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Spruce tree-ring proxy signals during cold and warm periods

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Abstract: The strength and temporal rigidity of climate signals are important characteristics of proxy data used to reconstruct climate variability over pre-instrumental periods. Here, we assess the performance of different tree-ring proxies, including ring width, maximum latewood density, δ¹³C, and δ¹⁸O, during exceptional cold (1800–1850) and warm periods (1946–2000). The analysis was conducted at a spruce (Picea abies) timberline site in the Swiss Alps in proximity to long homogenized instrumental records to support calibration tests against early temperature and precipitation data. In this cold environment, tree-ring width, maximum latewood density, and δ¹⁸O are mainly controlled by temperature variations. δ¹³C is influenced by various factors including temperature, precipitation, sunshine, and relative humidity. When comparing the response patterns during cold and warm periods, ring width and maximum latewood density revealed temporally stable temperature signals. In contrast, the association between the stable isotopes and climate changed considerably between the early 19th and late 20th centuries. The temperature signal in δ¹⁸O was stronger during the recent warm period, whereas the opposite is true for δ¹³C. In δ¹³C, the temperature signal weakened from the early 19th to the late 20th centuries, but an (inverse) precipitation signal evolved indicating that soil moisture conditions additionally limited recent carbon isotope ratios. An attempt to combine the tree-ring proxies in a multiple regression model did not substantially improve the strength of the dominating temperature signal retained in the latewood density data as this proxy already explained a significant fraction of summer temperature variability. Our findings underscore the importance of split calibration/verification approaches including cold and warm periods, and challenge transfer models based on only late 20th century observational data.

Keywords: stable isotopes, maximum latewood density, reconstruction model, Picea abies, Engadin, Alps

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Introduction

Instrumental records provide valuable information on climate variability over the past 100–200 years (Böhm et al., 2001, 2010). To improve our understanding of pre-instrumental climate, reconstructions based on proxy data are needed (Frank et al., 2010; Jones et al., 2009). Among the most widespread proxies are tree-ring width (TRW) and maximum latewood density (MXD) chronologies used to reconstruct annually resolved temperature and hydroclimatic variations at regional (e.g., Büntgen et al., 2016; Cook et al., 2000; Davi et al., 2015; Esper et al., 2007, 2012; Gennaretti et al., 2014; Myglan et al., 2012), continental (e.g., Cook et al., 2015; Luterbacher et al., 2016), and hemispheric scales (e.g., D’Arrigo et al., 2006; Esper et al., 2002; Schneider et al., 2015; Wilson et al., 2016). However, the potential of trees to record additional climate elements including relative humidity, sunshine and cloud cover changes has not been fully explored, and the combination of widely used TRW and MXD chronologies with other tree-ring proxies such as stable isotope ratios, height increments and cell parameters might further improve climate reconstructions (e.g., Bräuning, 2001; Carrer et al., 2016; Fonti & Babushkina, 2016; McCarroll et al., 2003). Only few studies have been conducted evaluating the climatic information recorded in both the classical tree-ring growth proxies, TRW and MXD, together with the stable isotope ratios, δ¹³C and δ¹⁸O (e.g., Esper et al., 2015a; Gagen et al., 2006; Hartl-Meier et al., 2015; Kirdyanov et al., 2008; Treydte et al., 2001).

Tree-ring δ¹³C and δ¹⁸O are controlled by climate through effects on stomatal conductance, photosynthetic rates and source water isotopic signatures (Leavitt, 2010). Other environmental factors such as air pollution or thinning might disturb the link between isotopes and climate (e.g., Saurer et al., 1995; Warren et al., 2001). Meanwhile several isotope/climate calibration studies have been completed (overview in Frank et al., 2015; Treydte et al., 2007), but only few focus on high elevation sites where the classical TRW and MXD growth proxies are known to contain significant temperature signals (e.g., Gagen et al., 2006; Konter et al., 2014; Kress et al., 2010; Treydte et al., 2001, 2006). Disentangling climate signals from species and site specific responses, based on observational data, remains a major challenge in high resolutions paleoclimatology (Rebetz et al., 2003; Treydte et al., 2007, 2009), and compared to the classical tree-ring proxies, little is known about the coherence of stable isotopes with pre–20th century climate data. The majority of isotope-calibration studies focus on the last 100 years (e.g., Hemming et al., 1998; McCarroll & Pawellek, 2001; Saurer et al., 2014; Treydte et al., 2007), and only few include the late 19th century or even longer periods (e.g., Masson-Delmotte et al., 2005; Saurer et al., 2000).

