Drought response of five conifer species under contrasting water availability suggests high vulnerability of Norway spruce and European larch

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Abstract

The ability of tree species to cope with anticipated decrease in water availability is still poorly understood. We evaluated the potential of Norway spruce, Scots pine, European larch, black pine, and Douglas-fir to withstand drought in a drier future climate by analyzing their past growth and physiological responses at a xeric and a mesic site in Central Europe using dendroecological methods. Earlywood, latewood, and total ring width, as well as the $\delta^{13}C$ and $\delta^{18}O$ in early- and latewood were measured and statistically related to a multiscalar soil water deficit index from 1961 to 2009. At the xeric site, $\delta^{13}C$ values of all species were strongly linked to water deficits that lasted longer than 11 months, indicating a long-term cumulative effect on the carbon pool. Trees at the xeric site were particularly sensitive to soil water recharge in the preceding autumn and early spring. The native species European larch and Norway spruce, growing close to their dry distribution limit at the xeric site, were found to be the most vulnerable species to soil water deficits. At the mesic site, summer water availability was critical for all species, whereas water availability prior to the growing season was less important. Trees at the mesic were more vulnerable to water deficits of shorter duration than the xeric site. We conclude that if summers become drier, trees growing on mesic sites will undergo significant growth reductions, whereas at their dry distribution limit in the Alps, tree growth of the highly sensitive spruce and larch may collapse, likely inducing dieback and compromising the provision of ecosystem services. However, the magnitude of these changes will be mediated strongly by soil water recharge in winter and thus water availability at the beginning of the growing season.

Keywords: carbon isotope, Central Europe, climate change, *Larix*, oxygen isotope, *Picea*, *Pinus*, *Pseudotsuga*, tree ring, water deficit

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Introduction

Drought is one of the main factors that determine tree growth, vitality, and survival in many regions of Europe (Bigler *et al.*, 2006) as well as worldwide (Allen *et al.*, 2010; Hartmann, 2011; McDowell, 2011). Particularly, inner-Alpine dry forests have been severely affected by unprecedented episodes of drought-induced tree mortality and forest decline in the last decade (Vertui & Tagliaferro, 1998; Oberhuber, 2001; Vacchiano *et al.*, 2012). In the Alps and lowlands of Central Europe, an increase in drought duration and frequency have already been noticed (Brunetti *et al.*, 2002; Begert *et al.*, 2005; Ciccarelli *et al.*, 2008; Ceppi *et al.*, 2012), and climate scenarios for the coming decades usually indicate even drier summers in these

regions (Christensen *et al.*, 2007; CH2011, 2011). Therefore, forests in these areas are likely to experience more frequent water deficits.

Impacts of drought on tree growth and physiology are difficult to quantitate due to lags between drought occurrence and the tree responses (Pasho *et al.*, 2011; Vicente-Serrano *et al.*, 2013). This is exacerbated by differences in physiological and anatomical adjustments among tree species to cope with drought (Eilmann *et al.*, 2009). Variation in drought severity, duration, and timing make the situation even more complex and render it difficult to compare drought events in time and space. Therefore, when dealing with species-specific responses to drought, it is crucial to properly consider and quantitate drought severity, seasonality, and duration, as well as the temporal scale of tree responses, including lag effects.

Drought depends not only on the amount of precipitation but also on factors such as temperature

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(i.e., evaporative demand) and soil characteristics. Simple drought indices based on a few climatic variables such as temperature and precipitation may not capture this complexity, and more sophisticated drought indices have been developed over the last decades, e.g., indices based on extensive water balance models such as the Palmer Drought Severity Index (cf. Zargar *et al.*, 2011). However, most of these indices ignore the multiscalar character of drought phenomena; i.e., the multiple temporal scales (days to years) at which water shortages have an impact on a given ecosystem (Vicente-Serrano *et al.*, 2010). Knowledge of the dominant temporal scales at which drought influences tree growth and physiology may be critical for the early detection of forest dieback, but also for identifying response patterns that determine the resistance and resilience of tree species to drought (Vicente-Serrano *et al.*, 2013). So far, only a few studies have analyzed tree radial growth responses to drought at various temporal scales based on tree-ring width (e.g., Pasho *et al.*, 2011; Vicente-Serrano *et al.*, 2013), but none of them focused on physiological responses, which can be inferred from stable isotopes in tree rings.

The stable isotope composition in tree rings provides retrospective information on the response of trees to past environmental conditions. For the stable carbon isotope ($\delta^{13}C$), the underlying physiological mechanisms behind carbon fixation and variation in stomatal conductance (g_s) are well known, thus making the interpretation of the isotopic signal straightforward (Farquhar *et al.*, 1989). The $\delta^{13}C$ ratio in tree rings is directly proportional to the CO_2 uptake (A_N) at a given g_s, or inversely, proportional to g_s at a given A_N (Farquhar *et al.*, 1982, 1989). Thus, $\delta^{13}C$ varies with changes in the carbon and water balance, which is reflected in the intrinsic water-use efficiency of trees, and is therefore an excellent proxy to estimate the degree of drought stress experienced by trees (e.g., Barber *et al.*, 2000; Eilmann *et al.*, 2010). However, by analyzing shifts in $\delta^{13}C$ alone, changes in water-use efficiency can be due to adjustments in assimilation rates and/or stomatal conductance. By contrast, the oxygen isotope ($\delta^{18}O$) ratio provides information on precipitation, relative humidity, and air temperature, as well as transpiration, as it is determined by (i) the isotopic signature of the source water; (ii) evaporative enrichment at the leaf level due to transpiration; and (iii) biochemical fractionation, which can be assumed to be constant (Dongmann *et al.*, 1974; Ehleringer, 1993; Farquhar & Lloyd, 1993). Thus, the combined analysis of $\delta^{13}C$ and $\delta^{18}O$ in tree rings enables the distinction between the independent effects of photosynthetic vs. stomatal responses to drought (Scheidegger *et al.*, 2000).

In this study, we analyzed tree radial increment as well as carbon and oxygen isotopic composition separately for early- and latewood in five conifer species at two ecologically contrasting sites, one in the dry inner-Alps and the other in the moist Swiss lowlands. Three species are native to these regions [European larch (*Larix decidua* Mill), Norway spruce (*Picea abies* (L.) Karst.) and Scots pine (*Pinus sylvestris* L.)], whereas black pine (*Pinus nigra* Arn.) and Douglas-fir [*Pseudotsuga menziesii* var. *menziesii* (Mirb.) Franco] are not. European larch is a pioneer and shade-intolerant species of mid-to-high altitudes, able to tolerate high thermal amplitude and moderate water deficits (Ellenberg, 2009). Norway spruce is an intermediately shade-tolerant species widely distributed across the Alps and sensitive to summer water deficits (Lebourgeois *et al.*, 2010). Scots pine and black pine are light demanding pioneer species, the latter being more drought tolerant (Eilmann & Rigling, 2012; Lebourgeois *et al.*, 2012). Scots pine is one the most widely distributed conifer species in the world and occurs in wide range of habitats from Spain to Siberia, and at elevation from sea level to 2600 m a.s.l. (Matías & Jump, 2012). Black pine is native to the Mediterranean and Vienna basins, where summer droughts are frequent, and has been identified as a potential substitute for Scots pine under future climatic conditions in Central Europe (Thiel *et al.*, 2012). Douglas-fir (var. menziesii) is an intermediately shade-tolerant species native to western North America (Canada, USA). It is fast growing and a potential alternative to the more drought sensitive Norway spruce in Central Europe (Eilmann & Rigling, 2012).

The dry inner-Alpine valleys of the Central Alps are close to the xeric distribution limit of Norway spruce, Scots pine, and European larch in Central Europe (Ellenberg, 2009). In these areas, Scots pine has experienced significant drought-induced decline in the last decades (Vacchiano *et al.*, 2012; Rigling *et al.*, 2013), whereas such phenomena has not yet been documented for European larch and Norway spruce. However, evidence suggests that species with small niche breadths and geographic ranges, such as Norway spruce and European larch in the dry inner-Alps, may be more sensitive to climate change (Morin & Lechowicz, 2013). Similarly, it is still poorly understood how the expected decrease in water availability will affect tree growth at mesic sites close to the optimum conditions for Norway spruce, Scots pine, and European larch. Furthermore, investigating nonnative species becomes necessary as native species may be unable to cope with a drier climate, hence challenging current forest management practices (Eilmann & Rigling, 2012) and the provision of ecosystem goods and services (Elkin *et al.*, 2013). Such analyses could provide a basis for the selection of tree species that can cope with a drier climate.

