistowko, Poland (49°N, 19°E, 1500 m a.s.l.) developed by Fritz Schweingruber was obtained from the World Tree-Ring Databank and used as a reference master chronology for cross-dating (Schweingruber 2005). The reference chronology is based on the ring-width and density measurements of 15 trees and covered the period of 1699–1978.

Ring-width chronologies for each site were developed with the ARSTAN software (Cook 1985), and were detrended (standardized) with straight lines or negative exponential curves. This detrending method has been used to preserve most of the low-frequency variance given the lengths of the series. In addition, we applied a data-adaptive power transformation to stabilize the variance and mitigate non-normality in the series before standardization (Cook and Peters 1997). The power was calculated as  $1 - x$ , where  $x$  is the slope of a linear regression in logarithmic space between the local spread and local level (Emerson and Strenio 1983). Then, indices were calculated as the differences between power-transformed ring-width measurements and fitted curves. These chronologies are considered to be standard chronologies. This method avoids possible “end-effect” bias in the resulting tree-ring chronologies due to index inflation after calculating ratios (Cook and Peters 1997).

All tree-ring series showed significant first-order autocorrelation, meaning current-year ring-width is significantly

correlated with prior-year ring-width (Fritts 1976). ARMA (autoregressive-moving-average modeling) generated residual chronologies – time series of ring-width indices with no dependence on past values (Box and Jenkins 1976). This operation called prewhitening, removes biologically related persistence from the series so that the residual may be more suitable for studying the influence of climate factors on tree growth. The autoregressive modeling is analogous to a multiple regression model, except the predictor variables are past values of the dependent variable. The AIC (Akaike information criterion) was used as a measure of goodness-of-fit (Akaike 1974). The residual tree-ring chronologies were developed by calculating a biweight robust mean for each site to further remove the random signals related to local disturbances (Cook et al. 1990).

Chronology statistics, such as the mean sensitivity (a measure of the annual variability in tree rings), the average correlation between all series (RBAR), the expressed population signal (EPS) and the first-order autocorrelation of standard chronologies (a measure of the association between growth in the previous year and that in the current year), were obtained to show the statistical characteristics of the tree-ring chronologies (Table 3).

RBAR is a measure of common variance between single series, independent of the number of measurement series. (Wigley et al. 1984). EPS measures how well the finite-sample chronology compares with the theoretical population chronology based on an infinite number of trees (Wigley et al. 1984). It varies from 0.0 to 1.0. The rough

cutoff point for accepting EPS is considered by Wigley et al. (1984) to be 0.85. RBAR and EPS values were computed using a 30-year moving window with a 15-year overlap.

#### Climate data

Monthly temperature data for the period from 1941–1956 to 1989–1991 were available from the nine nearest reporting weather stations in the region (within a  $1.0^\circ \times 1.0^\circ$  latitude and longitude grid) and were uploaded from the National Oceanic and Atmospheric Administration (NOAA), Boulder, CO (<ftp://ftp.ncdc.noaa.gov/>; Table 1). The temperature data for every month of every year were significantly correlated with the elevation among the nine weather stations, which encompassed a comparable elevation range as that of the ten sites ( $p < 0.05$ ,  $R$  varied from 0.97 to 0.99). These data enabled calculation of robust region-specific temperature lapse rates for each month and year of the available climate record. Standard least-square regressions were applied to the original weather station data in order to separately calculate monthly temperature data for each month of each year from 1951 to 1989 for all ten study sites, using elevation as the independent variable. Regression analysis revealed a mean lapse rate of  $0.51^\circ\text{C}$  per 100 m of elevation. The relationships between monthly precipitation of the available climate record and elevation were non-linear and highly variable. As a result, the modeling of the precipitation for study sites could result in less reliable estimations of the precipitation/growth relationships. Therefore, we did not use precipitation data in the analysis of site-based growth/climate response.

#### Climate/growth relationships

We chose the mean monthly temperature data over a 15-month period – from July of the previous year to September of the current year as predictor variables for current-year tree-ring indices for the period from 1951–1989 as it was the common period for available temperature data. Correlation coefficients were calculated between monthly temperature data and residual tree-ring chronologies.

