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Research paper

Uniform climate sensitivity in tree-ring stable isotopes across species and sites in a mid-latitude temperate forest

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Tree-ring stable isotopes, providing insight into drought-induced eco-physiological mechanisms, are frequently used to reconstruct past changes in growing season temperature and precipitation. Their climatic response is, however, still not fully understood, particularly for data originating from non-extreme, mid-latitude environments with differing ecological conditions. Here, we assess the response of $\delta^{13}\text{C}$, $\delta^{18}\text{O}$ and tree-ring width (TRW) from a temperate mountain forest in the Austrian pre-Alps to climate and specific drought events. Variations in stem growth and isotopic composition of Norway spruce, common beech and European larch from dry, medium and moist sites are compared with records of sunshine, temperature, moisture, precipitation and cloud cover. Results indicate uniform year-to-year variations in $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ across sites and species, but distinct differences in TRW according to habitat and species. While the climate sensitivity of TRW is overall weak, the $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ chronologies contain significant signals with a maximum sensitivity to cloud cover changes ($r = -0.72$ for $\delta^{18}\text{O}$). The coherent inter-annual isotopic variations are accompanied by substantial differences in the isotopic signatures with offsets up to $\sim 3\text{‰}$ for $\delta^{13}\text{C}$, indicating species-specific physiological strategies and varying water-use efficiencies. During severe summer drought, beech and larch benefit from access to deeper and moist soils, allowing them to keep their stomata open. This strategy is accompanied by an increased water loss through transpiration, but simultaneously enables enhanced photosynthesis. Our findings indicate the potential of tree-ring stable isotopes from temperate forests to reconstruct changes in cloud cover, and to improve knowledge on basic physiological mechanisms of tree species growing in different habitats to cope with soil moisture deficits.

Keywords: carbon isotopes, dendroecology, drought, oxygen isotopes, radial growth, tree physiology.

Introduction

Temperate forests are of importance to society and economies since these ecosystems constitute a large fraction of utilized biomass (FOREST EUROPE 2011). Forest ecosystem functioning and productivity, however, are expected to be affected by

intensified climate anomalies such as the summer heat wave in 2003 (Luterbacher et al. 2004, Schär et al. 2004, Rebetez et al. 2006), and even more importantly by co-occurring drought events (Fuhrer et al. 2006, Straile and Stenseth 2007). More detailed knowledge about the physiological processes

underlying climate-induced growth changes of different tree species, and their varying capabilities to cope with drought events, is required for the estimation of future forest adaption strategies to climate change.

At sites located at the distribution limit of forest ecosystems, tree growth is usually constrained by one climatic factor while in temperate forests, the delineation of growth responses to a single controlling factor often fails (Friedrichs et al. 2008, Kress et al. 2010). Reliable hydro-climatic reconstructions based on radial growth measures are thus mostly restricted to moisture-sensitive sites (Wilson et al. 2005, Esper et al. 2007). In the moist mid-latitudes, comprehensive dendroecological investigations based on annual stem increments have been performed to study the growth response of the most important native European tree species to climate and particularly drought events (Affolter et al. 2010, Zang et al. 2011, 2014, Hartl-Meier et al. 2014a, 2014b). While these studies have focused on radial growth only, additional information on the physiological responses of trees can be inferred from stable isotopes in tree rings (Gessler et al. 2014 and references therein).

Stable carbon ($\delta^{13}\text{C}$) and oxygen ($\delta^{18}\text{O}$) isotopes in tree rings differ from the classical dendrochronological variables as they reflect more directly the plant physiological response to climate and other environmental variables rather than net tree growth (Treydte et al. 2007, 2014, Gessler et al. 2013, 2014). $\delta^{13}\text{C}$ values depend on factors affecting the photosynthetic uptake of CO_2 and are mainly controlled by stomatal conductance and the rate of carboxylation during photosynthesis (Farquhar et al. 1989). $\delta^{18}\text{O}$ values are constrained by the isotopic ratio of the source water (Roden et al. 2000) and locally integrate the stomatal response to vapour pressure deficit via leaf water enrichment, coupled with transpiration (Yakir and DeNiro 1990, Barbour et al. 2004). These factors controlling isotopic fractionation are closely related to meteorological variables. Thus, stable isotopes can provide information on past precipitation and drought variations in regions where tree-ring width (TRW) and maximum late wood density (MXD) are mainly driven by temperature (Treydte et al. 2001, Kirilyanov et al. 2008, Kress et al. 2010), or contain information on climate variability at temperate sites with relatively weak signals recorded in TRW and MXD (Masson-Delmotte et al. 2005, Saurer et al. 2008, 2012, Haupt et al. 2011, Rinne et al. 2013).

Despite the dendroecological inferences that can be drawn from tree-ring stable isotopes, we still lack knowledge on how climatic signals, and their strengths, may vary among species growing in similar temperate climatic conditions but with varying access to soil water. Norway spruce (*Picea abies* [L.] Karst.), European larch (*Larix decidua* Mill.) and common beech (*Fagus sylvatica* L.) differ in their strategies of water uptake and, hence, in their capacity to cope with drought. Spruce is an intermediately shade-tolerant species widely distributed across the Alps and sensitive to summer water deficits (Ellenberg 2009, Lebourgeois

et al. 2010, Zang et al. 2011, Zang 2012, Lévesque et al. 2013, Pretzsch et al. 2013) at least below the montane elevation belt (Hartl-Meier et al. 2014a, 2014b). As an evergreen species with a shallow root system, it relies upon internally stored and superficial soil water supplies (Tranquillini 1976, Valentini et al. 1994). European larch is a pioneer and shade-intolerant deciduous conifer in mid-to-high elevations (Ellenberg 2009) capable of tolerating summer drought in lower montane elevations (Hartl-Meier et al. 2014a). It develops deep root systems accessing soil water pools even in extended dry periods (Tranquillini 1976, Valentini et al. 1994). Common beech is the most abundant broadleaf tree species in Central Europe (Dittmar et al. 2003). It is less drought sensitive than spruce (Zang et al. 2011, 2014, Hartl-Meier et al. 2014a), as it reaches deeper soil regions containing water throughout sustained drought periods (Pretzsch et al. 2013).