Thus, the objectives of this study were as follows: (i) to assess the contrasting vulnerability to drought of five conifer species at their xeric distribution limit in the dry inner-Alps and under mesic conditions; and (ii) to determine the duration and seasonality of soil water deficits that most strongly impact the growth and physiology of these species. The fulfillment of these objectives will allow to understand the response patterns that determine the resistance and resilience of these five species to the anticipated decrease in water availability.

Materials and methods

Study sites

Two afforestations with contrasting climatic and soil-moisture conditions (xeric vs. mesic) were selected. The xeric site is located at Verrayes in the dry inner-Alpine Aosta Valley in Northern Italy, on a southwest facing slope (slope 75%; 45°46′N, 7°32′E; 1150 m a.s.l.). This afforestation was established between 1905 and 1910 (Vescoz, 1909) and was left unmanaged until the early 2000s when some suppressed and dead trees were removed from the stand. The climate is dry with a mean annual temperature of 7.6 °C and a mean annual precipitation sum of 701 mm (data from 1960 to 2009) with a high probability of water deficit during the summer (Fig. 1a). The mesic site is located 3 km northeast of the city of Biel in Switzerland on a south-facing slope at the foothills of the Jura mountains (slope 35%; 47°09′N, 7°17′E; 750 m a.s.l.). This afforestation dates back to 1889 (Marcet, 1975), and occasional harvesting of single trees has occurred in the last decades. The site is characterized by mesic climatic conditions with a mean annual temperature of 8.0 °C and a mean annual precipitation sum of 1184 mm (data from 1960 to 2009) being distributed rather uniformly

over the year (Fig. 1b). At each site, a soil profile was dug to determine soil type and soil properties. The physical and chemical properties of the different soil horizons were measured up to a depth of 1 m. The available water capacity of the soil (AWC) between 0 and 100 cm depth was estimated using data on soil texture, bulk density, content of coarse fragments, and depth of each soil horizon. The soil type at the xeric site is a regosol with an AWC of 51 mm, whereas that of the mesic site is a leptosol with an AWC of 119 mm. At both sites, we analyzed a mixed stand of European larch, Norway spruce, Scots pine, black pine, and Douglas-fir. All sampled trees were between 100 and 115 years old. Thus, all trees were at least 50 years old at the beginning of the investigated period in 1960.

Tree-ring width analysis

In summer 2010 near Biel and in winter 2011 in Aosta Valley, between 12 and 15 codominant or dominant trees per species were sampled at each site by taking two increment cores at ca. 0.5 m height. This coring height was used due to the forest owners' preference. Although standard dendrochronological procedures suggest taking core at breast height (1.3 m aboveground), samples taken at 0.5 m height yield similar climatic signals (Chhin & Wang, 2005). Cores were air-dried and their surfaces were prepared using a core-microtome (Gärtner & Nievergelt, 2010). Earlywood, latewood, and total ring widths were measured separately under a stereo microscope to the nearest 0.01 mm using a Lintab digital positioning table and the software TSAP (Rinntech, Heidelberg, Germany). Early- and latewood tree-ring sections were defined according to visual aspects (darkening and cell size). For species with gradual transition between early- and latewood (Norway spruce), we defined the earlywood/latewood boundaries as the middle of the transition zone. Then, the individual tree-ring chronologies of each species were visually crossdated and
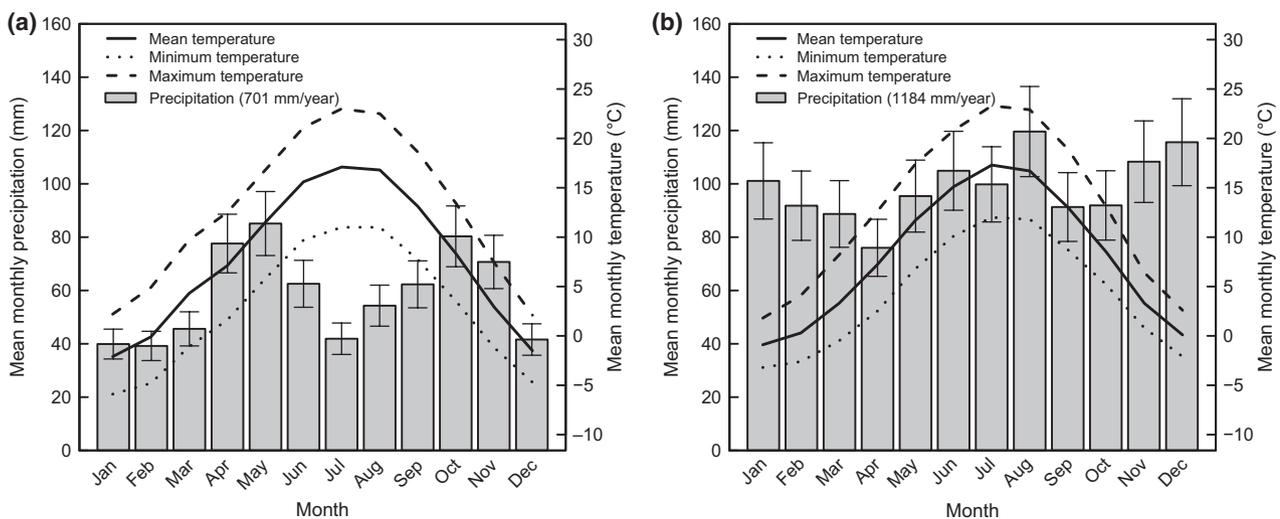

Fig. 1 Mean monthly precipitation sum (± 1 SE) and mean monthly temperature (minimum, mean, and maximum) for the observation period 1960 to 2009 at the xeric site in Aosta (a), and at the mesic site in Biel (b).

verified statistically using the computer program COFECHA (Holmes, 1983). Cores that could not be correctly crossdated were removed from further analysis. Individual tree-ring width series were detrended with ARSTAN (Cook, 1985) to remove long-term trends and past management effects (occasional single-tree harvesting) using a 15 year cubic smoothing spline with a 50% frequency cut-off. This standardization procedure retains 99% of the variance at 5 years and 50% of the variance at 15 years (Cook & Kairiukstis, 1990). Although no perfect standardization procedure exists to remove past forest management effects on tree-ring width chronologies, Esper *et al.* (2012) showed that occasional harvesting of single trees, as done at the mesic site, has no or only marginal effects on the climate-growth relationships in temperate forests. The residual series were averaged using a biweight robust mean to create a species-site chronology. To assess the signal strength of each species-site chronology, we calculated the interseries correlations (Rbar) and the expressed population signal (EPS) (Wigley *et al.*, 1984). We also calculated the mean sensitivity to assess year-to-year variability and the first-order autocorrelation of each chronology.

Stable isotope analysis

For the $\delta^{13}C$ and $\delta^{18}O$ analyses in earlywood and latewood, we selected the four trees per species showing the highest correlations with the species-site chronology. The eight cores per species and site were put in a Soxhlet apparatus with 95% ethanol for 24 h to extract resin and mobile extractives, washed in boiling distilled water, and air-dried. Due to the scarcity of material resulting from some very narrow tree rings, the stable isotope analyses were done on wood instead of cellulose samples. The early- and latewood of each annual ring for the period 1960–2009 were separated from each core with a scalpel under a stereo microscope and the samples from the four different trees of the same year were pooled regardless of mass (Leavitt, 2008). The samples were homogenized using a mill (Ultra Centrifugal Mill ZM 200, Retsch, Haan, Germany).