Our results showed that there was a very close significant relationship between growth/climate responses evaluated using a standard chronology and a residual chronology. Correlation coefficients varied from 0.84 to 0.97 ( $p < 0.01$ ) for the ten study sites. However, the standard chronology was less sensitive to temperature variations, especially at the lower-elevation sites, showing low correlations with temperature variations. In part, trees at lower altitudes may not be as sensitive to climate variations as trees at high altitudes. Considering that we analyzed climate/growth relationships for relatively short time intervals (1951–1989) due to a lack

of longer-term climate data, and that the standard chronologies contained a high first-order autocorrelation (Table 3), the procedure masked the effect of inter-annual climate variations on tree growth at the lower elevations, decreasing the sensitivity to climate variations. Therefore, the analysis of climate/growth relationships was conducted with use of the residual tree-ring chronologies rather than with standard chronologies (Fritts 1976). In general, this did not change the outcome of our analysis, but increased the level of statistical significance of the results.

#### Differences in response with elevation

Differences and similarities in growth/climate responses between the sites were analyzed by applying Ward's multivariate technique to cluster tree-ring chronologies in order to identify those with maximum similarities within each cluster and evaluate the distance between the obtained clusters (Anderberg 1973). We also calculated correlation coefficients of tree-ring chronologies at the ten sites with mean monthly temperatures and plotted the coefficients as a function of the distance in elevation from the lowest site (839 m) in order to compare changes in climate/growth relationships with increasing elevation.