Here, we present $\delta^{13}\text{C}$, $\delta^{18}\text{O}$ and TRW chronologies of Norway spruce, European larch and common beech from three sites in the mid-latitudes of Europe. We assess the response of these tree species to climate and severe drought events with respect to differences in site moisture and species-specific strategies to cope with drought. Our objectives are twofold: (i) testing the performance of $\delta^{13}\text{C}$, $\delta^{18}\text{O}$ and TRW from different species growing together under different soil moisture conditions in temperate conditions to record climate information; and (ii) providing insight into the physiological mechanisms driving both the long-term response to climate and the short-term response to specific drought events. To accomplish these objectives we study: (i) site- and species-specific differences and coherences of the chronologies; (ii) the response of these chronologies to different climate variables including sunshine duration, temperature, Thornthwaite's (1948) moisture index, precipitation and cloud cover; and (iii) their response to extreme drought events. The combined information on tree growth and physiology should help to assess the potential of different tree species from temperate sites to adapt to climate change.

Materials and methods

Study area and sampling design

Our study area is the long-term ecosystem monitoring site 'LTER Zöbelboden' (N47°50'25", E14°26'30", Figure 1a) (<http://www.umweltbundesamt.at/im>, July 2014, date last accessed) at 880–900 m above sea level in the northern part of the Austrian National Park 'Northern Limestone Alps'. The climatic conditions are characterized by high annual precipitation (~1370 mm year⁻¹) and a seasonal temperature range of 18.5 °C with a mean annual temperature of 7 °C (all data referring to the 1971–2000 period).

Ten dominant spruce, larch and beech trees were selected at a south-facing slope, a north-facing slope and a plateau site (hereafter termed South, North and Plateau; Figure 1b). Note that larch is missing on the dry, south-exposed site.

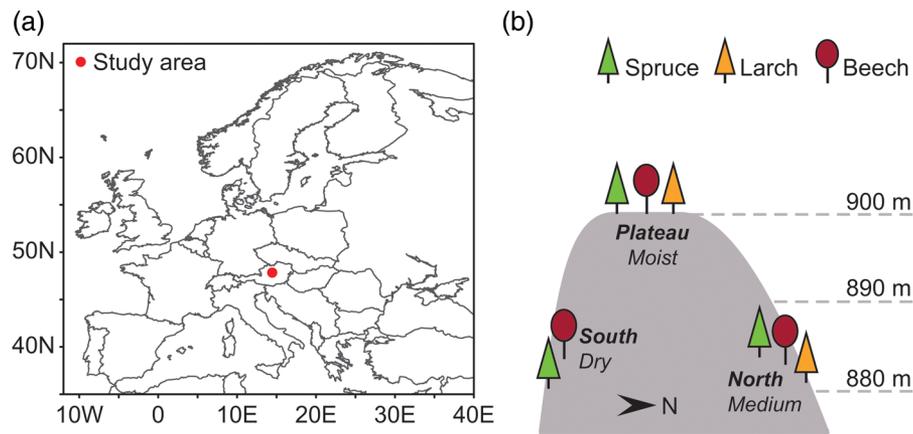


Figure 1. Study area 'LTER Zöbelboden' in Austria (a) and sampling design (b). At each site 10 individuals per species were sampled. All 10 trees were used for TRW measurements, and eight trees were used for carbon and oxygen stable isotope measurements. Micro-habitats were differentiated according to site exposure to dry, moist and medium soil conditions (see the text and Table 1). Note that the dry, south-exposed site is composed of spruce and beech only, i.e., larch is missing here.

Table 1. Site characteristics.

Site/ exposure	Moisture conditions	Slope (%)	Soil depth (cm)	Altitude (m a.s.l.)	Soil type	Forest type
South	Dry	100	28	880–890	Lithic and Rendzic Leptosols	Beech-dominated forest
North	Medium	25	52	880–890	Lithic and Rendzic Leptosols	Mixed beech, spruce, maple and ash forest
Plateau	Moist	4	60	900	Chromic Cambisols	Spruce-dominated forest

We sampled two 5-mm diameter increment cores per tree at breast height. All three sites are located within a horizontal distance of 900 m and an elevational difference of ~20 m. The sampling sites differ in soil moisture and depth mainly controlled through exposure and slope differences (Table 1). South is located on a steep grade (100%) with shallow soils (28 cm), North is less steep (25%) with much deeper soils (52 cm), and the Plateau is almost flat with the deepest soils (60 cm). The soil moisture categories are supported by high-resolution (30 min) soil-water content data available for the period 2001–10 at North and Plateau (Jost et al. 2011). Although no such data are available for South, it appeared obvious that this is the driest site due to the shallow soil, steep slope, southern exposure and plant community. Tree composition at the Plateau has been influenced by a plantation early in the 20th century following a clear cut around 1910 (Hülber et al. 2008).

Sample preparation and data treatment

Tree-ring width was measured at 0.01 mm resolution using a LINTAB 6 table and the TSAP-Win software (Rinn 2003). Species- and site-specific cross-dating accuracy was checked both visually and statistically using the program COFECHA (Holmes 1983). To remove age-related growth trends and potential disturbance signals (e.g., due to forest management), the TRW measurement series were detrended individually using a cubic smoothing spline with a 50% frequency cut-off at 15 years (Cook and Peters 1981). Species-specific

site chronologies were produced by averaging the detrended single series using a robust mean (Mosteller and Tukey 1977). Inter-series correlation (R_{bar}) and expressed population signal (EPS) statistics (Wigley et al. 1984) are used to estimate the internal coherence of each chronology.