In this paper, we contribute to this issue and analyze the dependency of TRW, MXD, δ¹³C and δ¹⁸O on climate during an early 19th century cold and a late 20th century warm calibration period. The early calibration period (AD 1800–1850) includes the termination of the Little Ice Age characterized by cold conditions at regional (Büntgen et al., 2006) to hemispheric scales (Schneider et al., 2015). According to long instrumental data, annual temperatures were substantially colder (−0.6°C) compared to the second half of the 20th century (Casty et al., 2005). The early calibration period includes some of the coldest Alpine summers of the past 500 years, including the 1816 ‘year without a summer’ forced by a major volcanic eruption in the tropics (Esper et al., 2013) and a period of low solar activity (Dalton Minimum) until the late 1820s (Luterbacher et al., 2004, 2016). The 1840s were characterized by high annual precipitation sums (Casty et al., 2005).

In contrast, the recent calibration period (AD 1946–2000) is characterized by overall warmer conditions, likely including some of the warmest summers of the past millennium (Luterbacher et al., 2016). Summers were particularly warm from 1946–1950 and from 1970–2000, with the latter period accompanied by a decrease in precipitation (Casty et al., 2005). We here consider these two similarly long, cold and warm periods, to (i) assess the climatic signals recorded in TRW, MXD, δ¹³C and δ¹⁸O, (ii) evaluate the temporal changes in signal strength from the early 19th to the late 20th centuries, and (iii) test the effects of combining tree-ring proxies to improve reconstruction skill. The study is conducted at a high elevation Picea abies site in the Swiss Engadin in the vicinity of long instrumental temperature and precipitation data covering the past 200+ years. In addition, we consider sunshine hour and relative air humidity data over the recent calibration period to compare climate signals over the late 20th century.

Data and Methods

Tree-ring proxies

The tree-ring sampling site is located in the Upper Engadin in the Swiss Alps at the northern slope of Piz Mezzaun in proximity to the Albula Pass (Fig. 1). The Engadin is situated in the rain shadow of surrounding mountain ranges and is classified as an “inner-alpine dry valley”. Mild summers, cold winters, low humidity and above-average sunshine characterize the local climate. Mean annual and summer temperatures recorded at the nearby station in Sils Maria (1961–1990) are 1.8°C and 10.5°C, respectively.
Annual precipitation equals 980 mm and includes a minor summer maximum of 335 mm. Precipitation primarily originates from west- to south-westerly air masses entering over the Maloja Pass.

Two core samples from 36 spruce trees of different age classes were collected (Table 1). The trees are situated in 1900 m a.s.l. near the species’ distribution limit on well drained soils from acidic bedrock (gneiss) on a 40% inclined slope. The plant community consists of an unmanaged, open (40% tree cover) conifer forest including Larix decidua, Pinus cembra and Picea abies. Forest understory is dominated by Vaccinium myrtillus, Rhododendron ferrugineum and Calamagrostis villosa. Herb layer coverage is ~80%, shrub coverage is ~10%.

We measured TRW on the 72 core samples using the TSAP software (Rinn, 2003) and crossdated the series visually and using the software COFECHA (Holmes, 2000). Fourteen of the older (~250 years) trees were selected for MXD measurement following standard X-ray densitometry procedures (Schweingruber et al., 1978). Among these, another four trees, from which two additional core samples were collected, were selected for isotope analysis. We used the latewood of these samples for stable isotope measurements to avoid carry-over effects of carbohydrate reserves, and discarded the innermost 30 rings of each tree to avoid potentially biasing effects due to juvenile discrimination trends (Leavitt, 2010; but see also Esper et al., 2010; Helama et al., 2015). The latewood samples were pooled using a Retsch mill (Leavitt & Long, 1984; Treydte et al., 2001) and cellulose extracted following standard procedures (Brenninkmeijer, 1983; McCarroll & Loader, 2004). Samples were combusted to CO₂ for carbon isotope measurement and pyrolized to CO for oxygen isotope measurement using an elemental analyzer coupled to a mass spectrometer. In some years, insufficient cellulose was extracted, causing gaps in the δ₁³C (1809, 1825, 1845, 1966, 1974, 1982) and δ₁⁸O chronologies (1800, 1840, 1966, 1974, 1992).

All isotopic values are given in δ notation relative to a standard in per mill \( \delta = \left( \frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right) \cdot 1000 \) (Leavitt, 2010). δ₁³C is the ratio of ¹³C to ¹²C from the combustion of pooled latewood samples and a reference fossil belemnite from the Pee Dee Formation of the upper Cretaceous in South Carolina. δ₁⁸O is the ratio of ¹⁸O to ¹⁶O from latewood samples relative to the Pee Dee Formation standard.