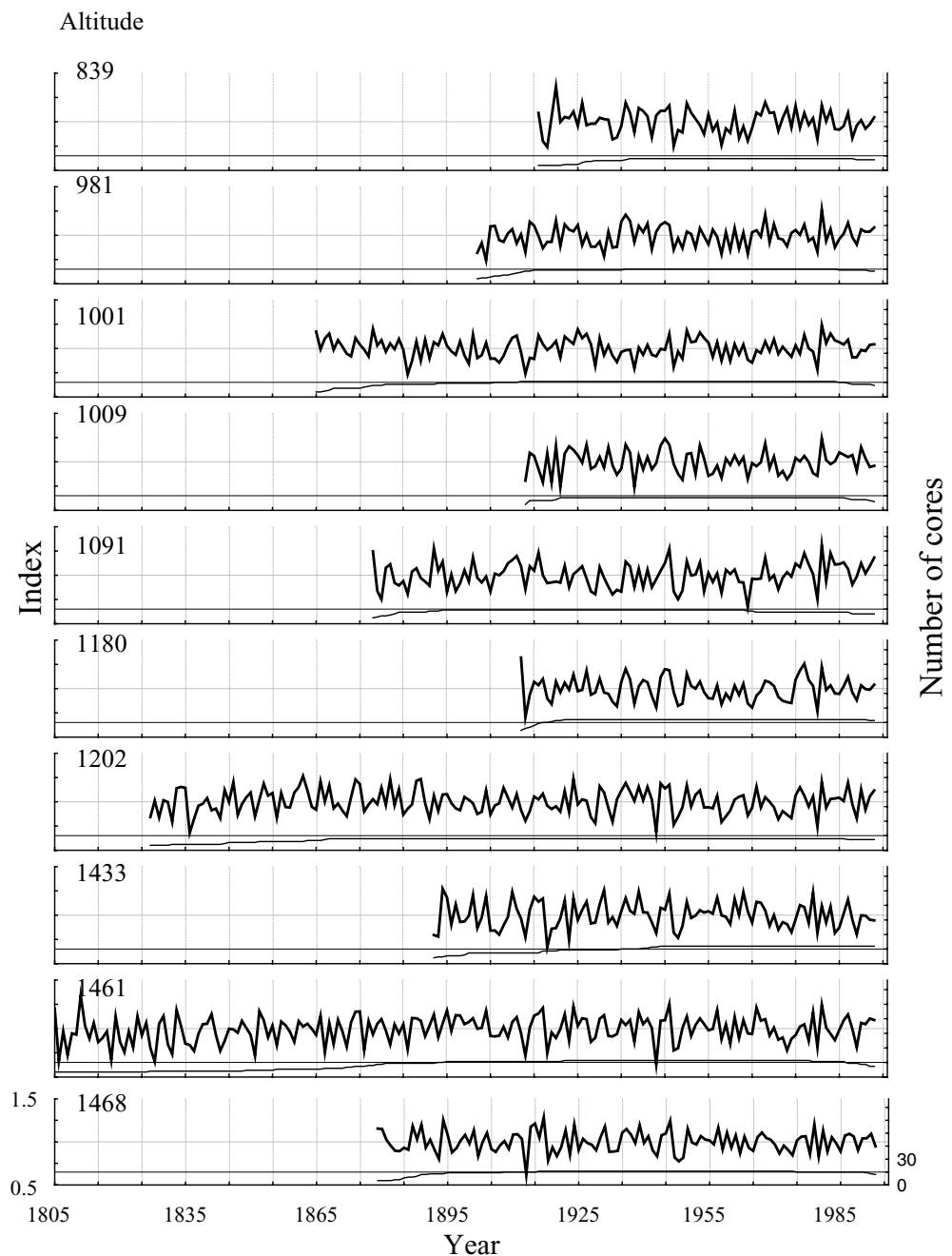
## Results

#### Statistical characteristics of tree-ring chronologies

Tree-ring chronologies were developed for each site (Fig. 1). The statistics for the tree-ring chronologies are shown in Table 3. The values of mean sensitivity varied from 0.144 to 0.175 among the ten sites, indicating that ring-width variability was relatively low. According to Ferguson's classification, a mean sensitivity greater than 0.3 is considered to be high (Shiyatov 1986). The values of the first-order autocorrelation (0.17–0.70) indicate that tree-ring growth of the previous year was correlated with tree-ring growth of the current year. The values of the second-order autocorrelation were also high for most of the sites and ranged from 0.20 to 0.70, except for the stand at 1433 m.

The values of RBAR and EPS are shown in Table 3 and Fig. 2. Mean RBARs were relatively high and range from 0.298 to 0.415. The changes in these characteristics were not constant through time. Running RBARs illustrate changes in the strength of common external forcing through time. In general, RBAR was relatively high for the whole period for all sites, showing the strength of a common signal. EPS values were mainly high for the period during which the chronology comprised the largest sample sizes. EPS values were persistently stable and exceeded the rough cutoff value of 0.85 after about 1870 (Fig. 2).

**Fig. 1** Ring-width chronologies of *Picea abies* developed for ten sites in the Tatra Mountains, Poland. The elevations (m) of the sites are shown for each tree-ring chronology. The *upper plots* show the annual tree-ring indices. The *lower plots* show the sample size for each year. All chronologies are truncated at sample size <5 series



