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The climate sensitivity of Norway spruce *(Picea abies* (L.) Karst.) in the southeastern European Alps.

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Abstract

To investigate the potential of Norway spruce (*Picea abies* L. Karst) as a palaeoclimate archive in the southeastern European Alps, tree ring chronologies were developed from trees growing at two sites in Slovenia which differed in their ecological and climatological characteristics. Ring width, maximum latewood density, annual height increment and latewood cellulose carbon isotope composition were determined at both sites and the resulting time-series compared with and verified against instrumental climate data for their common period (AD1960-AD2002). Results indicate that ring width sensitivity to summer temperature is very site-dependent, with opposing responses at alpine and lowland sites. Maximum density responds to September temperatures, indicating lignification after cell division has ceased. Stable carbon isotopes have most potential, responding strongly to summer temperature in both alpine and lowland stands. Height increment appears relatively insensitive to climate, and is likely to be dominated by local stand dynamics.

Key words: wood formation, height increment, latewood density, stable carbon isotope, southeastern Alps

Introduction

Norway spruce (*Picea abies* (L.) Karst.) is a long-lived tree (up to 400 years) and one of the most widespread conifers in Europe, extending naturally from the Arctic Circle in the north to the southwest and western range of the Alps, the Carpathians and Balkans, and to the extreme north of Greece. Today, it is even more widespread as a significant proportion of Norway spruce forests grow as monocultures beyond the boundaries or at lower elevations than their natural distribution. Mature spruce stands on shallow soils are more vulnerable to insects outbreaks, diseases, wind throws and other natural and human induced stresses (Jakša, 2007).

A comprehensive study of the influence of climate on tree-ring widths and maximum latewood density of *Picea abies* (L.) Karst., *Larix decidua* Mill., *Pinus cembra* L. and *Abies alba* Mill. has been conducted for the central and western Alps (Frank and Esper, 2005), but the southeastern part of the European Alps was not taken into consideration. Similarly, in a study on spruce growth along a transect from Southern Germany to the spruce arctic timberline (Mäkinen et al., 2002), sites in the southeastern part of the Alps (SE Alps) were excluded. Norway spruce does, however, have potential as a palaeoclimate archive in this region (Lindner, 2000; Stanovnik, 1998). The trees are relatively long-lived (up to 400 years), very widespread and the timber has been used in old buildings (Čufar et al., 1995; Levanič, 2004). Despite this potential, little is known about Norway spruce response to climate in the southeastern part of the Alps. A detailed multi-parameter approach based on intra- and inter-annual monitoring of the growth of trees and climatic data might greatly improve knowledge on tree response to climate and help to predict future responses. Here we perform such a study, at two contrasting sites, recording radial and height growth, latewood density and the stable carbon isotope ratios of the latewood as well as monitoring cambial activity and cell growth over three years.

Our aims are:

(i) to examine how climate has influenced spruce trees growing under different conditions in the southeastern European Alps using a range of growth proxies;

(ii) to evaluate whether the multi-parameter approach to dendroclimatology is applicable to spruce in this region;

(iii) to use high-resolution analysis of cambial dynamics (pinning) to investigate the seasonal dynamics of wood formation and its connection with local climate and

(iv) to investigate the potential of spruce as a palaeoclimate archive in the southeastern Alpine region.

Materials and Methods

Experimental site and trees

For the study we selected Norway spruce trees growing at a typical lowland plantation (Sorško polje, 350 m a.s.l., N 46°10’31”, E 14°23’22”) and at a typical natural alpine site (Pokljuka, 1250 m a.s.l., N 46°21’46”, E 13°58’39”) (Figure 1). The average annual temperature at Sorško polje, measured at the nearby meteorological station of Ljubljana (316 m a.s.l., 18 km S from the site), is 9.8°C, with January being the coolest (-1.0°C) and July the warmest month (20.0°C). The distribution of precipitation should favour spruce growth, May-September are well supplied with precipitation (47% of 1409 mm annual precipitation falls in this period) (Figure 2a). However, due to the presence of a thick layer of gravel just below the organic horizon, water drains quickly into deeper layers and gets inaccessible to the spruce roots. Trees growing on such shallow, organic soils are therefore subjected to high seasonal oscillations in soil water, resulting in summer water stress, increased bark beetle attacks and *Heterobasidion* spp. root and butt rot infections (Jakša, 2007).

The Alpine site Pokljuka is a typical, natural, sustainably managed sub-alpine spruce forest site *(Piceetum subalpinum)*. The site is characterized by low winter temperatures and high amounts of snow; annual mean temperature measured at Mrzli Studenec meteorological station (1350 m a.s.l, 4 km E from the site) is 3.5°C (Figure 2b). January and February are the coolest and driest months respectively at Pokljuka site (mean monthly minimum temperature and precipitation for January -4.4°C, 117 mm; February -5.2°C, 115 mm). July and August are the warmest months, with monthly mean temperatures of 12.3ºC and 11.9°C, respectively. Precipitation is abundant throughout the year, with September (185 mm), October (193 mm) and November (227 mm) being the wettest months. Precipitation in October and November could also fall as snow. Average annual precipitation at the Pokljuka site is 1978 mm, with an absolute maximum of 2604 mm and minimum of 1351 mm. The site is moist and relatively cool in summer and therefore optimal for Norway spruce growth. Ground vegetation at the site is scarce due to high stand density.

At each site, Norway spruce trees with comparable biometric characteristics and age (about 70 years) and at least 15 m from skidding trails were selected – see Table 1 for number of trees and samples. The mean diameter at breast height (1.3m) was 44 cm at Sorško polje and 35 cm at Pokljuka. Crowns of the sampled trees were in the stand canopy and normally developed (social position 2 by Kraft's classification), stems and surface roots were without any visible mechanical damage.

Meteorological data

The meteorological data sets used originate from the Environmental Agency of the Republic of Slovenia and are validated and corrected for errors. Ljubljana has the longest record in Slovenia, which spans from 1851 for temperature and from 1853 for precipitation till present, with no missing data. In this study, period 1960-2002 was used for both experimental sites. Distance from Ljubljana meteorological station to Sorško polje site is approx. 18 km and to Pokljuka site approx. 40 km. A meteorological station Mrzli studenec, close to the Pokljuka site has a short record (1953-present) with completely missing observations between 1965 and 1997 (64% of the whole data set) was therefore used only to check that the Ljubljana records are appropriate. The correlation (Pearson's r) between long-term monthly temperature values for meteorological stations Ljubljana and Mrzli studenec is 0.99 and for monthly sum of precipitation 0.88.