Table 1. Tree-ring proxy summary statistics for the 1800–1850 and 1946–2000 periods. TRW and MXD data are 300-year spline detrended, δ₁³C corrected for changes in the atmosphere due to fossil fuel combustion.

<table>
<thead>
<tr>
<th></th>
<th>TRW</th>
<th>MXD</th>
<th>δ₁³C</th>
<th>δ₁⁸O</th>
</tr>
</thead>
<tbody>
<tr>
<td>No. of trees</td>
<td>36</td>
<td>14</td>
<td>4</td>
<td>4</td>
</tr>
<tr>
<td>No. of cores</td>
<td>72</td>
<td>29</td>
<td>8</td>
<td>8</td>
</tr>
<tr>
<td>1800–1850</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>No. of years used in correlation</td>
<td>51</td>
<td>51</td>
<td>48</td>
<td>49</td>
</tr>
<tr>
<td>Inter-series correlation</td>
<td>0.28</td>
<td>0.44</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>EPS</td>
<td>0.93</td>
<td>0.93</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>1946–2000</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>No. of years used in correlation</td>
<td>55</td>
<td>55</td>
<td>51</td>
<td>51</td>
</tr>
<tr>
<td>Inter-series correlation</td>
<td>0.32</td>
<td>0.42</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>EPS</td>
<td>0.96</td>
<td>0.95</td>
<td>–</td>
<td>–</td>
</tr>
</tbody>
</table>

Fig. 1. Location of the *Picea abies* sampling site (triangle) in the Engadin, Switzerland. Circles indicate the meteorological stations in Davos (46.80°N, 9.82°E), Sils Maria (46.42°N, 9.76°E), and Milan (45.47°N, 9.17°E), as well as the GNIP station in Grimsel (46.56°N, 8.34°E)
standard mean ocean water. Measurement accuracy was estimated considering the standard deviation from commercial cellulose at ±0.2‰ for carbon and ±0.15‰ for oxygen isotope ratios. We measured latewood cellulose $\delta^{13}C$ and $\delta^{18}O$ over the periods 1800–1850 and 1946–2000.

The TRW and MXD measurement series were standardized by power transforming the data (Cook & Peters, 1997) and calculating residuals from 300-year fixed splines (Fig. 2). Inter-series correlations were slightly lower among the detrended TRW series ($r = 0.28$ and 0.32 over the early and late calibration periods) compared to MXD ($r = 0.44$ and 0.42).

![Fig. 2. Tree-ring proxies.](image)

Fig. 2. Tree-ring proxies. **a**, *Picea abies* TRW series after removing age trend using 300-year splines. Black curve is the bi-weight robust mean chronology. Bottom panel shows the temporally changing sample replication. **b**, Same as in **a**, but for MXD. Panels **c-f** show the TRW, MXD, $\delta^{13}C$, and $\delta^{18}O$ chronologies over the 1800–1850 and 1946–2000 periods. Gaps in the $\delta^{13}C$ and $\delta^{18}O$ chronologies result from insufficient latewood cellulose extraction.
However, calculation of the expressed population signal (EPS; Wigley et al., 1984) revealed that both proxies exceed the widely recognized EPS = 0.85 threshold used to identify periods over which tree-ring proxy records retain meaningful information on past climate variability (Table 1). Mean chronologies of the detrended TRW and MXD series were used for comparison with the stable isotope series and instrumental data. For $\delta^{13}C$, we corrected these data for changes in the atmospheric CO$_2$ isotope ratio attributable to fossil fuel combustion (Francey et al., 1999) to avoid spurious correlations due to artificial long-term trends (Treydte et al., 2009).

**Observational data and calibration**

For proxy calibration, we used the long temperature station record from Milan ($r_{1946–2000} = 0.82$ with the shorter Sils Maria summer temperature record) $\sim 120$ km southwest of the tree-ring sampling site (Böhm et al., 2001), and the long precipitation record from the nearest grid point of a $0.5^\circ \times 0.5^\circ$ network (see Casty et al., 2005 for covariance assessments). In addition to these long records, we used sunshine hour and relative humidity data from the nearby Davos climate station (1590 m a.s.l.) for calibration over the 1946–2000 period, as well as $\delta^{18}O$ in precipitation from the GNIP (Global Network of Isotopes in Precipitation) station in Grimsel (1950 m a.s.l.) over the 1971–1992 period.