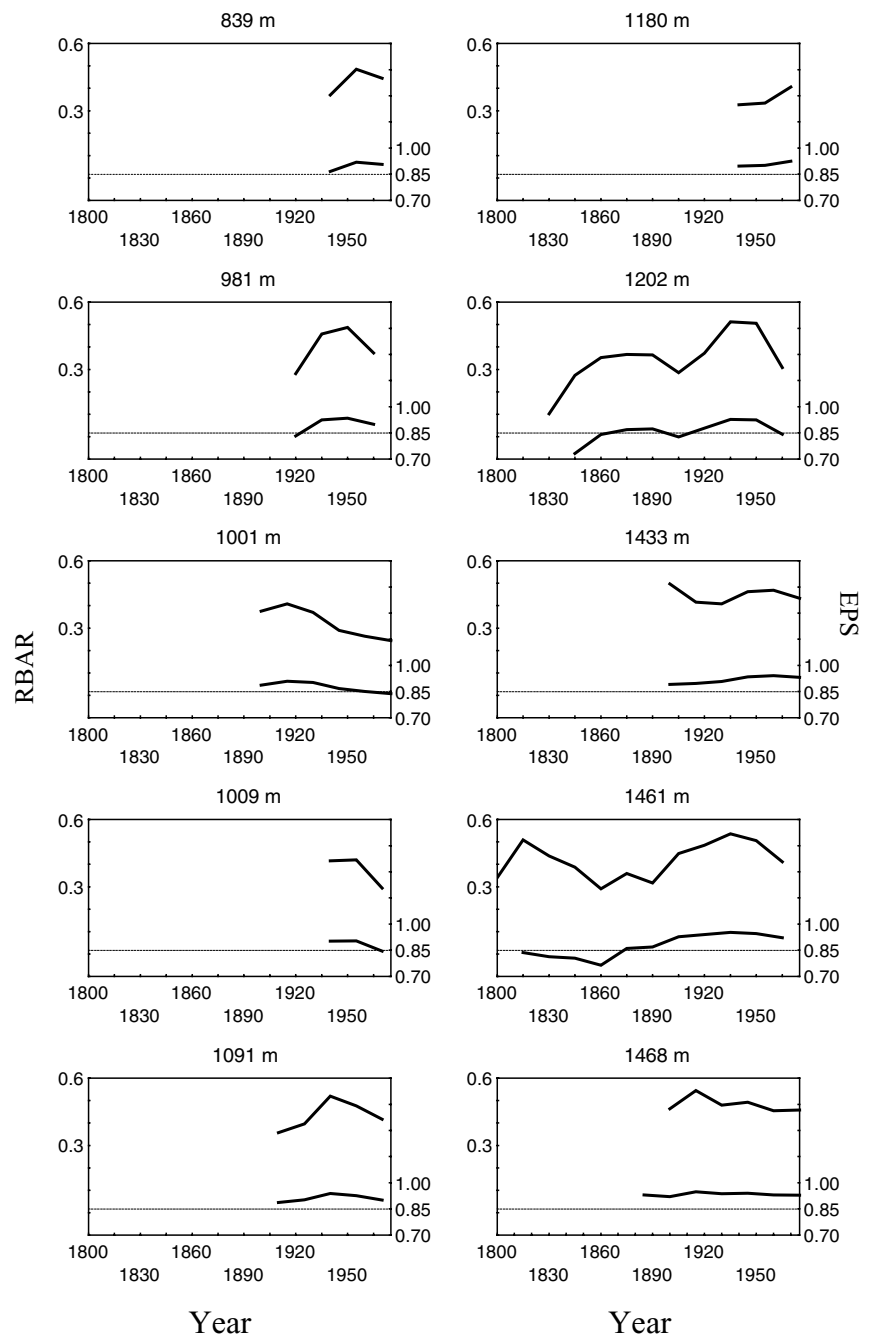
### Climate/growth relationships

Correlation coefficients of tree-ring chronologies with mean monthly temperature variations were developed for each of the ten sites (Fig. 3) in order to examine site-specific growth relationships to climate. There was a positive effect of the mean monthly temperature in June and July on radial growth, especially evident for the three highest elevation sites at 1433, 1461 and maximal for the highest elevation 1468 m. A positive effect of the mean temperature in March–April on radial growth was visible mainly among the low-elevation sites below 1180 m. The temperature in October of the pre-

vious year positively influenced radial growth of trees at all sites. There were statistically significant relationships only for two sites (1009 and 1433 m). Increasing mean monthly temperature in January negatively affected growth of trees at the high-elevation sites.

Growth of trees at the high-elevation sites was better explained by the temperature conditions than was growth at the lower-elevation sites. Values of the coefficient of multiple determination ( $R^2$ ) explained by the temperature variations were significant at  $p < 0.05$  for the three high-elevation sites (1433–1468 m,  $R^2$  from 0.44 to 0.58), slightly lower ( $R^2 = 0.40$ ) for the intermediate-elevation site (1202 m) and

**Fig. 2** Running average correlation between all series (RBAR, *upper plots*) and expressed population signal (EPS, *lower plots*) of the ten tree-ring chronologies of *Picea abies* based on a 30-year window with 15-year overlaps. The rough cutoff point for accepting EPS is 0.85



the lowest for other lower-elevation sites (839–1180 m,  $R^2$  from 0.24 to 0.36).