Measurements of tree-ring widths (TRW)

To build tree-ring width chronologies for each site, we used cross-sections from stem disks of 5 trees that were used for pinning and thereafter felled. Moreover, we took two 5 mm diameter cores at 1.30 m from ten additional trees at each plot. All trees were visually assessed before coring, and only healthy trees without any visual injuries to the crown, stem, or root system were selected for sampling. All samples were prepared according to standard dendrochronological procedures (Fritts, 1976; Schweingruber, 1989). Cross-sections and cores were sanded with sanding paper of increasingly higher grade until a perfectly smooth surface was achieved. Tree-ring widths were measured on a LINTAB^{TM} measuring table with a 0.01 mm precision (www.rinntech.com) equipped with an OLYMPUS binocular and polarized light source and further processed with PAST-4 dendrochronological software (www.sciem.com). Synchronisation and verification was done in PAST-4 using both visual comparisons and well established statistical parameters, including t_{BP} (Baillie and Pilcher, 1973), GLK% (Eckstein and Bauch, 1969), and Date Index - DI (Schmidt, 1987). Values of t_{BP} greater than 6.0, GLK% values greater than 65% and DI values greater than 100 were considered significant. Quality control using the programme COFECHA was applied to check for measuring mistakes (Grissino-Mayer, 2001; Holmes, 1983). If necessary, measurements were repeated and re-checked with COFECHA and removed from further processing if recognised as unusable. Pointer years, used as an additional cross-check tool, were defined as years where 80% of at least 10 trees reacted with a growth increase or decrease compared to the previous year. All calculations of pointer years were performed on non-standardised (raw) tree-ring series (Schweingruber et al., 1990).

Despite the fact that Sorsko polje is a spruce plantation with a thick layer of gravel just below the organic horizon, we did not find any false or missing rings. The only anomalies were narrow rings and, in some trees, compression wood and density fluctuations. Pokljuka site, in contrast, is characterised by a very stable growth rhythm and narrow rings with little width oscillation. No density fluctuation, missing or false rings were detected.

Analysis of maximum latewood density (MXD)

For examination of the tree-ring relative density, a system provided by Walesch electronics (www.walesch.ch) was used. Cores, 12 mm in diameter, or radial sections of stem discs were taken for this purpose from 15 trees per site (30 trees altogether). Samples were prepared on a double bladed saw and resin was extracted using Soxhlet apparatus (see Schweingruber et al., 1978). X-ray images were processed according to the procedures developed at the WSL laboratory, Switzerland (Schweingruber et al., 1978).

Stable carbon isotope composition (δ^{13}C)

Radial samples from dated disks were sampled for their stable carbon isotope composition. The latewood from each ring was extracted manually using a scalpel. For each sample α-cellulose was isolated from the slivers of wood through a series of chemical steps using a modified batch processing technique (Loader et al., 1997; Rinne et al., 2005). Between 300 and 350μg of dry α-cellulose were weighed into tin foil capsules and combusted on-line to CO_2 at 1000°C over chrome(III) oxide using an ANCA Elemental Analyser interfaced to a PDZ Europa 20/20 isotope ratio mass spectrometer. Combustion gases were purified online and the CO_2 resolved chromatographically prior to mass spectrometer analysis. Results are presented as per mille deviations from the VPDB standard using the conventional delta $\delta^{13}C$ notation (McCarroll and Loader, 2004). The precision on replicate analyses of an internal cellulose reference material is typically better than 0.1 per mille (n=15).

Height increment (HI)

Height increment was measured as the lengths of the annual shoots in the stem. The dating of the annual shoots was controlled by counting of absolutely dated tree rings in the discs sampled from inter-whorl increments located along the stem (for details see Kurkela and Jalkanen, 1990). Height increments were measured from the same felled trees used in cambial dynamics studies and radial growth measurements and combined into two site chronologies. Altogether there were 13 and 15 trees used for height increment analysis in Sorško polje and Pokljuka respectively. Because of damaged tree top (heavy storm prior to felling) we were not able to analyse height increment on two trees from Sorško polje experimental site, therefore we only took samples for TRW, MXD, $\delta^{13}C$ and WFD analysis.

Wood formation dynamics (WFD)

Five spruce trees per stand were pinned weekly between the end of April and end of October in the years 2002, 2003 and 2004. Six pinning holes per stem were set in a semi-helical pattern at the same date, using a 1.75 mm thick needle (Wolter, 1968). The pinning holes were marked and numbered. The pinned trees were felled at the end of the growing season, and samples containing wounded tissue were removed, fixed in FAA (formalin-ethanol-acetic acid solution) and dehydrated in ethanol series (30%, 50% and 70%). Transverse sections of approximately 25 µm thick were prepared using a Leica SM 2000R sliding microtome, stained with safranin and astra blue and finally mounted in Euparal.

Microscopic observations and analysis were carried out with a Nikon Eclipse E800 light microscope (bright field or polarized light) and a Lucia G 4.8 image analysis system. We counted the number of cells of the xylem increment formed from the onset of cambial growth to the time of pinning in at least three radial files of tracheids. To calculate relative increments we counted the number of cells on the extreme sides of the cross-sections that were free of a wound response.

A Gompertz function was applied to describe the seasonal dynamics of wood formation of the sampled trees at both sites in each year (Rossi et al., 2003).

Standardisation of the different proxies

The ARSTAN programme (Cook, 1985; Cook and Holmes, 1999) was used to remove age trends in the ring width, density and height data and build site chronologies. De-trending was achieved using a negative exponential or linear function. Indices were calculated as ratios between the actual and fitted values. Index values were then prewhitened using an autoregressive model selected on the basis of the minimum Akaike information criterion and combined across all series using bi-weight robust estimation of the mean to exclude the influence of the outliers (Cook, 1985; Cook et al., 1990).

Signal strength in the individual, detrended proxy series was tested using EPS – Expressed Population Signal (Briffa and Jones, 1990; Wigley et al., 1984). Only those series with a high common signal ($EPS \geq 0.85$) were included in the analysis.