For isotope measurements, eight trees per species and site and one core per tree were selected based on straight ring borders and absence of missing rings. Tree rings from 1970–2010 were cut off and the corresponding years of all cores and trees per site and species pooled before isotope measurement (Leavitt and Long 1984, Treydte et al. 2001, 2006, 2007, Leavitt 2008). The wood of the pooled samples was milled using an ultra-centrifuge ZM200 (Retsch, Haan, Germany) with a mesh size of 0.5 mm. Cellulose was extracted following standard procedures (Boettger et al. 2007) and packed into tin capsules for mass spectrometry. For carbon isotope measurement, cellulose samples were combusted to CO_2 using a EURO EA Elemental Analyser (EuroVector, Milan, Italy); for oxygen isotope measurements, cellulose was pyrolyzed to CO using a HT oxygen analyser from HEKAtech (Wegberg, Germany). Stable isotope ratios were determined with a Delta V Advantage from Thermo Scientific (Bremen, Germany). All isotope measurements were conducted at the WSL Central Lab at a precision of $\pm 0.3\text{‰}$ for oxygen and $\pm 0.02\text{‰}$ for carbon. $\delta^{13}\text{C}$ chronologies were corrected for changes in the atmospheric $\delta^{13}\text{C}$ value due to anthropogenic activities (Treydte et al. 2009). All further analyses refer to the CO_2 -corrected data, termed raw $\delta^{13}\text{C}$.

Other potential non-climatic trends in both the raw $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ time series (Treydte et al. 2006, 2009, Esper et al. 2010) were accounted for by calculating residuals from linear trends.

Climate data and drought events

Monthly climate data were obtained from the HISTALP database (Auer et al. 2007). For temperature and precipitation, the grid point closest to our site (N47°50' E14°20', grid mode 2), and for sunshine duration and cloud cover coarse resolution subregional means data (region NE-Alps) were used. A simple moisture index was calculated after Thornthwaite (1948) based on monthly precipitation sums and monthly sums of potential evapotranspiration as a function of temperature and latitude (see Kress et al. 2010 for details).

Severe drought events were classified by combining the 10 most extreme values of June/July/August temperature, precipitation and moisture index. Considering the mean of all parameters indicated 1983, 1992, 1994 and 2003 as the most extreme drought events of the analysis period 1970–2010 (Figure 2).

Statistical analyses

Chronologies were characterized considering the first year autocorrelation (lag-1) and average growth rates (AGR)

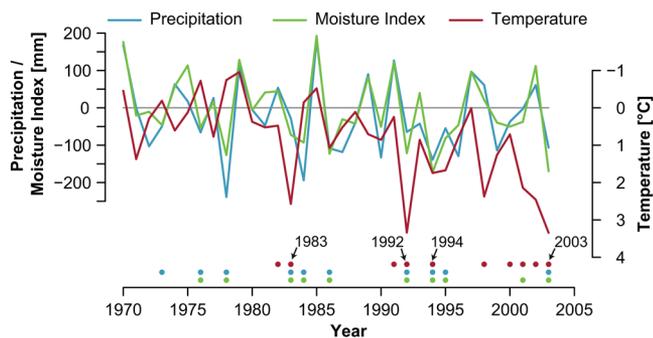


Figure 2. Precipitation, moisture index and temperature (note inverse scale) anomalies in the study area for June to August of the common period 1970–2003. Dots indicate the ten strongest extreme values of each climate parameter. The drought events 1983, 1992, 1994 and 2003 are identified by an overlap of the extremes for all climate parameter.

(Table 2). Differences in the raw $\delta^{13}\text{C}$, $\delta^{18}\text{O}$ and TRW chronologies, between sites and species, were assessed by analyses of variance followed by a Tukey HSD post hoc test. Coherency, here expressed as the similarity of the year-to-year variations among sites and species, was quantified using Pearson's correlation coefficients (i.e., the inter-chronology correlation).

The relationship of $\delta^{13}\text{C}$, $\delta^{18}\text{O}$ and TRW with climate variables was calculated using bootstrapped correlations, and the statistical significance was determined at $P \leq 0.05$. Since the focus of this study is on summer drought, the climate response was determined for June/July/August averages (temperature, cloud cover) and sums (sunshine duration, precipitation, moisture index) over the 1970–2003 period.

The response to drought events was assessed using superposed epoch analysis (SEA) (Panofsky and Brier 1958), by analysing the 4 years before and after the 1983, 1992, 1994 and 2003 drought events. In SEA, tree-ring parameters are expressed as scaled anomalies with respect to the mean of the 4 years preceding a drought event (years -4 to -1). All statistical procedures were performed using R 3.0.1 (R Development Core Team 2013) and the packages dpLR (Bunn et al. 2012) and bootRes (Zang and Biondi 2013).

Results

Chronology characteristics

Maximum tree ages were reached at South (241 years, Table 2), trees at North were slightly younger (222 years) and trees were youngest at Plateau (102 years). Almost all species at a site were even-aged. Rbar values ranged from 0.39 to 0.64, indicating the highest internal coherency for the beech chronologies. All EPS values exceeded the widely considered threshold of 0.85 (Wigley et al. 1984), indicating sufficient internal signal strength for all chronologies (Table 2). Lag-1 autocorrelation was generally high in TRW and fluctuated between 0.47 and 0.67. The values for $\delta^{13}\text{C}$ were lower but also more variable with 0.20 to 0.64. For the $\delta^{18}\text{O}$ chronologies,

Table 2. Characteristics of the TRW, $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ chronologies. Rbar, inter-series correlation; EPS, expressed population signal; AGR, average growth rate; Lag-1, first year autocorrelation; ¹referring to detrended TRW-data; ²calculated for the 1970–2010 period.

Species	Site	Tree age (years)			TRW				$\delta^{13}\text{C}$		$\delta^{18}\text{O}$	
		Min.	Max.	Mean	Rbar ^{1,2}	EPS ^{1,2}	AGR ² (mm)	Lag-1 ²	Mean (‰)	Lag-1	Mean (‰)	Lag-1
Spruce	South	189	241	217	0.46	0.94	0.67	0.52	-20.90	0.39	30.18	0.26
	North	83	222	130	0.39	0.93	1.21	0.58	-21.80	0.50	29.96	-0.07
	Plateau	88	101	94	0.42	0.94	1.90	0.58	-22.33	0.64	30.10	-0.08
Larch	North	86	103	93	0.43	0.94	1.21	0.65	-22.90	0.20	29.51	-0.09
	Plateau	88	102	95	0.48	0.95	1.08	0.67	-23.42	0.22	29.53	0.19
Beech	South	142	235	193	0.58	0.97	1.21	0.59	-23.76	0.44	29.78	0.24
	North	153	218	194	0.53	0.96	0.99	0.59	-24.44	0.34	29.55	0.26
	Plateau	71	102	89	0.64	0.97	1.84	0.47	-24.70	0.55	29.11	0.14

serial correlations ranged between -0.07 and 0.26 , indicating almost no lag effects inherent to these data (Table 2).