Climate correlations were calculated using the (i) original, and (ii) high-pass filtered tree-ring proxy and instrumental data over the early 1800–1850 (only temperature and precipitation) and late 1946–2000 calibration periods (1971–1992 for precipitation $\delta^{18}O$). “Original” data refers to the 300-year spline detrended TRW and MXD chronologies, the corrected $\delta^{13}C$ chronology, and the untreated $\delta^{18}O$ chronology, as well as the monthly and seasonal climate data. For assessments in the high frequency domain, all proxy and instrumental data were high-pass filtered by calculating residuals from a 5-year Kernel filter (Gasser & Müller, 1984). Significance estimates were adjusted for changing degrees of freedom due to varying serial correlations (Trenberth, 1984).

To facilitate the development of a reconstruction model based on multiple predictors, we first tested the climate sensitivity of TRW, MXD, $\delta^{13}C$ and $\delta^{18}O$ simultaneously using Redundancy Analysis (RDA), a non-symmetric method summarizing the redundant variance among tree-ring parameters explained by the climate variables (van den Wollenberg, 1977). We ran a series of RDAs using standardized climate variables and estimate significance based on 1000 re-samplings within a Monte Carlo approach (ter Braak & Smilauer, 2002). We then established transfer functions for the significant climate variables explaining most of the tree-ring proxies’ variance. Ordinary least-squares and partial least squares regressions are tested (Hastie et al., 2001) using the PLS and CAR R-packages (Fox, 2002; R Core Team, 2014), and predictors retained leading to a $>5\%$ reduction of the root mean squared error (RMSE) (Birks, 1995). Using leave-one-out validation, a technique based on subsampling and rebuilding models using n−1 data, we selected a ‘minimal adequate model’ (Crawley, 1993) reaching the highest coefficient of determination ($R^2$) and lowest RMSE.

**Results**

**Inter-proxy correlations**

Cross-correlations among the four tree-ring proxies over the early and late calibration periods ranged from $r_{1946–2000} = -0.20$ (TRW-$\delta^{13}C$) to $r_{1946–2000} = 0.41$ (MXD-$\delta^{18}O$; Table 2). The latter correlation even increased to $r = 0.49$ if the high-pass filtered data were considered (values in parenthesis in Table 2). The correlation values changed considerably between the early and late calibration periods, except perhaps for TRW versus MXD. Most notably, the correlation between $\delta^{13}C$ and MXD shifted from $r_{1900–1950} = -0.36$ to $r_{1946–2000} = -0.08$ indicating a complete loss of common variance from the early cold to the late warm period. Low correlations between TRW and stable isotopes are partly explained by the sampling scheme, as TRW is typically dominated by earlywood whereas the isotopes ratios were obtained from latewood produced.

Table 2. Correlation coefficients among tree-ring proxies over early (1800–1850) and late (1946–2000) calibration periods. Values in parentheses are calculated using 5-year high-pass filtered chronologies. Bold values are significant at $p<0.05$, underlined values at $p<0.01$.

<table>
<thead>
<tr>
<th>Period</th>
<th>TRW</th>
<th>MXD</th>
<th>$\delta^{13}C$</th>
<th>$\delta^{18}O$</th>
</tr>
</thead>
<tbody>
<tr>
<td>1800–1850</td>
<td></td>
<td></td>
<td>0.20 (0.20)</td>
<td>0.21 (0.23)</td>
</tr>
<tr>
<td></td>
<td>TRW</td>
<td></td>
<td>0.36 (0.22)</td>
<td>0.25 (0.03)</td>
</tr>
<tr>
<td>1946–2000</td>
<td>0.29 (0.35)</td>
<td>MXD</td>
<td>0.08 (0.11)</td>
<td>0.41 (0.49)</td>
</tr>
<tr>
<td></td>
<td>$\delta^{13}C$</td>
<td>0.00 (0.00)</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
TRW and MXD climate response

Both TRW and MXD are characterized by a dominating warm season temperature signal (Fig. 3). The signal is substantially stronger in MXD, though in both growth proxies it is temporally stable, i.e. similar between the early and late calibration periods. In TRW, the signal is stronger in the high-pass filtered data.

The TRW chronology correlated positively with May-July temperatures \(r_{1800-1850} = 0.33\), \(r_{1946-2000} = 0.34\) reaching maximum values in the high-pass filtered data with June-July temperatures \(r_{1800-1850} = 0.56\), \(r_{1946-2000} = 0.53\); Table 3 and Fig. 4). Besides temperature, other climate parameters affected TRW including March-April precipitation during the early cold period \(r_{1800-1850} = -0.33\), as well as May relative humidity \(r_{1946-2000} = -0.30\) and May sunshine \(r_{1946-2000} = 0.30\) during the late warm period. Note that humidity and sunshine are also inter-related (e.g., \(r = -0.49\) during May).