The stable isotope series, also yielding $EPS > 0.85$, were mathematically corrected to remove the effect of anthropogenic changes in the $\delta^{13}C$ composition of atmospheric carbon dioxide (McCarroll and Loader, 2004; McCarroll and Loader, 2005). A second correction was employed to conservatively correct for changes in carbon isotope discrimination as a consequence of elevated atmospheric carbon dioxide concentrations (Gagen et al., 2007; Loader et al., in press). The carbon isotope analyses are reported only since 1960 in order to exclude the ‘juvenile effect’ which results in depleted but rising $\delta^{13}C$ values in the early decades of tree growth (about 50 years: Gagen et al., 2007; Loader et al., 2007). Having made these corrections, it is not considered necessary to statistically de-trend or index the isotope values (McCarroll and Loader, 2004; McCarroll and Loader, 2005).

All proxy chronologies were compared with climate data from Ljubljana meteorological station. Relationships between the climatic variables and the corrected and residual site chronologies were examined by simple regression analysis and Pearson's correlation coefficient. Measures used to assess the accuracy of statistical predictions, as recommended by the National Research Council (-, 2006) were the mean squared error (MSE), reduction of error (RE), coefficient of efficiency (CE), and the squared correlation (r^2). MSE is a measure of how close a set of predictions are to the actual values. It is usually normalized and presented in the form of either the RE statistic (Fritts, 1976) or the CE statistic (Cook et al., 1994). The RE statistic compares the MSE of the reconstruction to the MSE of a reconstruction that is constant in time with a value equivalent to the sample mean for the *calibration* data. The CE, on the other hand, compares the MSE to the performance of a reconstruction that is constant in time with a value equivalent to the sample mean for the *validation* data. CE will always be less than RE, and the difference increases as the difference between the sample means for the validation and the calibration periods increases. Where RE and CE statistics are negative or close-to-zero, a reconstruction is likely to have little if any skill. The CE statistic is the most difficult to pass, but the RE statistic is particularly useful for detecting whether or not a proxy responds to lower frequency changes in climate by tracking a shift in the mean value between the calibration and verification periods (Wahl and Ammann, 2007). The squared correlation statistic, denoted as r^2, measures the strength of a linear relationship between two variables but is insensitive to differences in the absolute values.

Results

The results for the four proxies for the common period 1960 to 2002, in both raw and corrected or indexed form, are presented in Figure 3. The tree ring widths from the lowland site (Sorško polje) are much more variable (range 0.5 mm – 3.7 mm) than at the alpine site (1.5 mm – 2.7 mm), and the mean ring width is larger at the lowland site Sorško polje compared to high elevation site Pokljuka despite very similar tree ages at the two sites (Table 2). The difference in the mean level of the maximum density results is even more striking, with much higher values at the lowland (1.02 g.cm^{-3}) than on the high elevation site (0.86 g.cm^{-3}), although the within-site ranges are similar (Table 2). The height increment values are similar in terms of both mean value and range - mean 39.2 cm.year^{-1} (range 9.9 cm – 64.0 cm.year^{-1}) on Sorško polje compared to 32.0 cm.year^{-1} (range 18.1 - 45.4 cm.year^{-1}) at Pokljuka (Table 2). Although the carbon isotope values from the two sites vary around similar means, there is a marked difference in sensitivity, with a much larger range of values at the lowland site Sorško polje; mean $\delta^{13}C$ value of –22.75 (range -24.22 to -20.81) compared to the high elevation site Pokljuka with mean $\delta^{13}C$ value of –22.27 (range -23.40 to -21.29) (Table 2). The difference in sensitivity is not an artefact of the different sample sizes and is apparent in the individual tree series.

The correlations between the proxies within each of the sites (Table 3a,b) are very low, with only that between height increment (lagged 1 year) and ring width at Sorško polje proving significant. The height values are shifted because they respond to conditions in the previous summer, as discussed below. If the sites are combined to give four 'average' chronologies (Table 3c), the only marginally significant correlation is between height increment and maximum latewood density. The between-site correlations (Table 4) show that only two of four proxies are significantly correlated – correlation between MXD values is 0.40 ($p< 0.05$) and between $\delta^{13}C$ 0.67 ($p<0.01$). Ring widths and height increments are not correlated between the sites and none of the proxies at one site correlate significantly with a different proxy at the other site.

When the proxy data are compared with mean temperature and precipitation amount data from Ljubljana, it is clear that only comparison with stable carbon isotope gives high correlation values (Figure 4). For ring widths there are no significant correlations with the temperature or precipitation observed for any single month at either of the sites, nor with combinations of the summer months. There is, however, a clear opposite response of the ring widths to temperature at the two sites. In May, June and July the correlations with temperature at the alpine site are weak and positive, but at the lowland site they are weak and negative (Figure 4).

For maximum latewood density the results are more consistent between the sites, giving positive correlations with the temperature of the summer months. The only significant single month is September, showing a positive correlation with temperature and a negative correlation with precipitation. The combination of May to September is also significant for both temperature and precipitation at Pokljuka but not Sorško polje. The correlations between height increment and climate parameters are not statistically significant ($p>0.05$). The values presented in Figure 4 compare the height increment with the climate of the previous year, because it has been shown for Scots Pine that height growth is controlled by the climate of the year immediately prior to shoot extension (Jalkanen et al., 1995; Jalkanen et al., 1998). However, spruce at both sites did not exhibit any strong correlations with either the climate of the year prior to growth or with the climate of the year of growth.

The relationship between the stable carbon isotopes and climate is significant and consistent at both sites. There are strong positive correlations with the temperature of spring (May) and mid-summer (July and August) at both sites, and the best combination of months is the mean of July and August, giving correlations of 0.61 and 0.66 at the lowland and alpine sites respectively. There is a negative correlation with the precipitation of the summer months.