Species- and site-specific differences

Significant differences were found between sites and species, particularly in the raw $\delta^{13}\text{C}$ chronologies (Figure 3; Table S1 available as Supplementary Data at *Tree Physiology* Online): at all sites, spruce consistently showed the highest, and beech showed the lowest $\delta^{13}\text{C}$ mean values. Intra-species comparisons indicated maximum $\delta^{13}\text{C}$ values at South and minimum values at Plateau (Table 2, Figure 4a). In contrast, $\delta^{18}\text{O}$ values did not change significantly among sites and species, although again spruce showed higher and beech slightly lower values (Figure 4b). Both $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ values decreased with increasing moisture conditions, most notably in beech (Figure 4c). Average growth rates showed a clear site dependency for spruce only, with the lowest growth rates at South and the highest at Plateau. Beech growth was also slightly higher at Plateau compared with the other two sites, but AGR of larch remained similar among sites.

Coherency between species and sites

Both the $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ time series were significantly coherent among species and sites (Figure 5, Table S1 available as Supplementary Data at *Tree Physiology* Online). The mean correlation within one species over all sites (intra-species coherency) ranged from 0.57 ($\delta^{13}\text{C}$ of beech) to 0.85 ($\delta^{13}\text{C}$ of larch).

Interestingly, coherence between the mean species records, integrating all isotope records throughout the sites (inter-species coherence) was even stronger with r -values ranging from 0.52 to 0.69 for $\delta^{13}\text{C}$ and 0.83 to 0.84 for $\delta^{18}\text{O}$. In contrast, the correlation between the TRW records of the different species over all sites was close to zero, except for spruce and beech with a relatively low r -value of 0.45 .

Within the sampling sites, the carbon and oxygen time series of the different species were again strongly correlated reaching $r=0.52$ – 0.62 for $\delta^{13}\text{C}$ and $r=0.65$ – 0.73 for $\delta^{18}\text{O}$. The TRW chronologies, however, only showed common variability at the driest site South ($r=0.53$) among the species and no relationship at the moist North and Plateau sites.

A comparison of the different tree-ring parameters (Figure 5c) indicated strong coherence between the $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ chronologies for beech ($r=0.58$), medium coherence for larch ($r=0.48$) and weak coherence for spruce ($r=0.33$). Tree-ring width and $\delta^{13}\text{C}$ were negatively correlated, most significantly for spruce ($r=-0.53$). No association was found between TRW and $\delta^{18}\text{O}$.

Response to summer climate

Distinct and homogenous inter-site and inter-species summer climate signals were inherent to the $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ data, while TRW showed divergent and weak relationships (Figure 6). Both $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ of all sites and species correlated positively with summer season sunshine duration and temperature, and

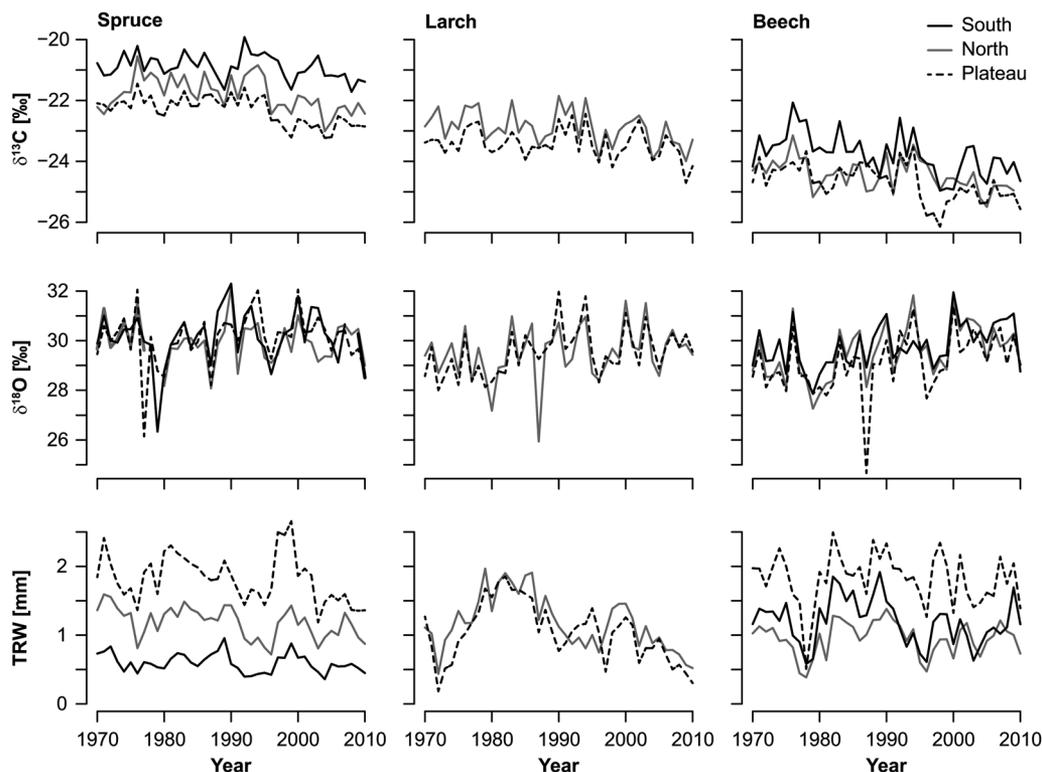


Figure 3. Raw $\delta^{13}\text{C}$, $\delta^{18}\text{O}$ and TRW chronologies of spruce, larch and beech at the three sites.