For $\delta^{13}C$ analysis, an aliquot of 0.6–0.8 mg of wood powder from each sample was weighed into a tin capsule, and combusted to CO_2 with excess of oxygen at 1020 °C in an elemental analyzer (EA-1110, Carlo Erba Thermoquest, Milan, Italy) linked to a Delta S mass spectrometer via a CONFLO II (both Finnigan MAT, Bremen, Germany), which was operated in continuous flow mode. For $\delta^{18}O$ analysis, 0.5–0.7 mg of wood powder from each sample was weighed into a silver capsule and pyrolyzed to CO at 1080 °C via a variable open-split interface (CONFLO-III, Finnigan MAT, Bremen, Germany) in an elemental analyzer (EA-1108, Carlo Erba Thermoquest, Milan, Italy) linked to a DELTAplus XP mass spectrometer (Finnigan MAT, Bremen, Germany). The isotopic values are expressed in the delta notation in ‰ relative to the international standards: $\delta_{sample} = (R_{sample}/R_{standard} - 1) \times 1000$, where R_{sample} is the molar fraction of the $^{13}C/^{12}C$, or $^{18}O/^{16}O$ ratio of the sample and $R_{standard}$, of the standards VPDB for carbon and VSMOW for oxygen. The precision of the analysis (standard deviation of laboratory cellulose standards) was ≤0.10‰ for $\delta^{13}C$ and ≤0.25‰ for $\delta^{18}O$.

Removal of nonclimatic trends in $\delta^{13}C$ and $\delta^{18}O$ chronologies

$\delta^{13}C$ time series were first corrected for changes in atmospheric $\delta^{13}C$ of CO_2 according to Francey *et al.* (1999) and McCarroll & Loader (2004). However, this correction procedure does not consider the increase in atmospheric CO_2 concentrations (c_a) that may influence the physiological response of trees. Therefore, a second correction procedure called the 'pre-industrial' (PIN) correction (Fig. S1 and S2), which takes into account the physiological response of trees to increasing atmospheric CO_2 concentrations, was applied to the $\delta^{13}C$ time series (McCarroll *et al.*, 2009). This procedure constitutes a constrained nonlinear detrending of the low frequency changes in the $\delta^{13}C$ time series based on the expected physiological response of trees to increased CO_2. It is also a subjective correction because there are some assumptions involved in its computation. The first constraint (passive response) is that a unit increase in c_a cannot cause more than the same unit increase in intercellular CO_2 concentrations (c_i), and the second constraint (active response) is that increases in intrinsic water-use efficiency are limited to maintaining a constant c_i/c_a ratio. Then, $\delta^{13}C$ and $\delta^{18}O$ time series were standardized (series scaled to zero mean and unit variance) and an autoregressive model of order 1 was fitted to each series to remove the serial autocorrelation. The resulting residual chronologies were used in the further analyses.

Climate data

Mean daily temperature and daily precipitation sum were obtained from the climate stations nearest to the study sites for the period 1960–2009. For the site near Biel, the closest station was located in Biel itself, 3 km from the study site (MeteoSwiss). Climate data in the Aosta Valley were provided by the Department of Soil Conservation and Water Resources (Autonomous Region of Valle d'Aosta, Italy) and obtained from the nearest station to the study site (5 km) located at the hydroelectric power station in Promiod Covalou. Missing data were filled in by linear regressions using data from the nearby stations of Saint-Christophe (13 km) and Brusson (15 km). Temperature data were adjusted using lapse rates to account for the difference in altitude between the meteorological stations and the study sites. Monthly lapse rates were obtained from data published in Lotter *et al.* (2002) for the site near Biel, whereas for the site in Aosta, they were calculated with data from seven climate stations spanning 545–2125 m a.s.l. for the period 2002–2010.

Standardized water deficit index calculation

As precipitation alone does not accurately represent water availability for trees (Piedallu *et al.*, 2013), we computed a standardized soil water deficit index (SWDI) based on daily mean temperature data, daily precipitation sums, and available water capacity of the soil. Monthly soil water deficit (SWD) is defined here as the difference between potential (PET) and actual evapotranspiration (AET), calculated using a

soil water balance model based on a modified Thornthwaite method (Willmott *et al.*, 1985). For a detailed explanation of the soil water balance calculation, see Bigler *et al.* (2007) and Camarero *et al.* (2011). We computed the soil water balance using an R function available online (http://geography.uore gon.edu/envchange/pbl/software.html). The calculated SWDs were then aggregated over different timescales (1–12 months), based on a modified version of the aggregation procedure by Vicente-Serrano *et al.* (2013), as follows:

$$\text{SWD}_n^K = \sum_{i=0}^{k-1}(\text{PET}_{n-1} - \text{AET}_{n-1}), n \ge k$$

where k (in months) is the timescale of aggregation and n is the calculation number. Following the aggregation procedure, the SWD time series were adjusted to a log-logistic distribution with a Gaussian kernel, so that the past months have a decreasing weight, and standardized (series scaled to zero mean and unit variance) using the algorithm developed by Vicente-Serrano *et al.* (2010) within the R package *SPEI* (Beguería & Vicente-Serrano, 2012). Values of SWDI are positive during wet conditions (SWDI > 0) and negative during dry conditions (SWDI < 0).

Data analysis

To determine the influence of drought on the growth and physiological responses of trees, we carried out correlation analyses between SWDI at different timescales (1–12 months) and the following seven tree-ring variables: earlywood width (EW), latewood width (LW), ring width (RW), $\delta^{13}C$ in earlywood ($\delta^{13}C_{EW}$), $\delta^{13}C$ in latewood ($\delta^{13}C_{LW}$), $\delta^{18}O$ in earlywood ($\delta^{18}O_{EW}$), and $\delta^{18}O$ in latewood ($\delta^{18}O_{LW}$). With respect to the evaluation of SWDI in combination with stable isotopes, an increase in SWDI (i.e., an increase in water availability) is expected to coincide with a decrease in $\delta^{13}C$ or $\delta^{18}O$, and vice versa. Bootstrapped correlation coefficients were calculated for the year prior to growth (June–December) and the year of growth (January–September) for the period 1961–2009 using the R package *bootRes* (Zang & Biondi, 2013). Correlation coefficients were

introduced into a principal component analysis (PCA) to elucidate the relationship between the different species and sites regarding soil water deficits.

Results

Tree-ring width, $\delta^{13}C$, and $\delta^{18}O$ chronologies

The high EPS values (≥0.89) for the species at both sites indicated that a sufficient number of trees were included in the chronologies to be representative of the entire population (Table 1). European larch (0.80 mm yr^{-1}) and Scots pine (0.72 mm yr^{-1}) had the lowest average radial growth rates at the xeric and mesic site, respectively. The mean sensitivity and Rbar values were higher at the xeric than at the mesic site (Table 1), indicating that at the xeric site, there is greater year-to-year variability in radial growth associated with interannual changes in weather conditions and a stronger common growth signal between trees. European larch and Norway spruce showed the highest mean sensitivity at the xeric site (0.50 and 0.42, respectively). A good synchronicity was observed between the species at the xeric and mesic sites for the EW, LW, and RW chronologies (Fig. 2).

$\delta^{13}C$ chronologies at the xeric site showed high synchronicity until 1990 for all species except Norway spruce (Fig. 2). After 1990, the chronologies became more asynchronous, especially in earlywood. The level of $\delta^{13}C$ enrichment was species-specific, with Norway spruce having the highest level over time (Table 2). For $\delta^{18}O$ chronologies at the xeric site, a good agreement between species was found in early- and latewood (Fig. 2). At the mesic site, $\delta^{13}C$ chronologies in earlywood were asynchronous between the species over time, whereas good synchronicity was found for the latewood section (Fig. 2). Douglas-fir and Norway spruce had the highest level of $\delta^{13}C$ enrichment over

Table 1 Tree characteristics (mean DBH, mean height), and time series statistics of the tree-ring width for the period 1960–2009[*]

Site	Species	DBH (cm)	Height (m)	RW (mm)	SD (mm)	AC1	MS	Rbar	EPS
Aosta (xeric)	Black pine	37.2	15.6	1.60	0.67	0.54	0.28	0.69	0.97
	Douglas-fir	42.4	18.9	1.60	0.72	0.64	0.29	0.75	0.98
	European larch	25.0	13.0	0.80	0.54	0.53	0.50	0.70	0.97
	Scots pine	24.7	9.5	1.02	0.61	0.70	0.34	0.58	0.95
	Norway spruce	26.4	14.1	1.42	0.79	0.54	0.42	0.64	0.96
Biel (mesic)	Black pine	44.8	25.0	1.42	0.49	0.63	0.23	0.55	0.95
	Douglas-fir	76.8	39.1	2.78	0.73	0.45	0.20	0.58	0.95
	European larch	51.5	31.3	1.43	0.74	0.72	0.27	0.46	0.90
	Scots pine	42.7	23.1	0.72	0.36	0.67	0.27	0.53	0.93
	Norway spruce	52.4	34.3	2.09	0.74	0.64	0.22	0.41	0.89