The potential for using the proxies to reconstruct past climate is tested using a split-period calibration and verification test, run in both directions (Table 5). In the case of MXD the target climate parameter is the mean temperature of September. The percentage of variance explained over the verification periods varies between 29% and 50%. In every case the RE statistics are positive. When the average of the two sites is taken, the correlation with September temperature over the full period is lower than at either of the individual sites. For stable carbon isotopes the climatic target is the mean July and August temperature. Over the full period the correlation is higher for Pokljuka than for Sorško polje, but when the sites are combined as a simple average the correlation is higher (0.68) and it is higher again if the values from the individual sites are standardised to equalise the variance prior to combining them (0.70). In every case the RE statistics are strongly positive. Since there is a difference of 1.6°C in the mean July/August temperatures of the two periods, these results confirm that the isotope-based reconstructions are able, to some extent, to track a change in the mean temperature, as well as reflecting the inter-annual variations. The negative CE values, however, demonstrate that the predicted temperature values in the verification periods do not perform as well as the verification mean, because some off-set remains. The best results are obtained when the isotope series are standardised prior to being combined, so that the difference in sensitivity is removed. The calibration and verification statistics for ring widths and height increments are also shown, with July - August (tree-ring widths) and previous August – September (height increment) temperature as the target, but since the correlations over the whole period are low it is unsurprising that the results are poor, with very little of the variance explained (Table 5).

The investigation of wood formation dynamics over the years 2002-2004 revealed that at Sorško polje, divisions in the cambium in all three years started at the end of April and finished at the end of July (year 2003) or at the end of August (year 2002 and 2004) (Figure 5). At Pokljuka, a delay of 2–4 weeks in the beginning of cambial cell divisions was observed, and the production of new cells stopped in the first half of August in all three years. At Sorško polje, the duration of the cambial activity was markedly longer (98–119 days) in 2002 and 2004 than in 2003 (77–84 days) (Figure 5). At Pokljuka, the differences in the duration of the cell divisions among years were less expressed (14 days) and the period of cambial activity was shorter, however rate of cell production was higher at Pokljuka (on average 0.46–0.60), than at Sorško polje (on average 0.39–0.42) – Table 6.

Discussion

The large between-site differences in the ring-width chronologies, and the poor fit with climate data are not unexpected. Mäkinen et al. (2003) studied radial growth of Norway spruce on a transect from southern Germany to the spruce northern timberline and stated that tree-ring widths of spruce growing under average climatic conditions respond less strongly to climatic variation than trees growing in extreme conditions. This coincides with our findings of tree-ring response to climate on both sites. Similarly, Frank and Esper (2005) found that in the central and western Alps ring widths in spruce are less sensitive to climate than maximum latewood densities. Spruce in the southeastern Alps is notoriously difficult to cross-date between sites, suggesting that local site factors dominate over the regional climate signal. In this case the difference is so large that the response to temperature at the two sites is even in opposite directions, with the colder alpine site showing positive values of correlation coefficients with the summer months and the lowland site negative values. The lowland site is more sensitive to water stress not because the summers are particularly dry and hot, but because the shallow soils overlie freely draining gravels, reducing the capacity of the thin organic soils to store water accessible by the trees. The shallow-rooted spruce trees are thus prone to periods of water stress, which can be sufficiently severe to terminate growth or to form partial rings. The cambial dynamics data show this effect during the hot summer of 2003, where radial growth was prematurely terminated at Sorško polje, forming a ring that was only 1.1 mm wide (normally between 1.6 and 1.7 mm) but enhanced at Pokljuka where a 1.4 mm wide ring was formed (normally between 1.2 and 1.3 mm).

For the maximum latewood density results there is a striking difference in the absolute values and sensitivities between the two sites, with much higher densities and smaller variability at the lowland site. This is likely to be linked to the higher site productivity and the longer growing season at lower altitude. Despite these differences there is a significant correlation between the two sites, suggesting that densities are less sensitive to local site factors than radial growth, as was also observed by Sander and Eckstein (2001). The strong and consistent correlation with the temperature of September, which according to the cambial dynamics results falls after radial growth has ceased, can be explained by lignification of the latest formed latewood tracheids, which can continue long after cambial cell division has stopped (Gindl et al., 2000; Gričar et al., 2005).

Height increment in spruce, as in pine, is a 2-year process involving the formation of the terminal bud in the first year and shoot elongation in the second year (Doak, 1935), so that summer temperatures of the previous year can control height increment (Salminen and Jalkanen, 2005). Annual height increment of Scots pine (*Pinus sylvestris* L.) has proven to be one of the strongest palaeoclimate proxies in the northern boreal zone (McCarroll et al., 2003; Salminen and Jalkanen, 2005). In the Giant Mountains of Czech Republic Sander and Eckstein (2001) found a good coherence in spruce between the needle production and height increment, and needle production correlated significantly with the temperatures of the previous March and October. The results presented here, however, indicate that the annual height increment of southern alpine spruce is relatively insensitive to climate. We could find no significant relationship between height growth of Norway spruce, and climate of the current or previous growing season. The average height growth at the two sites is similar, despite the large between-site differences in summer temperature and growing season length. The within-site and between-site correlations show some links between height growth and both ring width and density, as expected from a growth proxy, however no significant correlations were found with any of the measured climate parameters. The likely explanation is that in such dense and intensively managed spruce stands, local factors, including thinning, dominate over regional climate.

Stable carbon isotope ($\delta^{13}C$) analysis of tree-rings has demonstrated significant potential in dendroclimatological studies (Gagen et al., 2006; Gagen et al., 2007; McCarroll and Loader, 2004). In dry conditions the $\delta^{13}C$ signal is primarily dominated by stomatal conductance to CO_2, and $\delta^{13}C$ accumulated in tree-rings correlates well with factors influencing soil moisture status (and water stress in trees) e.g. vapour pressure deficit, precipitation and relative humidity (Gagen et al., 2004; Robertson et al., 1997). However, under conditions where moisture is not limiting, the internal partial pressure of CO_2 is controlled primarily by photosynthetic rate and $\delta^{13}C$ variability relates directly to the amount of light received by the plant for photosynthesis (photon flux) which may be correlated indirectly with temperature and sunshine hours (McCarroll and Pawellek, 2001; McCarroll and Loader, 2004).

Stable carbon isotope ratios have not previously been measured from spruce trees in this region, but the results are very encouraging. Despite the differences between the two sites, the carbon isotope results carry the same strong signal of summer temperatures at both sites. The dominance of regional climate over local site conditions is confirmed by the strengthening of the correlation with temperature when the values from the two sites are combined. Although the two site chronologies are strongly correlated, they differ in terms of the range of values, and thus their sensitivities. Some caution is therefore required in combining the data from different sites, and although the $\delta^{13}C$ data do not need to be indexed to remove growth trends, it may be necessary to stabilise the variance. In the example used here, stabilising the variance prior to averaging increased the strength of the correlation with climate and improved the verification statistics.