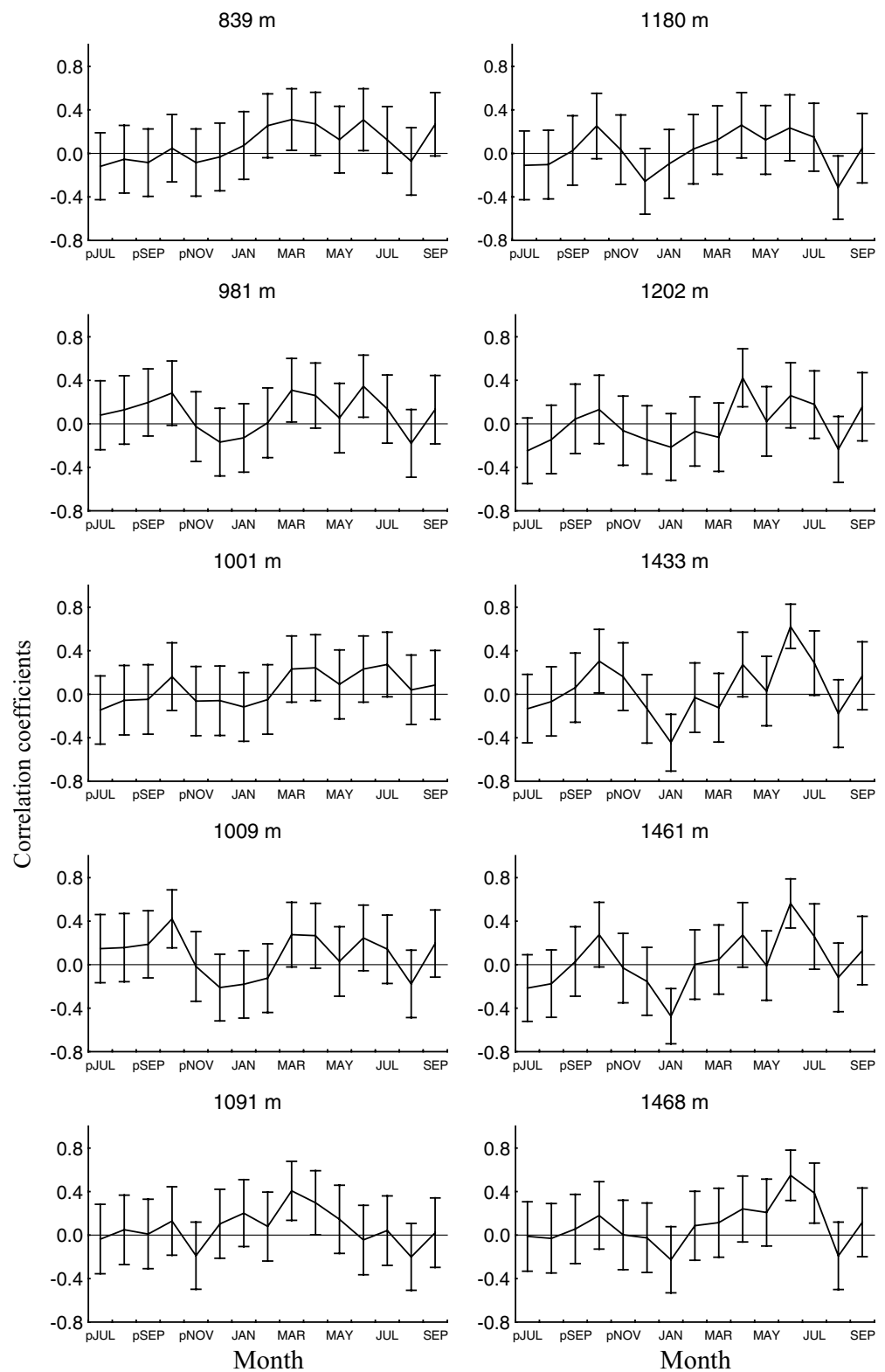
Differences in response with elevation

The similarity between tree-ring chronologies and growth/climate response among the sites is presented in Figs. 4 and 5. Cluster analysis classification techniques were used to group populations based on similarity of the tree-ring indices (Fig 4). Three distinct cluster groups were identified. The first cluster comprised trees from colder high-elevation