*Raw tree-ring chronologies: RW, mean total ring width; SD, standard deviation; AC1, first order autocorrelation. Residual chronologies: MS, mean sensitivity; Rbar, mean interseries correlation; EPS, expressed population signal.
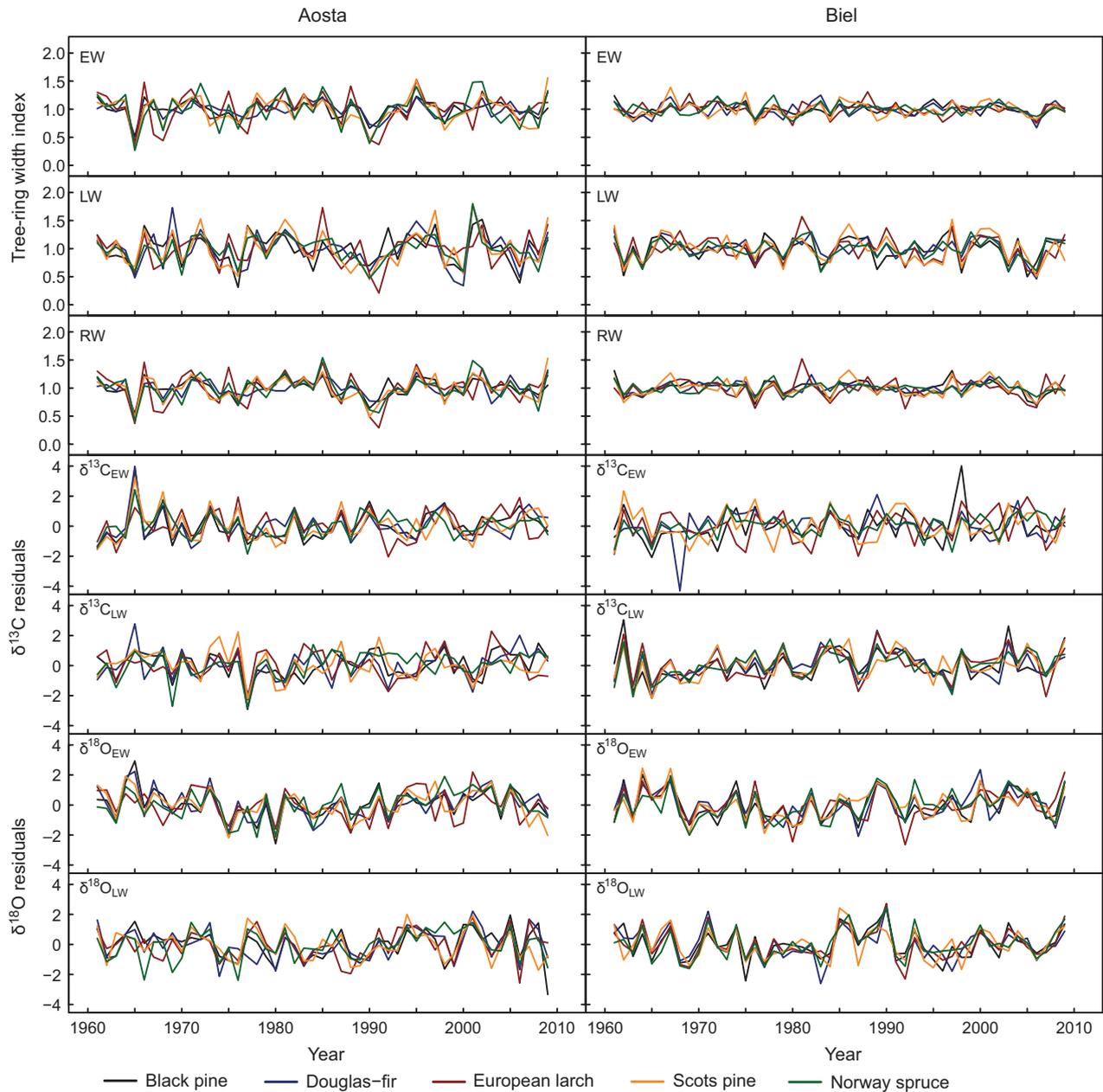
Fig. 2 Earlywood (EW), latewood (LW), and ring width (RW) residual chronologies, as well as $\delta^{13}C$ residual chronologies of earlywood ($\delta^{13}C_{EW}$) and latewood ($\delta^{13}C_{LW}$) and $\delta^{18}O$ residual chronologies of earlywood ($\delta^{18}O_{EW}$) and latewood ($\delta^{18}O_{LW}$) of the five species for the period 1961–2009 at the xeric site in Aosta and mesic site in Biel.

time (Table 2). $\delta^{18}O$ chronologies were very similar between species in early- and latewood (Fig. 2).

At the xeric site, earlywood and latewood chronologies of all species, except European larch, were highly significantly correlated with $\delta^{13}C_{EW}$ and $\delta^{13}C_{LW}$ chronologies, respectively (Table 3). Latewood chronologies of Douglas-fir, European larch, and Scots pine were significantly positively correlated with $\delta^{18}O_{LW}$ chronologies. $\delta^{13}C$ and $\delta^{18}O$ chronologies of black pine, Douglas-fir, and European larch were significantly

correlated. At the mesic site, all species showed significant correlations between the latewood and $\delta^{13}C_{LW}$ chronologies (Table 3). Only European larch and black pine had significant positive correlations between $\delta^{13}C$ and $\delta^{18}O$ chronologies.

Site-specific response to water deficit

Clear differences in the occurrence and duration of water deficit periods at the study sites were revealed by

Table 2 Time series statistics of the stable isotope series for the period 1961–2009[†]

Site	Species	Mean $\delta^{13}C_{EW}$ (‰)	$\delta^{13}C_{EW}$ AC1	Mean $\delta^{13}C_{LW}$ (‰)	$\delta^{13}C_{LW}$ AC1	Mean $\delta^{18}O_{EW}$ (‰)	$\delta^{18}O_{EW}$ AC1	Mean $\delta^{18}O_{LW}$ (‰)	$\delta^{18}O_{LW}$ AC1
Aosta (xeric)	Black pine	−22.79	0.24	−21.70	0.22[*]	27.01	0.12	27.05	0.10
	Douglas-fir	−22.90	0.04	−21.75	0.12	24.71	0.19	26.10	0.03
	European larch	−22.13	0.07	−21.64	0.00	25.56	−0.18	25.76	0.18
	Scots pine	−22.79	−0.01	−21.54	−0.04	26.05	0.12	26.01	0.32[**]
	Norway spruce	−21.35	0.53[***]	−20.34	0.29[*]	26.32	0.07	26.32	0.15
Biel (mesic)	Black pine	−24.44	0.11	−23.93	0.03	25.10	0.08	25.80	−0.03
	Douglas-fir	−21.79	0.30[*]	−21.60	0.24[*]	23.73	0.22[*]	25.31	0.14
	European larch	−24.62	0.00	−24.60	0.05	24.33	−0.01	25.35	−0.04
	Scots pine	−24.20	0.10	−23.60	0.01	23.54	0.18	24.54	−0.01
	Norway spruce	−22.83	0.66[***]	−22.54	0.39[*]	24.52	0.13	25.31	0.00

[†]$\delta^{13}C_{EW}$ and $\delta^{13}C_{LW}$ stand for $\delta^{13}C$ in earlywood and $\delta^{13}C$ in latewood and were corrected for changes in atmospheric $\delta^{13}C$ and CO_2 according to McCarroll *et al.* (McCarroll *et al.*, 2009). $\delta^{18}O_{EW}$ and $\delta^{18}O_{LW}$ denote $\delta^{18}O$ in earlywood and $\delta^{18}O$ in latewood, respectively. AC1 indicates first-order autocorrelation. Durbin-Watson tests were performed to test the significance of the AC1. The significance levels are indicated by
*$P < 0.05$.
**$P < 0.01$.
***$P < 0.001$.