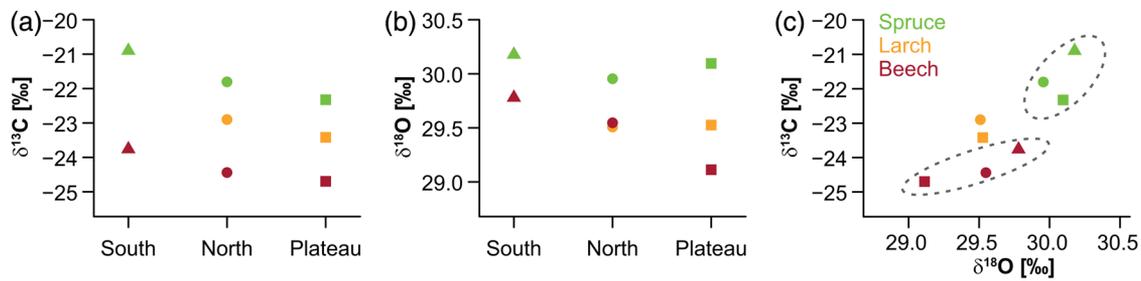


Figure 4. Mean (a) $\delta^{13}\text{C}$ and (b) $\delta^{18}\text{O}$ of spruce, larch and beech at the three sites and (c) the relationships between $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ (symbols in (c) indicate sites as in (a) and (b)).

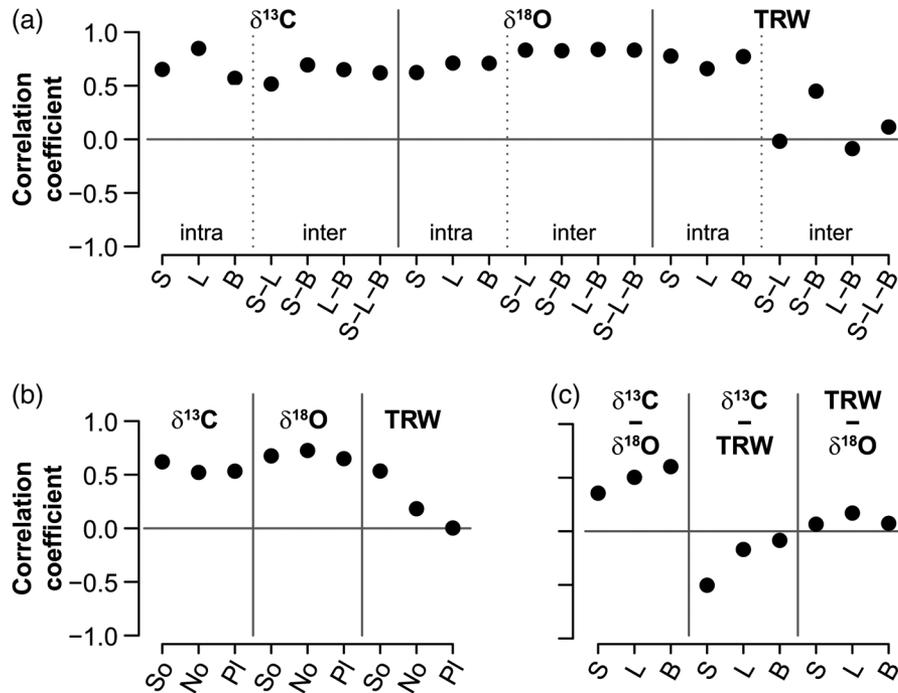


Figure 5. (a) Intra- and inter-species (mean species chronologies) correlations of detrended $\delta^{13}\text{C}$, $\delta^{18}\text{O}$ and TRW chronologies. (b) Inter-species correlation of detrended $\delta^{13}\text{C}$, $\delta^{18}\text{O}$ and TRW chronologies within the different sites. (c) Correlation between tree-ring parameter of the mean species chronologies. S, spruce; L, larch; B, beech; So, South; No, North; Pl, Plateau. $P < 0.01$ is reached at $r \sim 0.4$.

negatively with the moisture index, precipitation and cloud cover. Relationships between the climate parameters and the stable isotopes were frequently significant ($P \leq 0.05$) (Table S2 available as Supplementary Data at *Tree Physiology* Online). The correlation coefficients were coherent among sites and species, without a clear species (Figure 6a) or site-dependent response pattern (Figure 6b). Highest correlations with sunshine duration were inherent to the $\delta^{18}\text{O}$ data, with coefficients ranging from 0.37 to 0.49 for the species mean chronologies. The temperature signal was high in the $\delta^{18}\text{O}$ data ($r = 0.30$ – 0.37) as well, but the highest response was found in larch $\delta^{13}\text{C}$ ($r = 0.41$). The strongest moisture and precipitation signals were inherent to beech $\delta^{13}\text{C}$ with correlation coefficients of $r = -0.48$ and -0.45 , respectively. However, the overall strongest relationships in both C and O stable isotopes were observed with cloud cover, reaching $r = -0.71$ for larch and $r = -0.72$ for beech $\delta^{18}\text{O}$ data.

The correlation coefficients between TRW and climate data were weak, reaching a maximum of $r = 0.35$ between spruce and cloud cover. The low correlation patterns also appeared to be influenced by species (Figure 6a) and site effects (Figure 6b). For example, spruce growth was negatively correlated with sunshine duration and temperature, but positively correlated with moisture index, precipitation and cloud cover. The climate response of larch was largely inverse to the spruce pattern. Severe site effects were seen for larch indicating no correlation with precipitation at North, but -0.24 at Plateau, for example (Table S2 available as Supplementary Data at *Tree Physiology* Online).