The MXD chronology correlated best with July-September temperatures \(r_{1800-1850} = 0.64\), \(r_{1946-2000} = 0.62\), Fig. 4). Recent sunshine and relative humidity data also correlated significantly, but overall were of lesser importance to cell wall growth \(r = 0.48\) and \(-0.48\), respectively). During the recent period, an additional July-September moisture signal is retained \(r_{1946-2000} = -0.30\). This response is likely related to the increased co-variance between temperature and precipitation typically exceeding \(r = -0.30\) during the summer months in the European Alps (Casty et al., 2005).

δ\(^{13}\)C climate response

The δ\(^{13}\)C chronology correlated significantly with multiple climate parameters, ranging from \(r = -0.30\) to \(r = 0.56\), including a temporal strengthening of the precipitation signal (Fig. 3). July-August is the most important season for carbon isotope fractionation with the closest relationship recorded with recent sunshine hour data \(r_{1946-2000} = 0.56\). Temperature and precipitation also influenced δ\(^{13}\)C, but their relevance changed between the two calibration periods. Whereas temperature appeared to be the dominating forcing during the early period \(r_{1800-1850} = 0.49\), its impact is reduced in the recent period \(r_{1946-2000} = 0.29\). A reversed tendency was revealed for precipitation, with coefficients being more negative in the recent \(r_{1946-2000} = -0.44\), June-August) compared to the early period \(r_{1800-1850} = -0.27\). These changes indicate δ\(^{13}\)C sensitivity to temperature was enhanced in cooler conditions, whereas in the warmer late 20th century the proxy more closely reflected plant water status. The relationships found for δ\(^{13}\)C did not vary markedly in the higher

<table>
<thead>
<tr>
<th>Proxy</th>
<th>Parameter</th>
<th>Season</th>
<th>1800–1850</th>
<th>1946–2000</th>
</tr>
</thead>
<tbody>
<tr>
<td>TRW</td>
<td>Temperature</td>
<td>Jun-Jul</td>
<td>0.56*</td>
<td>0.53*</td>
</tr>
<tr>
<td></td>
<td>Precipitation</td>
<td>Mar-May</td>
<td>-0.33</td>
<td>-0.06</td>
</tr>
<tr>
<td></td>
<td>Sunshine</td>
<td>Jun-Jul</td>
<td>-</td>
<td>0.35*</td>
</tr>
<tr>
<td></td>
<td>Rel. humidity</td>
<td>May</td>
<td>-</td>
<td>-0.30</td>
</tr>
<tr>
<td>MXD</td>
<td>Temperature</td>
<td>Jul-Sep</td>
<td>0.64*</td>
<td>0.62</td>
</tr>
<tr>
<td></td>
<td>Precipitation</td>
<td>Jul-Sep</td>
<td>-0.02</td>
<td>-0.30</td>
</tr>
<tr>
<td></td>
<td>Sunshine</td>
<td>Jul-Sep</td>
<td>-</td>
<td>0.48</td>
</tr>
<tr>
<td></td>
<td>Rel. humidity</td>
<td>Jul-Sep</td>
<td>-</td>
<td>-0.48</td>
</tr>
<tr>
<td>δ(^{13})C</td>
<td>Temperature</td>
<td>Jul-Aug</td>
<td>0.43</td>
<td>0.28</td>
</tr>
<tr>
<td></td>
<td>Precipitation</td>
<td>Jun-Aug</td>
<td>-0.27</td>
<td>-0.44</td>
</tr>
<tr>
<td></td>
<td>Sunshine</td>
<td>Jul-Aug</td>
<td>-</td>
<td>0.56</td>
</tr>
<tr>
<td></td>
<td>Rel. humidity</td>
<td>Jul-Aug</td>
<td>-</td>
<td>-0.45</td>
</tr>
<tr>
<td>δ(^{18})O</td>
<td>Temperature</td>
<td>Aug</td>
<td>0.28</td>
<td>0.46</td>
</tr>
<tr>
<td></td>
<td>Precipitation</td>
<td>Aug</td>
<td>-0.35</td>
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</tr>
<tr>
<td></td>
<td>Sunshine</td>
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<td>-</td>
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<tr>
<td></td>
<td>Rel. humidity</td>
<td>Jul-Aug</td>
<td>-</td>
<td>-0.52*</td>
</tr>
</tbody>
</table>
Fig. 3. Pearson correlations between tree-ring proxies and monthly meteorological data from (previous-year) October to September, and the combination of months reaching maximum correlations (seasonal correlations exceeding \( p < 0.05 \)) are shown. Results for temperature (black) and precipitation (grey) shown in the left (1800–1850) and middle (1946–2000) columns. Right column panels show results for sunshine (black) and relative humidity (grey) over the 1946–2000 period. Horizontal lines indicate \( p < 0.05 \) significance levels.
frequency domain, except for the temperature response being stronger in the recent calibration period ($r_{1946-2000} = 0.39$).