Table 3 Pearson's correlation coefficients of the relationships between the residual chronologies of the different tree-ring variables: earlywood width (EW), latewood width (LW), carbon isotopic composition of earlywood ($\delta^{13}C_{EW}$), carbon isotopic composition of latewood ($\delta^{13}C_{LW}$), oxygen isotopic composition of earlywood ($\delta^{18}O_{EW}$), and oxygen isotopic composition of latewood ($\delta^{18}O_{LW}$)

Site	Tree-ring variables	Species				
		Black pine	Douglas-fir	European larch	Scots pine	Norway spruce
Aosta (xeric)	EW vs. $\delta^{13}C_{EW}$	−0.63[***]	−0.51[***]	−0.23	−0.65[***]	−0.55[***]
	LW vs. $\delta^{13}C_{LW}$	−0.48[***]	−0.45[**]	−0.13	−0.37[**]	−0.46[***]
	EW vs. $\delta^{18}O_{EW}$	−0.40[**]	−0.14	0.17	0.01	−0.05
	LW vs. $\delta^{18}O_{LW}$	0.18	0.45[**]	0.41[**]	0.55[***]	0.26
	$\delta^{13}C_{EW}$ vs. $\delta^{18}O_{EW}$	0.55[***]	0.30[*]	−0.03	0.17	0.03
	$\delta^{13}C_{LW}$ vs. $\delta^{18}O_{LW}$	0.01	0.06	−0.34[**]	−0.21	−0.08
Biel (mesic)	EW vs. $\delta^{13}C_{EW}$	−0.31[*]	−0.03	−0.12	−0.20	−0.26
	LW vs. $\delta^{13}C_{LW}$	−0.47[***]	−0.47[***]	−0.28[*]	−0.29[*]	−0.55[***]
	EW vs. $\delta^{18}O_{EW}$	−0.31[*]	−0.04	0.02	0.10	−0.09
	LW vs. $\delta^{18}O_{LW}$	−0.09	0.23	0.19	0.48[***]	0.15
	$\delta^{13}C_{EW}$ vs. $\delta^{18}O_{EW}$	0.22	0.14	0.41[**]	0.23	0.11
	$\delta^{13}C_{LW}$ vs. $\delta^{18}O_{LW}$	0.53[***]	0.08	0.37[**]	0.13	0.25

The significance levels are indicated by
*$P < 0.05$.
**$P < 0.01$.
***$P < 0.001$.

the SWDI at different monthly timescales for the period 1960 to 2009 (Fig. 3). The periods 1960–1964, 1969–1976, 1983–1992, and 2003–2009 were very dry in Aosta, whereas the periods 1970–1976, 1983–1986, 1989–1992, and 2003–2006 were dry in Biel. At longer timescales (6 and 12 months), drought periods were more frequent in Aosta than in Biel.

At both sites, $\delta^{13}C$ series of all species showed a non-climatic trend due to changes in atmospheric $\delta^{13}C$ and

CO_2 concentration over time (Fig. S1 and S2). After removing the influence of changes in atmospheric $\delta^{13}C$ and CO_2 on $\delta^{13}C$ time series, correlation coefficients increased in most cases (Table S1).

At the xeric site, water availability in the previous year, during winter and in spring of the current year significantly influenced the tree-ring variables of the five species (Table 4). Their EW, LW, and RW were significantly positively influenced by previous autumn
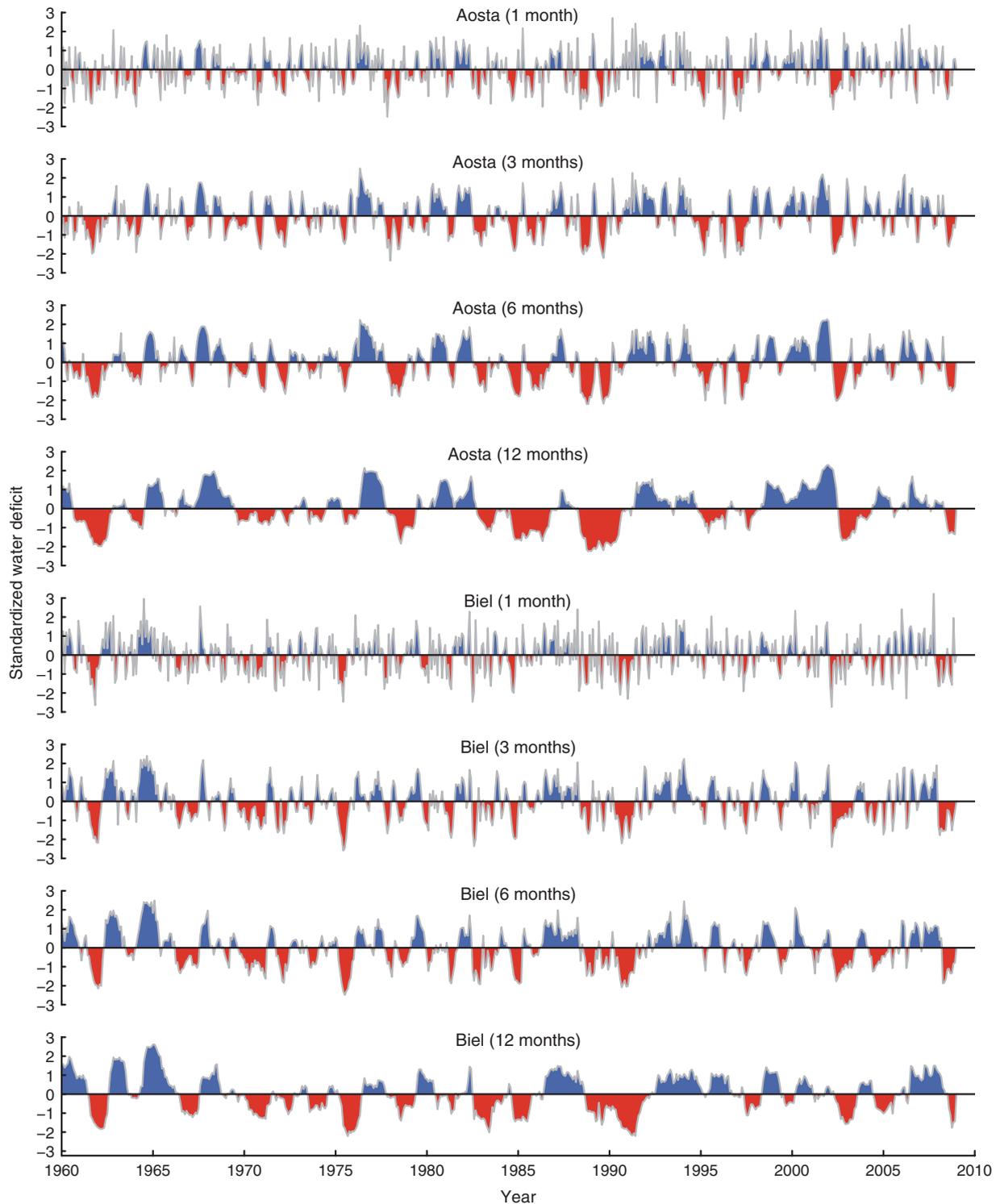
Fig. 3 Development of the standardized soil water deficit index at monthly timescales of 1, 3, 6, and 12 months for the xeric site in Aosta and the mesic site in Biel.

to current summer water availability ($r = 0.24$–0.47). The $\delta^{13}C_{EW}$ for all the species were significantly negatively correlated with water availability from the

current winter to early summer ($r = -0.38$ to -0.71). By contrast, the $\delta^{13}C_{LW}$ were significantly negatively correlated with water availability from winter to late

Table 4 Correlation coefficients between the tree-ring variables[†] and monthly standardized soil water deficit series for the xeric site in Aosta at the timescale and month of the year at which the highest correlation was reached. The months of the previous and current year in which significant correlations ($P < 0.05$) were found are also indicated