Response to drought events

The SEA revealed a distinct relationship of all $\delta^{13}\text{C}$ chronologies to drought, independent of species and site. The most significant ($P \leq 0.05$) $\delta^{13}\text{C}$ deviations were always reached in the

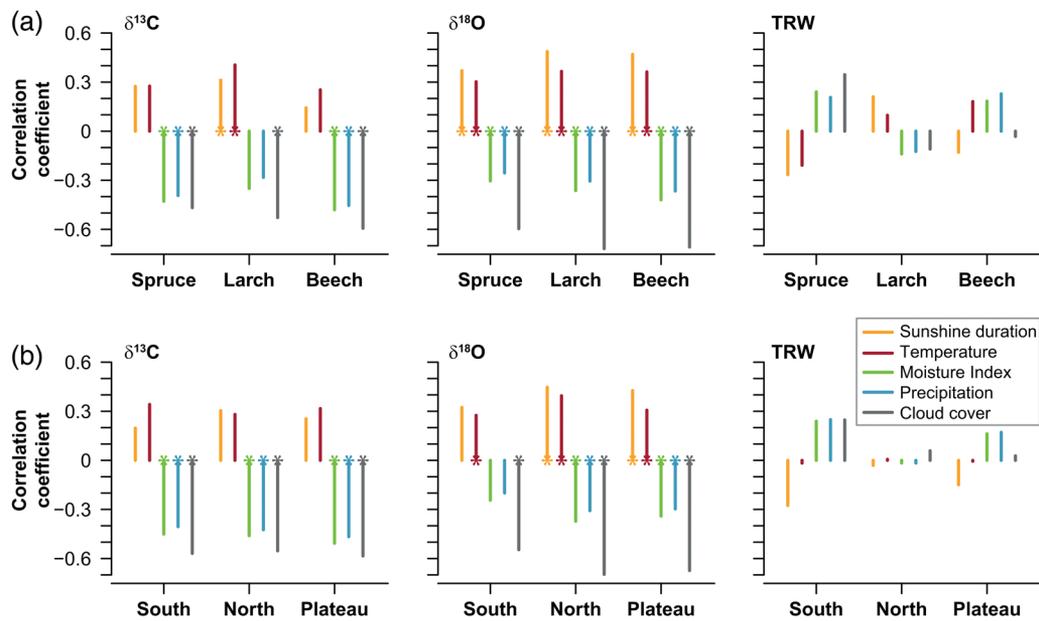


Figure 6. Relationships of (a) species and (b) sites to the climate variables of the June/July/August season. * $P \leq 0.05$ significant correlations.

year when the drought event occurred (Year 0) with almost no lag effects (Figure 7a). However, there were noticeable positive and negative peaks in the Years -2 and -3 , respectively. By comparing the species mean $\delta^{13}\text{C}$ deviations with the climate data, the strong relationship between $\delta^{13}\text{C}$ and climate, especially cloud cover, becomes apparent, indicating that $\delta^{13}\text{C}$ strongly depends on irradiance conditions (Figure 7b, Table S3 available as Supplementary Data at *Tree Physiology* Online).

For $\delta^{18}\text{O}$, the SEA-derived relationship to drought events is less pronounced and the strength of the response varied among sites (Figure 7a). Again, no lag effects were found, and the SEA revealed significant ($P \leq 0.05$) positive deviations in $\delta^{18}\text{O}$ during drought events at both larch sites (Plateau and North) and at Plateau for spruce and beech. The $\delta^{18}\text{O}$ SEA of the species mean (Figure 7b) revealed a species-specific response including stronger deviations in larch and beech, and a weaker response of spruce. As with $\delta^{13}\text{C}$, cloud cover seems to be the most important influencing factor of $\delta^{18}\text{O}$.

In contrast to the coherent isotopic patterns, TRW indicated strong site- and species-dependent drought responses (Figure 7). Although a growth decline was only significant ($P \leq 0.05$) 1 year after the drought event for spruce at South, the SEA nevertheless revealed strong negative growth reactions of the other sites and species, including the following species-specific patterns: spruce growth declined sharply during drought, and the reduction persisted until Year 4; larch growth showed no obvious reaction to drought; and beech growth deviated weakly during drought, then declined more strongly in Year +1, and persisted until Year +4. Besides the species-specific growth reaction, the response pattern within a species showed only minor site-specific differences including a stronger decline in South and faster recovery in Plateau. Because of the biological

persistence inherent to TRW, the SEA patterns were overall less distinct.

Discussion

Performance of $\delta^{13}\text{C}$, $\delta^{18}\text{O}$ and TRW as climate proxies

The common variance of both the C and O isotope chronologies, among sites and species, exceeded the strength of the inter-series correlation of the TRW chronologies. This high degree of uniformity is especially conspicuous, as the compared species included an evergreen conifer, a deciduous conifer and a deciduous broadleaved species (Leavitt 1993). Our results indicate a stronger dependency of the stable isotopes on atmospheric conditions (Saurer et al. 2008) compared with TRW, while the latter seems to be controlled by species-specific and especially local soil moisture conditions.

This is also confirmed by our climate response analyses indicating a stronger sensitivity of the isotopic signatures compared with TRW, a finding also reported by Andreu et al. (2008) and Mölder et al. (2011). Particularly for $\delta^{13}\text{C}$, other studies indicated a stronger precipitation signal compared with TRW (Saurer et al. 1995, Gagen et al. 2004, Andreu et al. 2008, Kirilyanov et al. 2008). Our results reveal that also the oxygen isotope variations show a more coherent and stronger sensitivity to climate variables. Moreover, a site- and species-independent precipitation signal, in both isotopic parameters, challenges the assumption that precipitation signals are stronger at locally drier sites (Saurer et al. 1995, McCarroll and Loader 2004). The absence of strong species-specific responses in the isotopic parameters supports the development of large-scale isotope networks from regions with weak signals in classical TRW and MXD data (Treydte et al. 2007).