### $\delta^{18}O$ climate response

The latewood $\delta^{18}O$ data contained a significant late summer temperature signal, but this signal was weaker during the early calibration period ($r_{1800-1850} = 0.28$) compared to the late 20th century ($r_{1946-2000} = 0.46$, Fig. 4). The temperature signal was also weaker when considering high-pass filtered data, where relative humidity and sunshine appeared to be the main drivers of recent inter-annual $\delta^{18}O$ variations (Table 3). However, the $\delta^{18}O$ temperature signal is additionally supported by a comparison with the GNIP station.

Fig. 4. Tree-ring proxies (black) shown together with the best correlating climate variables (grey) over the 1800–1850 and 1946–2000 calibration periods. Sunshine hour data were only available over the late calibration period (panel c). TRW and June-September temperature data were 5-year high-pass filtered (panel a). All records are scaled to zero mean and unit variance.
Combining tree-ring proxies

Using RDA we found that May-September temperatures explained most variance of the combined tree-ring dataset over the recent 1946–2000 calibration period (15.9%, p < 0.05). July-September sunshine hours explained 12.6%, July-September relative humidity 9.5%, and previous year June-March precipitation 7.7%. During 1800–1850, March-November temperature accounted for 24.5% and May-July precipitation for 13.4% of the combined proxy variance. As temperature explained most variance, we joined the early and late calibration period data. In this approach, RDA revealed July-September temperature to account for the largest fraction of proxy variance (16.8%) including 18.7% during 1800–1850 and 15.8% during 1946–2000 periods. Considering this season, we developed a proxy-based temperature model using multiple ordinary least-squares regression explaining 46% of July-September instrumental temperature variability (44.3% using partial least-squares regression, RMSE = 0.75–0.77°C). According to type-II variance analysis (Fox, 2002), only MXD and $\delta^{13}$C significantly explained July-September temperature variability in this regression model (Fig. 6).

Discussion

Our analysis shows that TRW, MXD, $\delta^{13}$C and $\delta^{18}$O contain relevant information on the variability of several meteorological parameters. TRW is mainly influenced by temperature fluctuations in the early to mid growing season (May-July), whereas high and late summer conditions (July-September) impact MXD and the tree-ring stable isotopes. We here focus on the changing climatic controls of the four climate proxies during the early and late calibration periods.
Temperature and sunshine

In the high elevation *Picea abies* site considered here, TRW and MXD are primarily controlled by temperature displaying temporally stable relationships. The temperature signal derives from the fact that these proxies are integrative products of the trees’ photosynthesis that, in turn, is directly regulated by air temperature and irradiance in high elevation sites (Frank & Esper, 2005). TRW and MXD exhibit differing sensitivities to varying frequencies of temperature change. Higher frequency temperature fluctuations from late spring to early summer are most significant to TRW. It is well established that temperature variations in the early growing season regulate cell division and enlargement (Tranquillini, 1979), and that higher temperatures stimulate cambial activity resulting in wider rings (Kirdyanov et al., 2003). This connection is even tighter for the proxy reflecting cell wall thickening (MXD) in thermally limited environments (Briffa et al., 1998; Esper et al., 2012, 2015b; Frank & Esper, 2005; Schneider et al., 2015). In contrast to TRW, MXD showed the highest sensitivity using the original (not high-pass filtered) data. Anatomical studies revealed MXD variability is better explained by changes in growing season length than changes in seasonal mean temperatures (Moser et al., 2010; Kirdyanov et al., 2003). Higher summer temperatures promote the synthesis of cell wall components, but limit the duration of tracheid development, resulting in relatively minor net effects on xylem densities (Antonova &斯塔索va, 1997).