sites (from 1433 to 1468 m). A second cluster included the intermediate-elevation sites (from 1001 to 1202 m). A third cluster group included the stands from warm, low-elevation sites (from 839 to 1009 m). The stands from the highest elevations formed a group distinct from the remaining two groups at a high linkage distance.

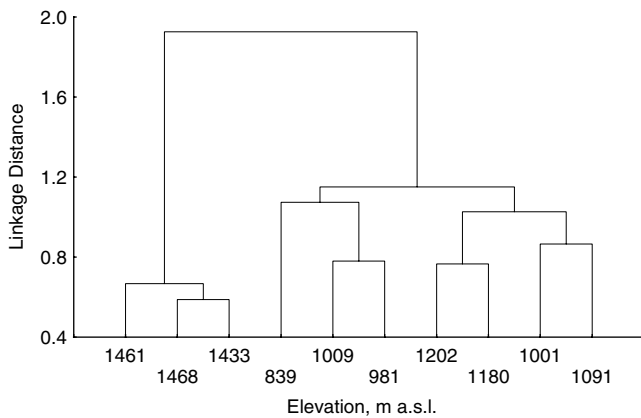
The similarity between growth/climate responses was expressed as a function of distance in elevation (Fig. 5). The correlation coefficient between tree-ring chronologies linearly decreases with increasing distance in elevation from the lowest site at 839 m ( $R^2 = 0.60, p = 0.01$ , Fig. 5A). Thus, the

**Fig. 3** Correlation coefficients relating mean monthly temperature to the tree-ring chronologies for *Picea abies* at the ten sites in the Tatra Mountains. The error bars of the coefficients that are significant at  $p < 0.05$  do not cross the  $x$ -axis. The dendroclimatic year is 15 months long and extends from July of the previous growth year (indicated by letter  $p$ ) to September of the current growth year



correspondence of factors controlling radial growth variability at sites of similar elevation was quite high and diminishes with increasing differences in elevation. This is probably due to a replacement of the factors controlling tree growth

or a redistribution of the magnitude of the influence of climatic factors on tree growth with changing elevation. The effect of mean temperature in March and January decreases ( $R^2 = 0.50$ ,  $p = 0.02$  and  $R^2 = 0.53$ ,  $p = 0.02$ ) and the effect



**Fig. 4** Dendrogram of cluster groupings of *Picea abies* at different elevations in the Tatra Mountains, based on the similarity of tree-ring chronologies

of temperature in June and July increases with increasing distance in stand elevation relative to the lowest site ( $R^2 = 0.45$ ,  $p = 0.03$  and  $R^2 = 0.47$ ,  $p = 0.03$ , respectively).