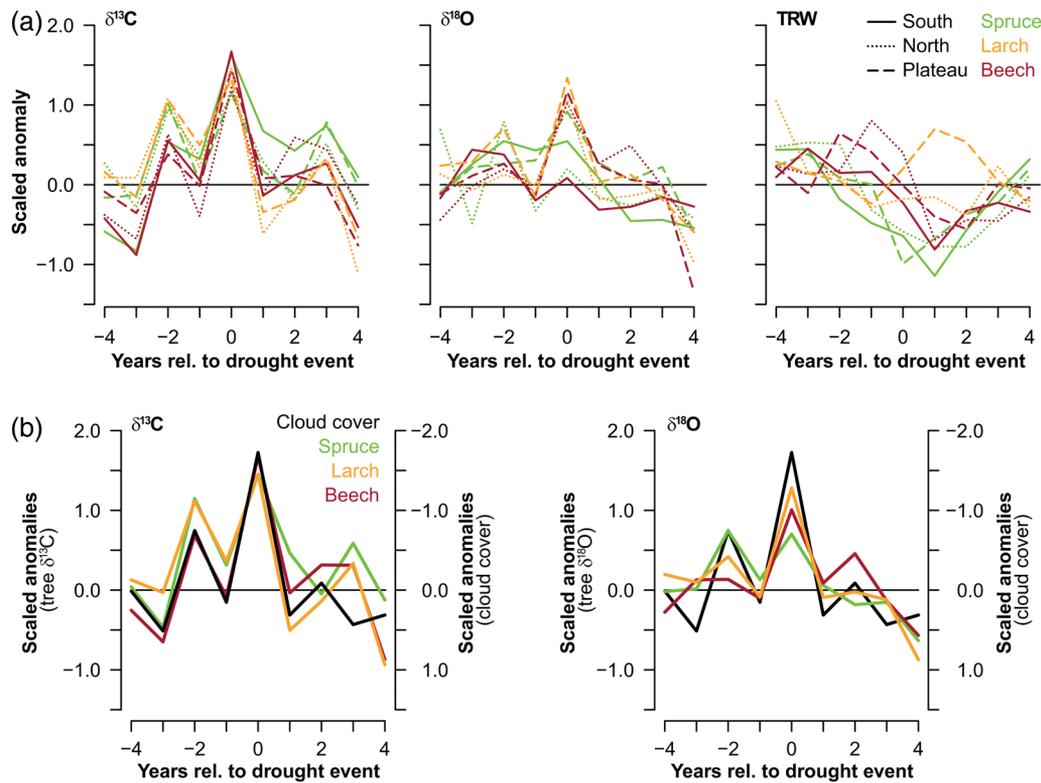


Figure 7. (a) Superposed epoch analysis for $\delta^{13}\text{C}$, $\delta^{18}\text{O}$ and TRW site chronologies of spruce, larch and beech. Curves represent scaled time series centred on the drought events (Year 0) in 1983, 1992, 1994 and 2003, and scaled to zero mean over Years -4 to -1 . (b) Comparison of the $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ mean species with cloud cover data.

Both $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ correlated best with the climate variables representing irradiance conditions (i.e., cloud cover and sunshine) with strongest relationships revealed in $\delta^{18}\text{O}$ of larch and beech. Correlations exceeding $r = -0.70$ indicate the potential for a $\delta^{18}\text{O}$ -based cloud cover reconstruction also in the temperate climatic zone to accompany similar efforts using $\delta^{13}\text{C}$ in the high latitudes of Scandinavia (Young et al. 2010, 2012, Gagen et al. 2011, Loader et al. 2013) and eastern European Alps (Hafner et al. 2013).

The correlations between TRW and the climate variables are rather inconsistent. Only spruce revealed a relationship between TRW and drought, whereas the weak correlations of larch and beech are typical for such regions/elevations (Hartl-Meier et al. 2014a). In general, the strength of the climate signal in TRW depends on local site conditions rather than on species.

The response of the different tree-ring parameters to severe drought, as derived from SEA, supports this conclusion. $\delta^{13}\text{C}$ uniformly displayed drought signals across sites most precisely, again questioning expectations of increased sensitivity to drought at drier sites (Saurer et al. 1995, Weitner et al. 2007, Eilmann et al. 2010). Leavitt (1993), however, reported common $\delta^{13}\text{C}$ variations from different sites in periods with distinct moisture deficit compared with pluvial periods. This also holds for our results, since the $\delta^{13}\text{C}$ values diverge in the years following the drought event. Surprisingly, we could not detect any significant

species-specific response to drought, although the mean values indicated different efficiency in the water use among species (see below). The O isotopes also increased during drought, though did not record the drought events as closely as $\delta^{13}\text{C}$ (Kress et al. 2010, Jansen et al. 2013). Interestingly the values particularly increased at the wet Plateau site, indicating that $\delta^{18}\text{O}$ is not necessarily associated with environmental stress conditions.

Although the SEA-derived response of radial growth is inconsistent among species and sites, it nevertheless provided insight into the recovery potential of the tree species. For spruce, we found a distinct growth decline during drought events followed by a rapid recovery. Differences in soil moisture conditions had no influence on the growth reaction of spruce, a finding in line with Hartl-Meier et al. (2014a, 2014b), reporting that the growth response of spruce to drought is rather driven by altitude, along with the corresponding hydrothermal changes. We also found growth reductions to be strongest in beech in the year following a drought event, and as indicated by Zang et al. (2014), that spruce exceeded the recovery potential of beech.

Physiological insights from the response to long-term climate and extreme drought events

Common variance and uniform climate response in both the C and O isotope data, throughout species and sites, are striking. In contrast, the mean isotope values differ substantially among

species and sites, particularly for $\delta^{13}\text{C}$. It has, however, to be noted that due to the pooling procedure an estimation of the inter-tree variability cannot be provided. Leavitt (2010) summarized for a number of studies the offsets in the mean values between trees, which can be up to 3‰ for $\delta^{13}\text{C}$ and 4‰ for $\delta^{18}\text{O}$, almost independent of species. These values exceed the differences among sites in our study, though the offsets reported here are consistent and systematic supporting the interpretation of differing species- and site-specific physiological strategies: The lower carbon and oxygen isotope values of the deciduous larch and beech trees than those of the evergreen spruce indicate higher stomatal conductance in correspondence with access to deeper soil water pools that are typically depleted in ^{18}O (Barbour et al. 2004, Marshall and Monserud 2006, Lévesque et al. 2013). Besides the more efficient water transport and deeper root system of the deciduous trees (Stuiver and Brazionas 1987, Leavitt 1993, Saurer et al. 1995, 1997, Lévesque et al. 2013), both species seem to enhance their photosynthetic capacity during the short period of assimilate production (Anfodillo et al. 1998). This strategy, however, involves risking water losses through increased transpiration and subsequent cavitation and hydraulic failure. The among-site, intra-species differences of the mean isotopes seemingly point to this strategy as well as to an obvious dependence on soil moisture conditions (Leavitt 1993, Saurer et al. 1995, 1997, Treydte et al. 2001, 2014). This holds particularly for $\delta^{13}\text{C}$, where the highest values are reached at the driest sites indicating reduced stomatal conductance and decreased water-use efficiency (Saurer et al. 1995, 2014, Treydte et al. 2001, Gessler et al. 2014).