Our analysis indicates tree-ring δ¹³C and δ¹⁸O to be influenced by temperature as well. Yet in comparison to TRW and MXD, the strength of temperature control varies considerably between early 19th and late 20th centuries. Stable isotope ratios are regulated by temperature via processes that differ fundamentally from the tree-ring growth proxies. The oxygen isotope ratio retained in latewood cellulose combines the isotopic signature of the source water with the signature from evaporative enrichment of leaf water regulated by the plant’s transpiration demand (Dongmann et al., 1974). The significant correlations between rainfall and tree-ring cellulose oxygen isotopes reported here demonstrate that, at our high elevation site, latewood δ¹⁸O is mainly recording the isotopic composition of precipitation during the growing season, and can thus be considered as a proxy of condensation temperature. Similar associations have been reported for spruce (Anderson et al., 1998; Jäggi et al., 2003) and other species from central European sites (Raffalli-Delerce et al., 2004; Saurer et al., 2000). Using diurnally resolved data, maximum daytime air temperatures during the growing season were shown to be the key driver of δ¹⁸O in fir trees from Central Switzerland (Rebetez et al., 2003). While the temperature sensitivity of δ¹⁸O is slightly more consistent compared to δ¹³C, the signal is still much tighter in the warm 20th century calibration period. This increased temperature sensitivity likely originates from altered fractionation processes in an overall warmer environment: higher temperatures cause higher δ¹⁸O in precipitation, enhanced evaporation enriches δ¹⁸O in soil water, and higher transpiration rates increase δ¹⁸O in leaf water (Raffalli-Delerce et al., 2004).

The temperature signal in δ¹³C is substantially increased during the cooler and wetter summers of the first half of the 19th century, whereas in the warmer late 20th century precipitation becomes more relevant. We hypothesize that during the less favorable thermal conditions of the early 19th century, photosynthetic rates (forced by temperature and irradiance) controlled fractionation, while during the late calibration period, stomatal conductivity (forced by soil moisture and air humidity) controlled the discrimination against ¹³C. This would also explain the stronger correlation with precipitation in the late period (discussed below).

Sunshine hours are often disregarded in calibration studies as this parameter generally correlates closely with temperature (e.g., r_{1946-2006} = 0.42 for June-September). Nevertheless, sunshine directly affects wood density and carbon isotopes, and anatomical studies showed that a decrease in light intensity and duration results in a decline in tracheid dimension and lighter latewood (Yasue et al., 2000). Sunshine hours were here identified as the leading climatic factor controlling δ¹³C variability during the recent calibration period. The association likely arises from direct effects on photosynthetic and soil evaporation rates (Farquhar et al., 1989). Similar findings have been reported for δ¹³C in latewood cellulose from *Pinus sylvestris* growing in high latitude environments (McCarron et al., 2003). Our study also reveals sunshine effects on δ¹⁸O particularly in the high frequency domain and during the cold season. While the cold season signal remains fairly unclear, we generally expect δ¹⁸O enrichment in leaf water during sunny days to mask potential source water signals at inter-annual scales.

Precipitation and relative humidity

As water availability is not a limiting factor of photosynthesis at the study site, its influence on the growth proxies appears to be restricted. We found spring precipitation to be negatively correlated with TRW, possibly by delaying snowmelt and therefore shortening the growing season (Kirdyanov et al., 2003). Adverse effects of increased cloudiness on photosynthetic activity are likely the reason for slightly negative correlations between summer...
precipitation and MXD (Yasue et al., 2000). Interestingly, relative humidity, which at this high elevation site may be considered as a proxy of overcast conditions, shows an even stronger negative connection with MXD.

$\delta^{13}C$ is the only proxy that appears to be directly affected by summer precipitation through soil moisture effects on stomatal regulation (Farquhar et al., 1989; Warren et al., 2001). The moderate correlation with precipitation ($r \leq -0.46$), compared to more continental sites in the Alps reaching $r = -0.75$ (Treydte et al., 2001), seems to be related to balanced soil moisture tensions buffering stomatal activity in our sampling site. Other work showed the magnitude of $\delta^{13}C$ climate signals to vary along environmental gradients. Whereas oak trees growing in oceanic conditions contain weaker signals not exceeding $r = 0.4$ (Raffalli-Delerce et al., 2004), Scots pine from high latitude and temperature limited environments reach correlations ranging from $r = 0.58$ to 0.78 (McCarroll et al., 2003). Our results indicate that the sensitivity of $\delta^{13}C$ to temperature and precipitation may not only vary in different bioclimatic belts, but also through time: As with temperature, the association between precipitation and $\delta^{13}C$ changes from the early 19th to the late 20th century.

The relatively weak link between $\delta^{18}O$ and precipitation is not fully surprising considering the good availability of soil water mitigating the trees’ transpiration demand. Nevertheless, when considering higher frequency variations, the thermal signal retained in precipitation $\delta^{18}O$ is much weaker, whereas the link to relative humidity (and sunshine, see above) strengthens, reaching significance. This effect seems to be a consequence of a stronger variability in leaf transpirative enrichment recorded in prevailingly wet and dry periods. The importance of summer precipitation and relative humidity on oxygen isotope variability was also reported for Abies alba, a drought-sensitive species sampled at an alpine site (Saurer et al., 2000). Winter precipitation acted as a driver of $\delta^{18}O$ variability in juniper trees in semi-arid high mountain sites in northern Pakistan (Treydte et al., 2006), and in species with highly responsive stomata, such as Pinus halepensis, the link of oxygen isotope ratios to the plant’s water status is even tighter (Ferrio & Voltas, 2005).