Conclusions

The results presented here suggest that the sensitivity of spruce trees to climate and climate change is likely to be very variable between sites. Increased temperatures are likely to stimulate growth at cool high altitude sites, which is the natural range of spruce distribution in this area, but to be deleterious at lower altitudes where spruce has been widely planted. With increasing summer temperatures radial growth is likely to decline (Pichler and Oberhuber, 2007; Reichstein et al., 2007). Water stress will become more common, increasing susceptibility to other impacts, including insect outbreaks, disease and wind throws (Jakša, 2007), which are amongst the most severe threats to forest management in this region.

Although spruce is now very widespread in the southeastern alpine region, and covers a wide altitudinal range, it would seem that there is limited potential for extracting a climate signal from the ring widths alone. Local site conditions and different forest management practices can dominate over the regional climate signal, and response to the same climate driver can work in opposite directions at different sites. It would be necessary to choose sites very carefully to maximise response to the signal of choice. Maximum latewood density appears to be a better climate proxy than tree ring widths, responding most strongly to the temperature of September. The pinning results presented here suggest that this is likely to reflect inter-annual variations in lignification after cell division has ceased (Gindl et al., 2000; Gričar et al., 2005). The relationship between maximum density and mean September temperature appears, from the results presented here, to be strong and consistent enough to be useful for palaeoclimate reconstruction. Height increment, in contrast, appears to carry no clear climate signal and at the sites studied is likely to have been dominated by local stand dynamics.

The most promising palaeoclimate proxy identified here is the stable carbon isotope ratios of the latewood cellulose. These are strongly correlated with mid summer temperatures (July/August), and the relationship is consistent between sites. These findings are in agreement with studies elsewhere, which suggest that stable isotopes are less sensitive to local site conditions and disturbance than the growth proxies (Gagen et al., 2004; Loader et al., 2007; McCarroll and Pawellek, 2001). An unexpected result here is that, although the dominant climate signal at the two sites was the same, and the two isotope chronologies are strongly correlated, there is a clear difference in sensitivity. This calls for caution in combining stable isotope data from different sites simply on the basis of strong correlations.

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Table 1: Number of trees, cores and actual number of samples used in the analysis for each site. TRW=tree-ring width, HI=height increment, MXD=maximum latewood density, δ^{13}C=stable carbon isotope composition, WFD=wood formation dynamics.

Table 2: Mean values and range for all studied proxies for Sorško polje and Pokljuka. TRW=tree-ring width, MXD=maximum latewood density, HI=height increment, δ^{13}C=stable carbon isotope composition.

Table 3: Inter- and intra-site correlations between proxies of Norway spruce. TRW=tree-ring width, MXD=maximum latewood density, HI=height increment, δ^{13}C=stable carbon isotope composition; statistical significance level: * - 5%; ** - 1%.

Table 4: Correlations between the averaged proxies of Sorško polje and Pokljuka; statistical significance level: * - 5%; ** - 1%.

Table 5: Measures of reconstruction accuracy for lowland site Sorško polje and high elevation site Pokljuka and average thereof for both, forward and backward calibration / verification.

Table 6: Wood formation dynamics (WFD) in Norway spruce at Sorško polje and Pokljuka in the years 2002, 2003 and 2004.

Table 1

Location	Number of trees	Number of cores / cross-sections	Number of samples used
SORŠKO POLJE			
TRW	15	2	11
HI	15	cross-sections	13
MXD	15	1	13
$\delta^{13}C$	5	1	3
WFD*	5 / year	150 samples / year	150 samples / year
POKLJUKA			
TRW	15	2	12
HI	15	cross-sections	15
MXD	15	1	13
$\delta^{13}C$	5	1	5
WFD*	5 / year	125 samples / year	125 samples / year

*number of samples in WFD section is calculated as number of weeks of pinning x number of trees; on Sorško polje we did pinning 30 weeks on 5 trees and on Pokljuka 25 weeks on 5 trees

Table 2

		Sorško polje		**Pokljuka**	
		mean	range	mean	range
TRW	*mm*	2.3	0.5 – 3.7	2.0	1.5 – 2.7
MxD	*g.cm^{-3}*	1.02	0.91 – 1.15	0.86	0.73 – 0.94
HI	*cm.year^{-1}*	39.2	9.9 – 64.0	32.0	18.1 - 45.4
δ^{13}C	‰	–22.75	-24.22 to -20.81	–22.27	-23.40 to -21.29

Table 3

	a			b			c		
	Within Sorško polje			Within Pokljuka			Combined proxies		
	TRW	*MXD*	*HI*	*TRW*	*MXD*	*HI*	*TRW*	*MXD*	*HI*
MXD	-0.04			0.06			-0.05		
HI	0.32*	0.14		0.22	0.19		0.25	0.32*	
$\delta^{13}C$	-0.14	-0.19	-0.18	0.08	0.10	0.23	-0.10	-0.02	-0.05

Table 4

Between-site correlations

	TRW_s	MXD_s	HI_s	$\delta^{13}C_s$
TRW_p	0.10	-0.24	0.12	0.12
MXD_p	-0.02	0.40*	0.18	0.07
HI_p	-0.17	0.19	-0.19	0.13
$\delta^{13}C$	-0.17	-0.20	-0.15	0.67**