For $\delta^{18}\text{O}$, the short distances between our sites exclude an influence of varying precipitation $\delta^{18}\text{O}$ signatures. It is, however, well known that soil water close to the surface is evaporatively enriched in ^{18}O compared with the deeper soil water pools (Roden et al. 2000, Sarris et al. 2013, Treydte et al. 2014). Soils are deepest at the Plateau site and thus, specifically the deep rooting beech (Pretzsch et al. 2013) shows lower isotope values. Since water uptake in the shallow rooting spruce (Przybylski 2007, Pretzsch et al. 2013) is limited to the enriched near-surface soils, spruce $\delta^{18}\text{O}$ appears to be less site dependent, compared with larch and beech.

Despite these fundamental differences, the temporal variations of the C and O isotope records contain substantial variance in common and respond uniformly to climate. This can be explained by the fact that the relative variations in the few atmospheric variables controlling the physiological processes are similar at all sites and therefore cause similar variations in the tree-ring isotopes. Cloud cover, the variable with strongest correlation to the tree-ring isotopes, is strongly linked to irradiance (i.e., photon flux), relative air humidity and vapour pressure deficit, the most important factors controlling stomata conductance, transpiration and partly also soil water evaporation.

Interestingly, all trees with good access to soil water (North and Plateau sites) are most sensitive to cloud cover and drought events. Obviously high soil water availability allows the stomata to stay open resulting in water loss through transpiration, but offering the advantage of enhanced CO_2 uptake and increased assimilate production. Since high transpiration is associated with high evaporative leaf water ^{18}O enrichment, the isotopic values of the newly produced assimilates used for cellulose synthesis show higher isotope values (Offermann et al. 2011, Gessler et al. 2013, 2014, Treydte et al. 2014). Under moist conditions, the relative variations in leaf water enrichment, due to increased transpiration, seem to outweigh the relative variations of soil water $\delta^{18}\text{O}$. The fact that the response of $\delta^{13}\text{C}$ to drought events does not show any similar site differences to $\delta^{18}\text{O}$ supports the assumption of increased photosynthetic activity with higher soil water availability: in this case the discrimination against ^{13}C is reduced due to increased photosynthetic activity. This seems to outweigh the common effect of increased discrimination due to higher stomatal conductance (Farquhar et al. 1982, Leavitt and Long 1989). The observed $\delta^{13}\text{C}$ response to warm-dry conditions may therefore not only be a stomatal signal, but also reflect changes in the assimilation rate (Gessler et al. 2014 and references therein).

The differing physiological strategies identified here may be related to stem biomass production represented in TRW. We found significant negative correlations between $\delta^{13}\text{C}$ and TRW at least for spruce, indicating that wood production is related to stomatal conductance. By linking this relationship to climate, it appears that low soil water availability during drought periods might reduce carbon fixation and subsequently tree growth (Francey and Farquhar 1982, Saurer et al. 1995, Weitner et al. 2007). This particularly holds for Norway spruce and reveals its isohydric character: stomata closure during early phases of drought stress, resulting in low growth rates but preventing stress damage and allowing fast recovery (McDowell et al. 2008, Matyssek et al. 2013, Pretzsch et al. 2013). For the other species, the differences in physiological strategies and sensitivity to climate are less clearly linked to variations of radial growth. During drought events, beech takes advantage of the access to deeper soil horizons, increases photosynthetic activity as described above, and continues biomass production. Since this capability is associated with increased water losses, this anisohydric strategy might lead to xylem embolism (Gessler et al. 2007) that might need to be compensated by using assimilates for restoration in subsequent years (Hartmann 2011, Matyssek et al. 2013, Pretzsch et al. 2013, Zang et al. 2014). The result is a slow recovery, including a prolonged low stem biomass production following extreme drought events. It seems that larch follows an anisohydric strategy (Anfodillo et al. 1998, Lévesque et al. 2013) similar to beech, at least with respect to transpiration vs enhanced photosynthetic activity, but the next year's assimilation products may nonetheless build up stem increment.

Conclusions

Our findings reveal that the temporal patterns of carbon and oxygen isotopes show generally strong common variation, and consequently respond uniformly to short- and long-term climate variability. Tree-ring stable isotopes from this temperate forest show high climate sensitivities independent of site and species, and much stronger than radial growth. High correlations with irradiance variables demonstrate the potential of tree-ring stable isotopes for reconstructing past climatic conditions in mid-latitude, temperate environments. During drought events, tree-ring stable isotopes (particularly $\delta^{13}\text{C}$) show distinct signals. Although the growth response is inconsistent between sites and species, TRW still provides important information about future tree-species suitability, since tree performance can be inferred from the strength of growth reductions and subsequent recovery.

Despite the high temporal synchronicity and coherence of climatic signals, the isotopic signatures also allow identification of different physiological strategies of different tree species. Significant offsets inherent to the carbon and oxygen isotopes arise from differing water-use efficiencies, varying among species and with local soil moisture conditions. Our findings suggest that higher soil water availability allows high stomatal conductance in beech and larch and simultaneously enhanced photosynthetic activity, leading to continued biomass production during drought. We conclude that stable isotopes in tree rings from temperate sites do not only provide valuable proxies for climate reconstruction, but also enable the identification of drought-induced changes in physiological strategies.

Supplementary data

Supplementary data for this article are available at [Tree Physiology Online](http://treephys.oxfordjournals.org/).

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Conflict of interest

None declared.

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