**Potential for a multi-proxy approach**

In locations where seasonal temperature or water stresses are small, classical tree-ring growth proxies do not contain adequate quantitative climate information, whereas reconstructions based on multiple proxies might provide more suitable results (Raffalli-Delerce et al., 2004). In our treeline site, combining temperature sensitive proxies did not substantially improve the strength of the linear relationship that could be obtained using a single proxy. This is because MXD alone contains a rather significant and time-invariant mid summer temperature signal ($r \geq 0.64$). Nevertheless, reconstructions integrating multiple proxies based on relatively independent physiological mechanisms likely provide more reliable estimates of past climate variability (Bräuning, 2001; Raffalli-Delerce et al., 2004). Since the physiological drivers of carbon and oxygen isotope variations differ, these proxies were shown to provide complementary estimates of climate variability (Ferrio & Voltas, 2005).

The minor difference between multiple- and single-proxy based models suggest that common signals due to shared eco-physiological factors are limited, even if substantial co-variance among the chronologies was recorded. This conclusion is supported by the cross-correlation results between $\delta^{13}C$, $\delta^{18}O$ and MXD during the early calibration period, when these proxies share temperature as the main controlling factor. The $\delta^{18}O$ and MXD chronologies also correlate significantly in the late calibration period, during which the sensitivity of oxygen isotope ratio to temperature even increased. Despite the fact that both $\delta^{13}C$ and $\delta^{18}O$ record environmental information via stomatal regulation (Farquhar et al., 1982), temporally consistent relationships between these stable isotope ratios are lacking. Weak associations between carbon and oxygen isotope chronologies are also reported from Pinus halepensis in semiarid to humid Mediterranean environments (Ferrio & Voltas, 2005) and from Pinus sylvestris in northern European sites (overview in Treydte et al., 2007). Interestingly, $\delta^{13}C$ and $\delta^{18}O$ are more closely coupled during warmer and dryer periods, when stomatal conductance seems to be more influential, particularly after emphasizing inter-annual variability using high-pass filtered data.

**Conclusions**

We present the first systematic analysis of climate signals in tree-ring stable isotopes and growth proxies during distinctly cold and warm calibration periods. Our results indicate that $\delta^{13}C$ and $\delta^{18}O$, together with TRW and MXD, contain substantial information on inter-annual climate variations in a treeline site in the Central Alps. Temperature, sunshine hours, precipitation and relative humidity all influence various fractions of the tree-ring growth and stable isotope proxies. Yet, in this subalpine environment, overall greater correlations ($r \approx 0.6$) are obtained with warm season temperature and sunshine data. Information on the inter-annual variability of summer precipitation is contributed by the $\delta^{13}C$ data, though
correlation coefficients are likely too low for reliable paleoclimatic reconstructions.

When evaluating the temporal consistency of climate signals, the tree-ring growth proxies showed more stable responses. In contrast, $\delta^{13}C$ is more temperature sensitive in the cold calibration period and more precipitation sensitive in the warm calibration period. These results are in line with the predominant physiological process discriminating against the heavy $^{13}C$. The $\delta^{18}O$ series mainly act as a proxy of the isotopic composition of summer rain, and therefore of local condensation temperatures. However, in the warmer 1946–2000 calibration period, higher precipitation $\delta^{18}O$ and increased evapotranspiration contributed to an enhanced signal recorded in the tree-ring cellulose. While an increasing sensitivity along environmental gradients has been described for carbon and oxygen isotope data (overview in Frank et al., 2015; Saurer et al., 2014; Treydte et al., 2007), our results clearly demonstrate that temporarily varying climate signals must be taken into account when considering long isotopic chronologies for reconstruction purposes. The European Alps are certainly a key area to further investigate these relationships.

The temperature sensitivity of various tree-ring proxies allowed the development of a reconstruction based on multiple regression explaining up to 46% of the inter-annual variance of this factor. However, at our high elevation sampling site, this approach does not notably improve the temperature signal compared to using only MXD, as this proxy alone accounts for the majority of reconstructed variance. Nonetheless, the different tree-ring proxies record climate variability based on relatively independent physiological processes, and comparing these relationships will likely improve the interpretation of climate reconstructions.

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