Tree-ring variable	Species	Timescale with highest correlation (month)	Month with highest correlation	Highest Correlation coefficient
EW	Black pine	7	January	0.44
	Douglas-fir	8	February	0.32
	European larch	12	February	0.31
	Scots pine	3	November[*]	0.41
	Norway spruce	12	June	0.44
LW	Black pine	12	July	0.47
	Douglas-fir	3	December[*]	0.31
	European larch	7	June[*]	0.24
	Scots pine	1	July	0.38
	Norway spruce	3	May	0.37
RW	Black pine	12	July	0.38
	Douglas-fir	12	May	0.33
	European larch	11	February	0.33
	Scots pine	6	December[*]	0.40
	Norway spruce	12	May	0.35
$\delta^{13}C_{EW}$	Black pine	12	April	−0.52
	Douglas-fir	12	April	−0.49
	European larch	12	June	−0.71
	Scots pine	12	May	−0.38
	Norway spruce	12	May	−0.41
$\delta^{13}C_{LW}$	Black pine	12	June	−0.54
	Douglas-fir	11	April	−0.50
	European larch	12	July	−0.62
	Scots pine	12	May	−0.58
	Norway spruce	11	July	−0.39
$\delta^{18}O_{EW}$	Black pine	4	May	−0.32
	Douglas-fir	6	May	−0.35
	European larch	4	June[*]	0.33
	Scots pine	9	May	−0.31
	Norway spruce	–	–	–
$\delta^{18}O_{LW}$	Black pine	5	August	0.54
	Douglas-fir	5	April	−0.22
	European larch	9	June[*]	0.26
	Scots pine	9	August	0.50
	Norway spruce	8	August	0.42

Color scale for the correlation coefficients

| < -0.7 | -0.6 | -0.5 | -0.4 | ≥ -0.3 | Not significant | ≤ 0.3 | 0.4 | 0.5 | 0.6 | > 0.7 |

*Previous year.

[†]EW, earlywood width; LW, latewood width; RW, total ring width; $\delta^{13}C_{EW}$, $\delta^{13}C$ in earlywood; $\delta^{13}C_{LW}$, $\delta^{13}C$ in latewood; $\delta^{18}O_{EW}$, $\delta^{18}O$ in earlywood; $\delta^{18}O_{LW}$, $\delta^{18}O$ in latewood. The $\delta^{13}C$ series were corrected for changes in atmospheric $\delta^{13}C$ and CO_2 following the "pre-industrial" (PIN) correction from McCarroll *et al.* (2009). The EW, LW, RW, as well as $\delta^{13}C$ and $\delta^{18}O$ residual chronologies were used.

summer of the current year ($r = -0.39$ to -0.62). $\delta^{13}C$ signals of all species responded to water deficits at longer timescales (11–12 months) compared with $\delta^{18}O$ signals (4–9 months). The $\delta^{18}O_{EW}$ of Douglas-fir, European larch, and Scots pine were significantly positively correlated with water availability of the previous year. The $\delta^{18}O_{EW}$ of black pine, Douglas-fir, and Scots pine were significantly negatively correlated with water availability in May of the current year. Signifi-

cant positive correlations were found between water availability and $\delta^{18}O_{LW}$ for the summer months of the current year.

At the mesic site, the correlations between the seven tree-ring variables and the SWDI were much stronger during the current summer months than at the xeric site (Table 5). EW was significantly positively influenced by moisture availability during the previous autumn and current winter ($r = 0.39$–0.53), except for

Table 5 Correlation coefficients between the tree-ring variables[†] and monthly standardized soil water deficit series for the mesic site in Biel at the timescale and month of the year at which the highest correlation was reached. The months of the previous and current year in which significant correlations ($P < 0.05$) were found are also indicated

Tree-ring variable	Species	Timescale with highest correlation (month)	Month with highest correlation	Highest correlation coefficient	Month with significant correlations — Previous year (J J A S O N D) / Current year (J F M A M J J A S)
EW	Black pine	12	June	0.39	
	Douglas-fir	10	February	0.53	
	European larch	7	August[*]	0.45	
	Scots pine	3	December[*]	0.39	
	Norway spruce	–	–	–	
LW	Black pine	7	August	0.66	
	Douglas-fir	4	July	0.55	
	European larch	5	July	0.38	
	Scots pine	5	July	0.38	
	Norway spruce	4	July	0.61	
RW	Black pine	7	July	0.53	
	Douglas-fir	4	July	0.33	
	European larch	4	July	0.33	
	Scots pine	–	–	–	
	Norway spruce	8	July	0.32	
$\delta^{13}C_{EW}$	Black pine	11	June	−0.51	
	Douglas-fir	8	September	−0.34	
	European larch	5	July	−0.58	
	Scots pine	11	August	−0.52	
	Norway spruce	12	June	−0.39	
$\delta^{13}C_{LW}$	Black pine	7	September	−0.72	
	Douglas-fir	7	September	−0.73	
	European larch	9	September	−0.70	
	Scots pine	9	September	−0.72	
	Norway spruce	9	August	−0.72	
$\delta^{18}O_{EW}$	Black pine	7	June	−0.52	
	Douglas-fir	10	June	−0.42	
	European larch	5	June	−0.55	
	Scots pine	10	June	−0.42	
	Norway spruce	10	June	−0.45	
$\delta^{18}O_{LW}$	Black pine	4	September	−0.56	
	Douglas-fir	3	September	−0.36	
	European larch	5	September	−0.38	
	Scots pine	1	September	−0.28	
	Norway spruce	4	September	−0.35	

Color scale for the correlation coefficients

< -0.7 -0.6 -0.5 -0.4 ≥ -0.3 Not significant ≤ 0.3 0.4 0.5 0.6 > 0.7

[*]Previous year.

[†]EW, earlywood width; LW, latewood width; RW, total ring width; $\delta^{13}C_{EW}$, $\delta^{13}C$ in earlywood; $\delta^{13}C_{LW}$, $\delta^{13}C$ in latewood; $\delta^{18}O_{EW}$, $\delta^{18}O$ in earlywood; $\delta^{18}O_{LW}$, $\delta^{18}O$ in latewood. The $\delta^{13}C$ series were corrected for changes in atmospheric $\delta^{13}C$ and CO_2 following the "pre-industrial" (PIN) correction from McCarroll *et al.* (2009). The EW, LW, RW, as well as $\delta^{13}C$ and $\delta^{18}O$ residual chronologies were used.

Norway spruce. Water availability during the current summer positively influenced the LW and RW of all species ($r = 0.32$–0.66), except for the RW of Scots pine. Significant negative correlations between $\delta^{13}C_{EW}$ and current spring to summer water availability were found for black pine, Douglas-fir, and European larch. The $\delta^{13}C_{EW}$ of Scots pine and Norway spruce were significantly negatively correlated with previous year autumn and current year water availability ($r = -0.34$ to -0.58).

The strongest and most consistent correlations of all species were observed for $\delta^{13}C_{LW}$. The $\delta^{13}C_{LW}$ were highly significantly negatively correlated with water availability in the current summer, particularly in August and September ($r = -0.70$ to -0.73). The $\delta^{18}O_{EW}$ were significantly negatively correlated with water availability in spring and summer of the current year ($r = -0.42$ to -0.55), whereas the $\delta^{18}O_{LW}$ were significantly negatively correlated with water availability in

September of the current year ($r = -0.28$ to -0.56). The $\delta^{18}O$ signal responded to water deficits at shorter timescales compared with the $\delta^{13}C$ signal, but not as strongly as at the xeric site.