s= Sorško polje; p= Pokljuka

Table 5

			FORWARD Calibration: 2002-1981 Verification: 1982-1960				**BACKWARD** Calibration:1982-1960 Verification: 2002-1981			
	Target variable	Pearson's r-value	R^2_{ver}	mse	RE	CE	R^2_{ver}	mse	RE	CE
TRW_s	JA	-0.43	0.12	2.61	0.15	-2.76	0,04	2,36	0,30	-1,41
TRW_p	JA	0.41	0.01	2.29	0.25	-2.30	0,17	3,70	-0,10	-2,78
TRW_{avg}	JA	-0.19	0.11	3.76	0.01	-3.41	0,00	3,18	0,05	-2,24
MXD_s	S	0.61	0.50	1.14	0.45	-0.35	0,29	1,30	0,40	-0,39
MXD_p	S	0.55	0.42	1.65	0.20	-0.95	0,37	1,75	0,19	-0,87
MXD_{avg}	S	0.51	0.52	1.63	0.21	-0.93	0,20	1,95	0,10	-1,08
HI_s	-AS	-0.07	0.09	3.33	-0.20	-3.72	0,09	3,13	0,01	-1,85
HI_p	-AS	0.14	0.19	3.08	-0.12	-3.37	0,19	3,39	-0,14	-4,03
HI_{avg}	-AS	0.03	0.00	2.84	-0.03	-3.03	0,00	3,00	-0,01	-3,45
$\delta^{13}C_s$	JA	0.61	0.30	1.76	0.43	-1.54	0,14	1,97	0,41	-1,01
$\delta^{13}C_p$	JA	0.66	0.12	1.37	0.55	-0.98	0,20	1,52	0,55	-0,55
$\delta^{13}C_{avg}$	JA	0.68	0.32	1.38	0.55	-1.00	0,19	1,46	0,57	-0,49
$\delta^{13}C_{inx}$	JA	0.70	0.31	1.29	0.58	-0.85	0,21	1,27	0,62	-0,30

Legend:

mse – mean squared error; RE – reduction of error statistics; CE – coefficient of efficiency; R^2_{ver} – squared correlation of the verification period; TRW_s, MXD_s, HI_s, $\delta^{13}C_s$ – proxies for Sorško polje; TRW_p, MXD_p, HI_p, $\delta^{13}C_p$ – proxies for Pokljuka; TRW, MXD_{avg}, HI_{avg}, $\delta^{13}C_{avg}$ – combined proxies for Sorško polje and Pokljuka; $\delta^{13}C_{inx}$ - indexed isotope proxy – values were standardised to equalise variance and then combined into average for both sites; JA –July-August temperature combination; S –September average monthly temperature; -AS – previous August-September temperature combination

Table 6

	Sorško polje			Pokljuka		
	2002	2003	2004	2002	2003	2004
Average number of cells in tree-ring	62.7	36.3	50.5	36.1	45.5	41.4
Average tree-ring width (mm)	1.73	1.06	1.62	1.23	1.42	1.25
Average number of cells produced per day during the growing season	0.39	0.41	0.43	0.46	0.60	0.47

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Figure 1: Location of the experimental sites Pokljuka and Sorško polje (black circle) and meteorological stations (white square).

Figure 2: Climate diagram of the meteorological stations Ljubljana, for the period 1900 - 2006 used in both Sorško polje and Pokljuka site (a). Meteorological station Mrzli studenec (reference for the Pokljuka site) for the period 1953 - 2002 was not used in calculations because of more than 60% missing values (b).

Figure 3: Raw and corrected / indexed chronologies of tree-ring width, maximum latewood density, height increment and stable carbon isotopes of Norway spruce for Sorško polje and Pokljuka for the common period 1960 - 2002.

Figure 4: Correlations between proxies of Norway spruce and mean monthly temperature and monthly sum of precipitation for Sorško polje and Pokljuka for a period 1960-2002. Combinations of months: MJ, JJ, JA, MJJ, JJA, MJJA and MJJAS are combinations of mean temperatures in **M**ay, **J**une, **J**uly, **A**ugust and **S**eptember. Dashed horizontal line represents 95% significance level for Pearson’s correlation coefficient at given degrees of freedom.

Figure 5: Onset, duration and cessation of cambial activity in Norway spruce at Sorško polje (gray bars) and Pokljuka (white bars) in the growing seasons 2002–2004. Error bars indicate one standard deviation of onset and cessation of cambial activity among trees.