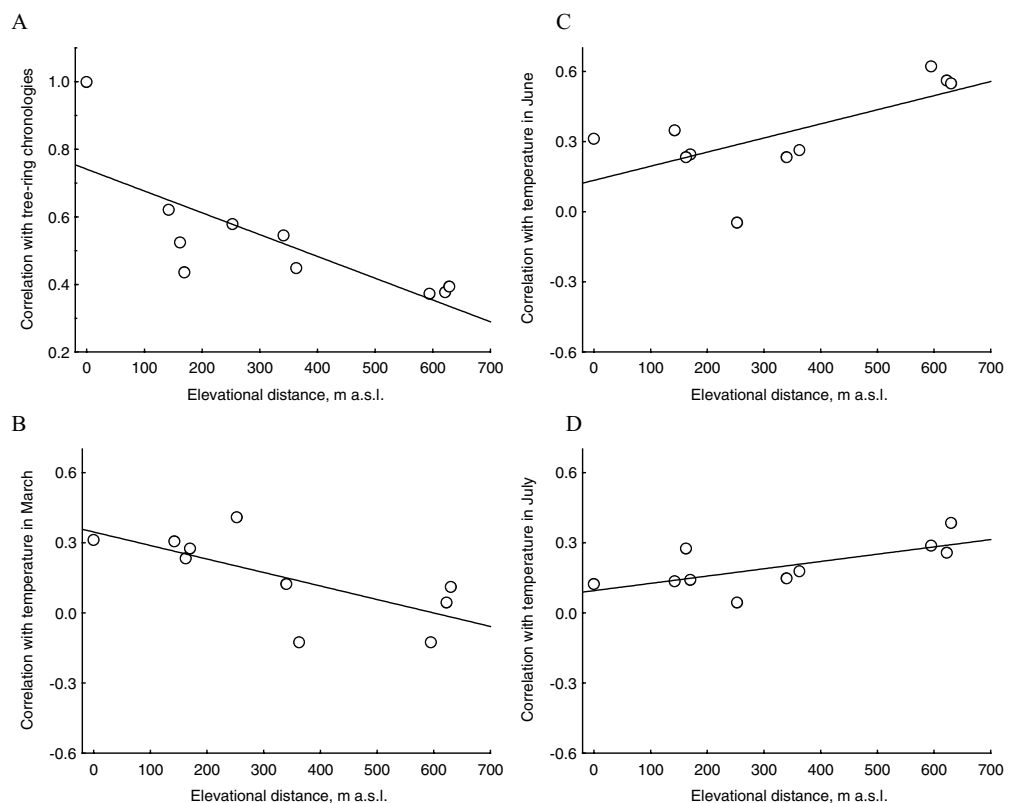
**Discussion**

Growth/climate response

Temperature of spring and summer months positively influenced tree growth of *Picea abies* in the Tatra Mountains. A

positive relationship between radial growth and the mean temperature in March and April was found for trees from the low-elevation sites (839–1091 m), the temperature in April for trees from the intermediate-elevation sites (1180–1202 m), and the temperature in June–July for the high-elevation sites (1433–1468 m). The shifting elevational pattern of the radial growth and mean monthly temperature correlation may be associated with the length of the growing season. Warm springs increase the length of the growing season and consequently the radial growth. The mean temperature in March varies from 0 to  $-3.6^{\circ}\text{C}$  and in April from 5 to  $1^{\circ}\text{C}$  with increasing elevation from 839 to 1468 m. This supports Mikola’s (1950) observations that the interannual variation in tree-ring growth in *Picea abies* was most dependent on the temperature in early part of the growing season. A positive influence of temperature in March on growth of *Picea abies* has been found in lowland sites in eastern Poland (Koprowski and Zielski 2006). Our results are consistent with studies of *Picea abies* along a latitudinal transect from central Finland to the Arctic timberline by Mäkinen et al. (2000). They concluded that mainly summer temperature in June–July affected the growth of trees. The importance of temperature in July increased from south to north. Neuwirth et al. (2004) reported on the importance of temperature and precipitation of May on the formation of tree rings of spruce along an altitudinal transect in Switzerland. In the European Alps, Frank and Esper (2005a) found a common temperature

**Fig. 5** Correlation coefficients between *Picea abies* tree-ring chronologies as a function of the distance in elevation for the ten sites in the Tatra Mountains ( $R^2 = 0.60$ ,  $p = 0.01$ ). **A** Correlation coefficients of *Picea abies* tree-ring chronologies with mean monthly temperatures as a function of the distance in elevation in the Tatra Mountains. **B** Correlation with mean temperature in March ( $R^2 = 0.50$ ,  $p = 0.02$ ). **C** Correlation with mean temperature in June ( $R^2 = 0.45$ ,  $p = 0.03$ ). **D** Correlation with mean temperature in July ( $R^2 = 0.47$ ,  $p = 0.03$ ). The distance equal to zero is the stand at the 839 m a.s.l. site. Positive distances occur when stands are from higher elevations



signal in ring-width chronologies related to June–August temperatures.