A clear separation of the site-specific responses was highlighted by the PCAs (Fig. 4). The first two axes of the PCA based on the correlation coefficients between monthly SWDI and radial growth variables accounted for 54.9% and 21.1% of the total variance, respectively (Fig. 4a–c). Previous year and current year monthly water deficits were positively associated with growth at the xeric site, whereas current summer water deficits were positively associated with growth at the mesic site. The first two axes of the PCA for the correlation coefficients between monthly SWDI and $\delta^{13}C_{EW}$ and $\delta^{13}C_{LW}$ explained 49.0% and 35.7% of the total variance (Fig. 4d–f). At the mesic site, $\delta^{13}C_{EW}$ was positively related to previous year water deficits, whereas $\delta^{13}C_{LW}$ was negatively related to current year water deficits. At the xeric site, $\delta^{13}C_{EW}$ and $\delta^{13}C_{LW}$ were positively associated with current year summer water deficits. The first two axes of the PCA for the correlation coefficients between monthly SWDI and $\delta^{18}O_{EW}$ and $\delta^{18}O_{LW}$ accounted for 71.8% and 10.7% of the total variance (Fig. 4g–i). At the xeric site, $\delta^{18}O_{EW}$ and $\delta^{18}O_{LW}$ were positively correlated with current year summer water deficits, whereas $\delta^{18}O_{EW}$ and $\delta^{18}O_{LW}$ were negatively correlated with current year summer water deficits at the mesic site.

Species-specific responses to water deficit

At the xeric site, winter to summer water deficits reduced the radial growth of black pine (Table 4). Dry periods between December and September significantly influenced the $\delta^{13}C$ of black pine. The radial growth of Douglas-fir was little affected by water deficits, but the $\delta^{13}C$ was sensitive to dry periods between January and July. The radial growth of European larch was significantly reduced by water deficits in previous autumn and current winter, whereas the $\delta^{13}C$ was highly significantly negatively correlated with water deficits between March and August. The radial growth of Scots pine was limited by water deficits in previous autumn and current winter. The $\delta^{13}C_{LW}$ of Scots pine was sensitive to drought period between December and July. The radial growth of Norway spruce was significantly limited by water deficits that occur between December and June, whereas $\delta^{13}C$ was sensitive to dry periods between March and August. The $\delta^{18}O_{LW}$ of Norway spruce was positively correlated with summer water deficits.

At the mesic site, summer water deficits significantly reduced the radial growth of black pine, whereas the $\delta^{13}C$ and $\delta^{18}O$ were significantly negatively correlated with spring and summer water deficits (Table 5). The EW of Douglas-fir was positively influenced by water availability in the previous year and winter. The $\delta^{13}C$ of Douglas-fir was sensitive to water deficits that occur between June and September, whereas the $\delta^{18}O$ significantly responded to water availability between May and September. Dry periods in the year prior of growth reduced the earlywood of European larch. The $\delta^{13}C$ and $\delta^{18}O$ of European larch were sensitive to summer drought. The radial growth of Scots pine was little affected by drought in spite of the high sensitivity of the $\delta^{13}C_{LW}$ throughout the year. The $\delta^{18}O$ of Scots pine was sensitive to water deficits between May and September. The latewood of Norway spruce was very limited by summer water deficits, whereas the $\delta^{13}C$ was sensitive to previous autumn, as well as current spring and summer water availability. Late spring and summer water availability significantly influenced $\delta^{18}O$ of Norway spruce.

Discussion

Site-specific response to drought

Trees at the xeric site were found to be affected more strongly by previous year and winter water deficits than at the mesic site, where they mainly responded to summer water deficits (Table 4 and 5; Fig. 4). The lower available water capacity of the soil (51 mm) at the xeric than at the mesic site (119 mm) and the strong seasonality of precipitation in the Aosta Valley may reinforce the differences between the sites. The annual precipitation maximum in the Aosta Valley occurs in early spring and autumn, whereas summers are generally dry (Fig. 1a). Hence, one drought-avoidance strategy is to complete most of the secondary growth before the onset of dry periods in summer (Zweifel *et al.*, 2006; Eilmann *et al.*, 2011; Sarris *et al.*, 2013), as indicated by the weak summer drought signals in the EW, LW, RW, $\delta^{13}C_{EW}$, and $\delta^{18}O_{EW}$ (Table 4). By contrast, trees at the mesic site do not regularly experience periods of water deficit as precipitation is abundant and rather uniformly distributed over the year (Fig. 1b). Moreover, the relatively high available water capacity of the soil allows for the buffering of short-term water deficits that occur early in the growing season, as long as the soil-moisture reservoir is refilled during the dormant season when evapotranspiration is minimal. However, the strong correlations found between radial growth variables, $\delta^{13}C$ and SWDI at the mesic site indicate that soil water deficits during summer months can strongly reduce carbon fixation and subsequently tree growth (Table 5). This coupling between carbon fixation and
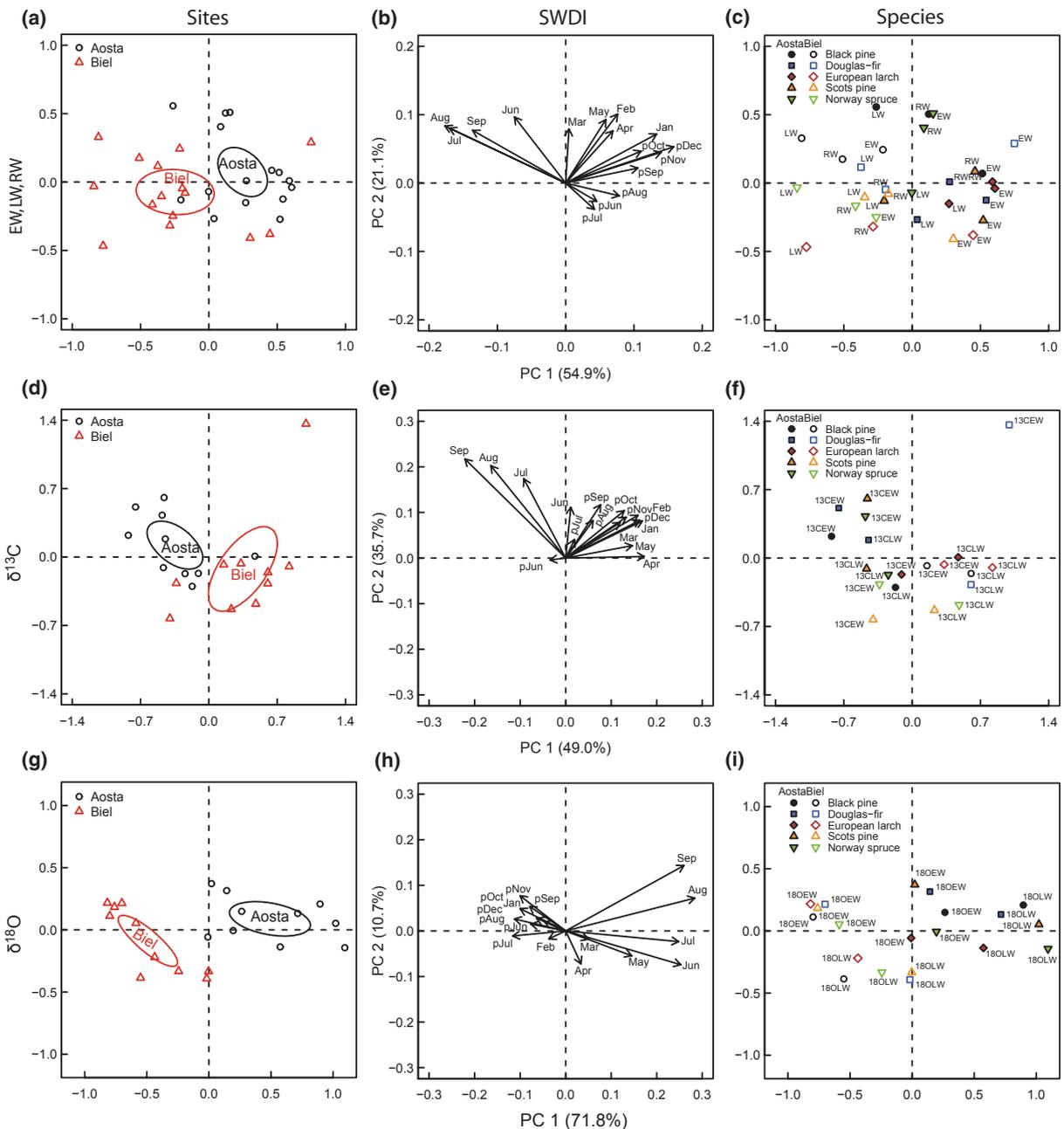
Fig. 4 Principal component analysis (PCA) of the correlation coefficients between species and monthly standardized soil water deficit index (SWDI) for earlywood (EW), latewood (LW), and total ring width (RW) (a–c); $\delta^{13}C$ in earlywood (13CEW) and $\delta^{13}C$ in latewood (13CLW) (d–f); and $\delta^{18}O$ in earlywood(18OEW) and $\delta^{18}O$ in latewood (18OLW) (g–i). Correlations coefficients were calculated between monthly SWDI and the residuals chronologies of the tree-ring variables from previous June to current September. SWDIs in the previous year are indicated with a 'p'. The correlation between the tree-ring variables and monthly SWDI is given by the cosine of the angle between two vectors, but only the apices (symbols) of the vectors of the tree-ring variables of the species are displayed for visual clarity. Vectors pointing in the same direction indicate a high positive correlation, whereas vectors pointing in opposite direction indicate a high negative correlation. Vectors crossing at right angle indicate no or marginal correlation. Monthly SWDI vectors with the longest vectors are the most important. Differences between sites are depicted with ellipses showing the 95% confidence interval.