Figure 1


AUSTRIA
HU
15E
POKLJUKA
SORSKO POLJE
ITALY
SLOVENIA
CROATIA
45N
N
W
S
100
0
100 Kilometers

Figure 2

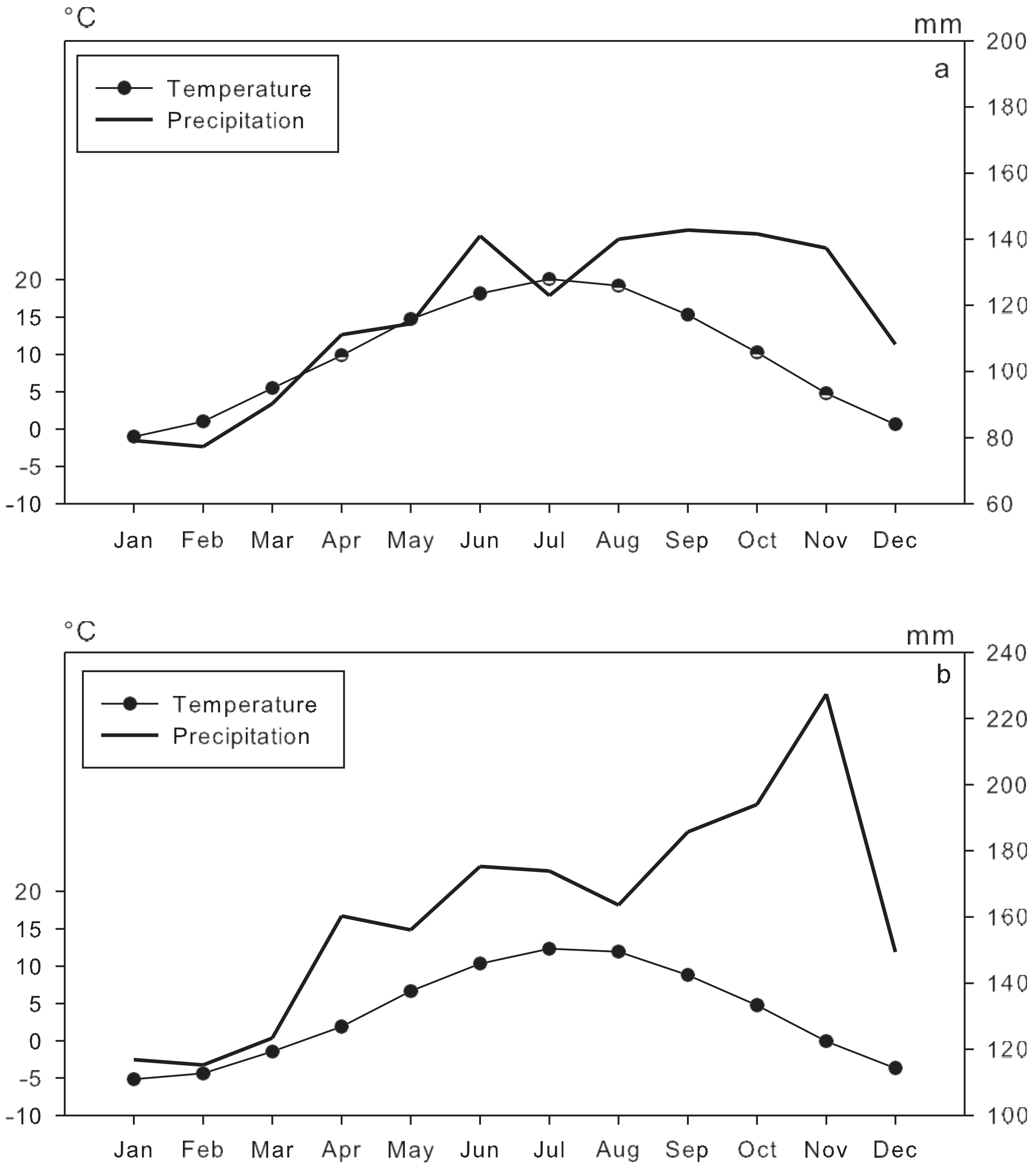

Figure 2

Figure 3