There is a positive effect of the temperature in October on growth of trees at all studied sites in the following year. High photosynthesis rates late in the fall could lead to high carbohydrate storage and thus to increased growth in the following year (Fritts 1976). A positive effect of temperatures in the previous autumn on growth was also reported by Oberhuber (2004) for *Pinus cembra* in the alpine timberline ecotone.

#### Differences in response with elevation

There was a negative correlation between winter temperatures (January) and radial growth of *Picea abies* mainly at the high-elevation sites. A study of spruce and fir in the southern French and Italian Alps by Rolland et al. (2000) showed that severe winter frosts, unusual summer droughts, or excessive wet and cold springs explained the occurrence of most negative indicator years in tree-ring series. Similar results were also found in studies of *Pinus cembra* in the alpine timberline ecotone by Oberhuber (2004), who showed that spatial and temporal variability of radial growth was caused by site-related differences in sensitivity to winter stress (i.e. desiccation). Also, Rolland et al. (1998) found that growth enhancements of spruce since 1860 and two pine species since 1920 near the upper timberline in the French Alps may be explained by increases in mean minimum temperatures (especially in January and from July to October), CO<sub>2</sub> concentration and N-deposition.

In general, high-elevation sites were more sensitive to interannual climate variation. A stronger positive correlation between summer temperature and radial growth as well as a higher sensitivity of trees to temperature changes at high than at low-elevation sites were found for other species such as *Lagarestrobos franklinii* (Buckley et al. 1997), *Nothofagus pumilio* (Villalba et al. 1997) and *Abies lasiocarpa* (Splechtina et al. 2000; Peterson et al. 2002). Our results indicated that growth/climate response changes with increasing elevation for *Picea abies* largely because the environmental factors controlling tree growth (coupled climatic and nutrient supply constraints) as well as the length of the growing season differ with elevation. Compared to low-elevation sites, trees at high elevations may increase growth significantly in response to comparatively small increases in summer temperatures because temperature constrains growth in a short growing season. However, increased temperatures may also lead to water stress and growth limitations at low-elevation sites on well-drained soils. For example, Jolly et al. (2005) studied the effect of the 2003 heat wave on trees of different species in Swiss Alps and showed a high-elevation tree growth enhancement and low-elevation growth suppression in response to these extreme summer temperatures. Warmer summer temperatures lengthened the snow-free growing sea-

son at high elevations, whereas high temperatures increased summer evaporation demand at lower elevations. To be sure, any approach using dendrochronology only describes the relative responsiveness of tree-ring series and not absolute growth differences. Our data supports this showing no significant correlation between mean absolute tree-ring-widths and coefficients of sensitivity of the ten sites (correlation coefficient  $r = -0.29$ ;  $p = 0.4$ ). The absolute radial growth of trees will differ among sites, in large part, depending upon environment. Thus, one might expect that high-elevation trees have lower growth rates than do lower-elevation trees at a common age.

One of the expected effects of climate change is an increase in temperature. Several studies have suggested that if possible climate warming is not accompanied by increased precipitation, rising temperatures could have a detrimental effect on forest ecosystems in Central Europe, arising from increased evapotranspiration and water deficits (Mäkinen et al. 2002b). However, our study showed that increased summer temperatures will likely result in radial growth increases, mainly among high-elevation sites where tree-ring growth is more strongly coupled to climate variation compared to the low-elevation sites. The largest proportion of total annual diameter growth is usually formed at the beginning of the growing season when early wood production occurs. In the latter part of the growing season radial growth slows and the thickening of cell walls occurs (Vaganov and Shashkin 2000). Cell wall thickness is probably more sensitive to soil water deficit at the latter part of the growing season when high temperatures at low elevations could cause soil water deficits and further slow cell growth and production. These findings suggest that high-elevation sites may be sensitive to potential future effects of temperature change, whereas trees from lower elevations would suffer from increased temperatures due to associated drought stress.

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