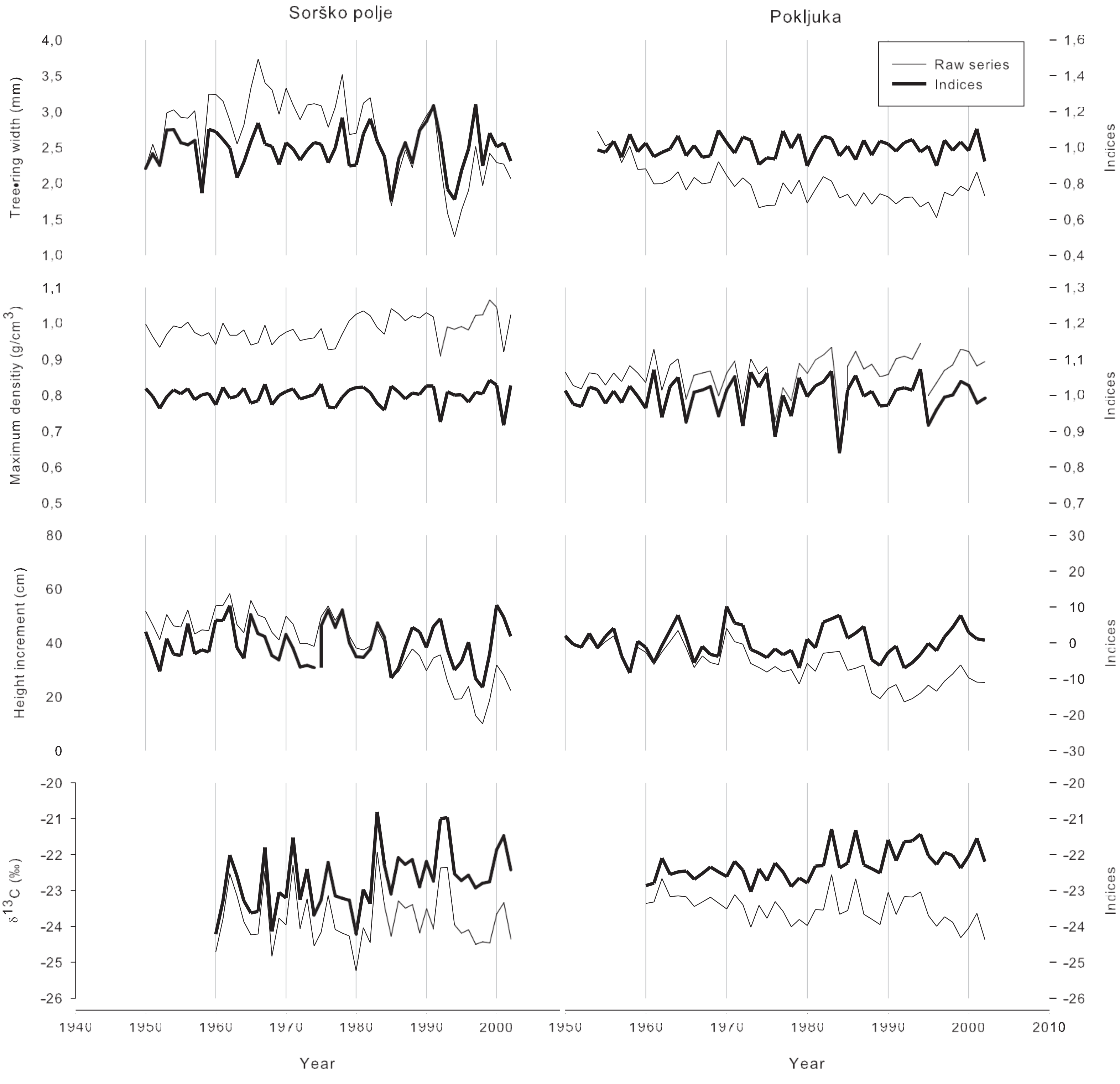

Figure 3

Figure 4

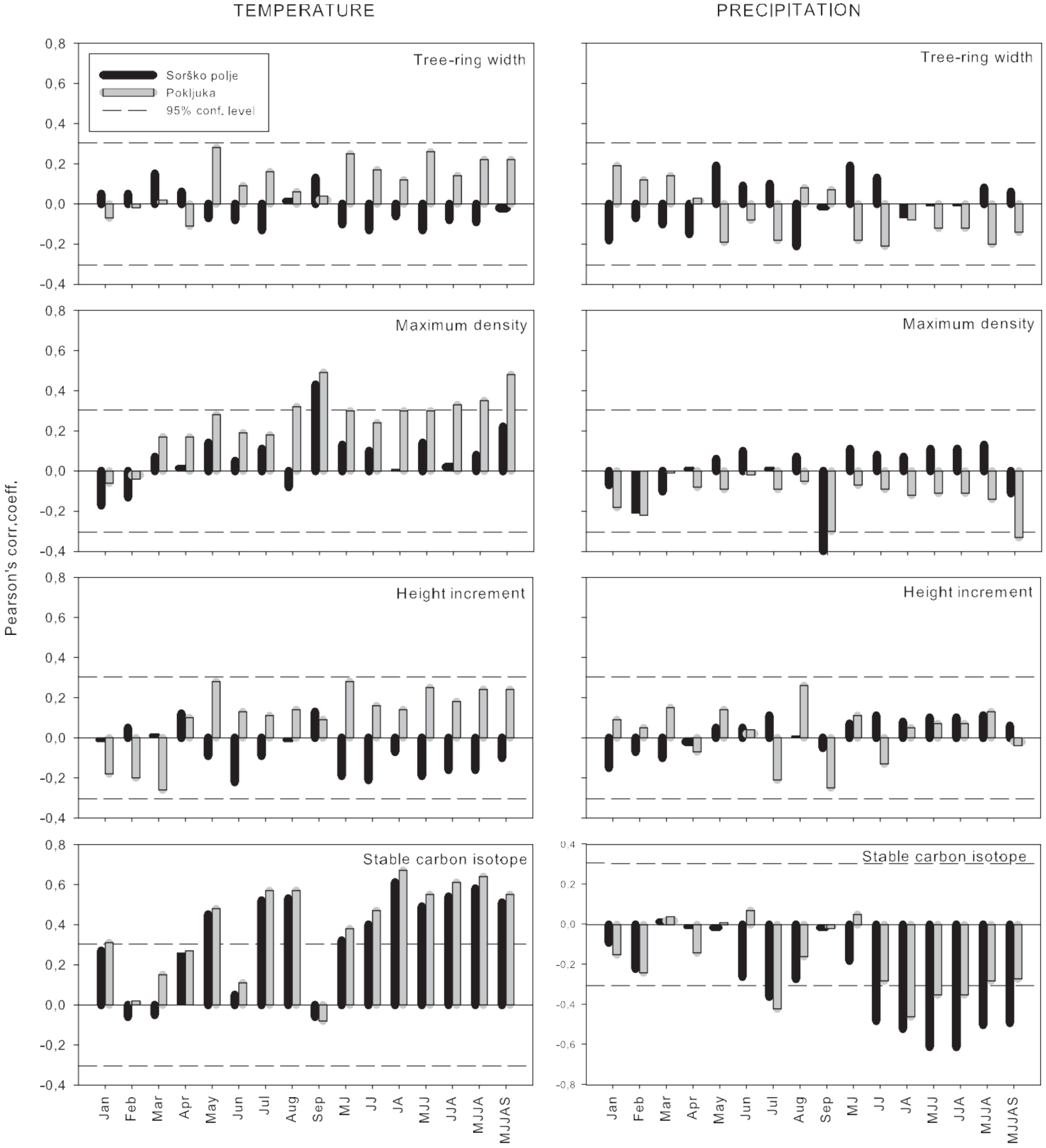

Figure 4

Figure 5

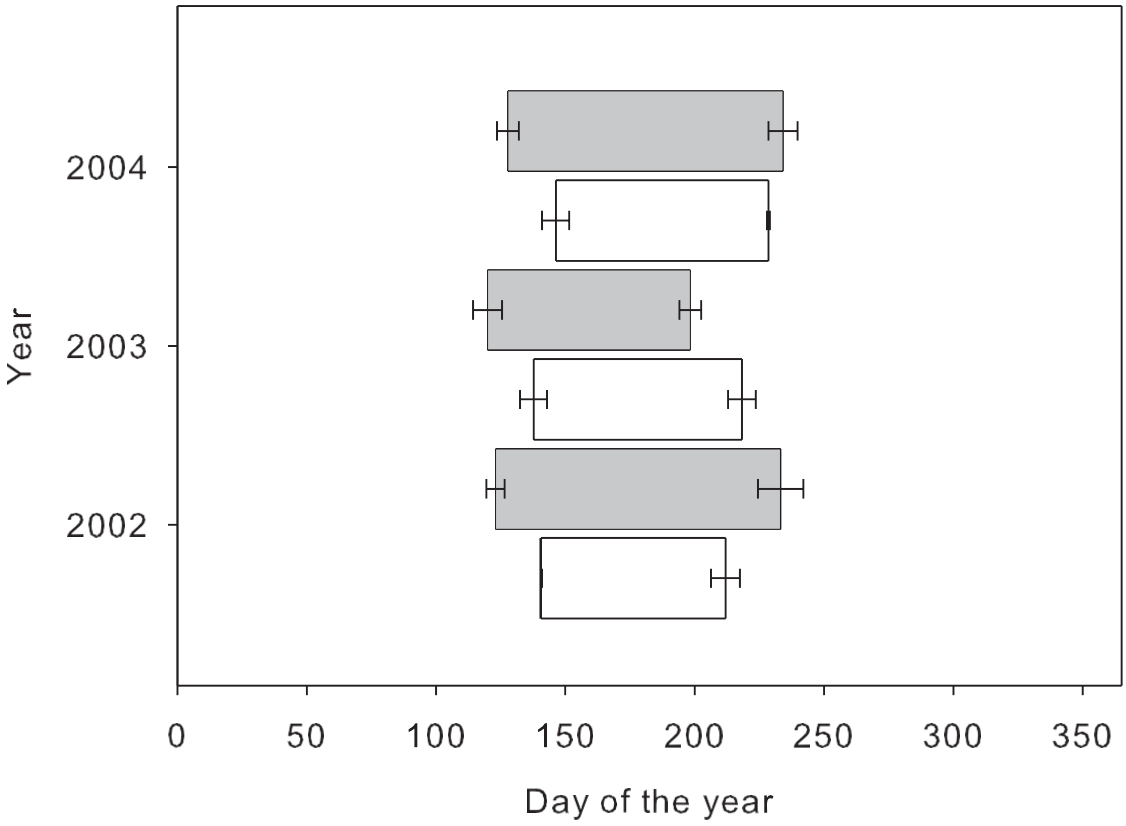

Figure 5