radial growth is supported by the significant negative correlations between $\delta^{13}C_{LW}$ and LW for all species at the mesic site (Table 3). The high vulnerability of trees to summer drought at the mesic site agrees with the susceptibility to summer water deficits of various conifer species reported recently from mesic forests in northeastern Spain and France (Lebourgeois *et al.*, 2010; Pasho *et al.*, 2011). However, as long as winter and

spring precipitation remains sufficient to refill the soil water reservoir, growth reductions should not be overly strong, such that increasing rates of tree mortality are rather unlikely even if summers become drier, as projected (Christensen *et al.*, 2007; CH2011, 2011).

At the xeric site, the $\delta^{13}C$ and RW responded to drought at long timescales (11–12 months), suggesting that trees have a certain adaptive capacity in response to drought of short duration. Trees in dry inner-Alpine forests have a lower stature, smaller canopy, and shorter needles with a higher stomatal density than those in mesic forests (Dobbertin *et al.*, 2010), which leads to a more efficient control of water loss and a reduced sensitivity to water deficits of short duration. By contrast, at the mesic site, trees were more vulnerable to water deficits of shorter duration. Radial growth was significantly reduced by water deficits lasting less than 8 months, whereas photosynthesis and carbon uptake, inferred from $\delta^{13}C$ values, were affected by drought periods lasting between 5 and 12 months (Table 5). Trees at the mesic site have large crowns with a high foliage mass and large stems (data not shown), implying a disadvantage under drought. Thus, it is possible that these aboveground characteristics make these trees more sensitive to drought of short duration, as reflected in the strong $\delta^{13}C$ response to summer conditions (Table 5), as they need more carbon, water, and nutrients to maintain their functions. The higher sensitivity of trees to drought of short duration at the mesic than at the xeric site agrees with the results of Vicente-Serrano *et al.* (2013) reported at the global scale. They found that trees in humid biomes respond to drought at shorter timescales than trees in dry biomes and explained this divergence by the different physiological mechanisms and adaptations of trees, which depend on site moisture conditions. At the xeric site, our results show that long-lasting drought periods (>11 months) can strongly reduce carbon fixation and the amount of carbohydrates within a tree (Table 4), leading to a severe reduction in radial growth, as indicated by the strong coupling found between $\delta^{13}C$ and radial growth (Table 3). By contrast, we found a much shorter response time for $\delta^{18}O$, which reflects changes in the water signal, than for $\delta^{13}C$, indicating a faster turnover of water than carbohydrates within the tree (Brandes *et al.*, 2007; Offermann *et al.*, 2011). Thus, the response of trees to drought under dry conditions can be seen as a two-stage process. First, water stored in the xylem will be used up as a short-term response. Then, carbohydrate reserves will diminish as the tree's capability to form and replenish carbohydrates decreases with increasing drought duration and frequency, which is ultimately reflected in lower radial tree growth. Therefore, if summer drought is severe and long-lasting, and

if multiple dry years occur, tree fitness and survival mainly depend on the availability of carbon reserves, which are already limited in dry environments (McDowell *et al.*, 2008; Breshears *et al.*, 2009; Eilmann *et al.*, 2010). In such cases, favorable conditions in spring, autumn, and even winter are becoming critical for tree survival in inner-Alpine dry forests.

Species-specific response to drought

At the xeric site, tree-ring $\delta^{13}C$ of all species, except European larch, was negatively correlated with water availability and radial growth, whereas tree-ring $\delta^{18}O_{LW}$ was positively correlated with water availability and latewood formation (Tables 3 and 4). This result indicates that radial growth declines when water availability decreases due to a reduction in stomatal conductance and photosynthetic activity, while an increased utilization of water from deeper soil layers is promoted. Under dry conditions, trees can improve their water acquisition by increasing their root-to-shoot ratio and fine root production (Saxe *et al.*, 1998; Chaves *et al.*, 2003). This in turn allows trees to reach water at deeper soil horizons that are less enriched in $\delta^{18}O$ than surface water (Dawson, 1993; Sarris *et al.*, 2013), and to increase water uptake near the soil surface in moist periods, as indicated by the positive correlations found for all species between $\delta^{18}O_{LW}$ and SWDI. Therefore, if the frequency, duration, and intensity of summer droughts increase, deep moisture pools become important for tree survival in inner-Alpine dry forests.

At the xeric site, the seasonality of water deficits had a different effect on the species, but no clear differences between the species were observed regarding their sensitivity to the duration of water deficits (timescale of drought). This is surprising given the differences in tree architecture and especially rooting patterns between species. For instance, Norway spruce, a shallow-rooted species (Schmid & Kazda, 2002), expected to be more sensitive to short-term variations in water availability than deep-rooted species, was not found to be more sensitive to water deficits of short duration than the other co-occurring species. However, the radial growth of Norway spruce was very sensitive to weather conditions, as indicated by its high mean sensitivity (0.42). Soil water availability between December of the previous year and July of the current year was also critical for this species (Table 4). Therefore, if spring and summer conditions become drier as projected (Christensen *et al.*, 2007), the radial growth and vigor of Norway spruce can be drastically reduced at dry sites in the Alps. Of all the investigated species, European larch shows a contrasting physiological strat-

egy to deal with water deficits: its radial growth remained insensitive and depended mainly on previous year water availability, despite its high sensitivity of tree-ring $\delta^{13}C$ to spring and summer water deficits (Table 4). The deciduous character of European larch makes it dependent on previous year soil water storage for budburst and foliage formation in early spring, and forces it to be photosynthetically active in summer irrespective of water deficits. This may explain the negative correlation found between tree-ring $\delta^{13}C_{LW}$ and $\delta^{18}O_{LW}$ of European larch (Table 3), which suggests that this species tends to increase its assimilation rate irrespective of soil water availability in summer. This finding agrees with the results of Anfodillo et al. (1998) who reported relatively high transpiration and assimilation rates for European larch during periods with moderate water deficits in the Alps. However, this strategy makes this species prone to cavitation, particularly during severe drought events when soil water availability is insufficient to meet the high water demand of the canopy. Consequently, ineffective stomatal control of water loss under drier climate increases the risk of hydraulic failure and mortality of European larch.

At the mesic site, the impacts of the duration of soil water deficits did not clearly differ between species. European larch and Norway spruce, both known to be rather drought sensitive, were not more affected by water deficits of short duration than drought-tolerant species such as black pine, Scots pine, and Douglas-fir (Table 5). The relatively high available water capacity of the soil may have masked any differences in response time to drought between species. However, we found that drought seasonality influenced the species differently. Previous year water availability negatively affected carbon assimilation and fixation of Scots pine and Norway spruce early in the growing season, as suggested by the strong negative correlation found between $\delta^{13}C_{EW}$ and SWDI. However, this reduction in carbon uptake only slightly reduced radial growth of these two species (Table 5). Still, long-lasting water deficit periods may strongly reduce carbon reserves and vigor of trees, which, in return, prolong their growth recovery (Galiano et al., 2011) and increase their vulnerability to pests and pathogens (Jactel et al., 2012).

Implications of the results in a global context

Our results and those from other studies (e.g., Zweifel et al., 2009; Eilmann & Rigling, 2012; Schuster & Oberhuber, 2013) indicate that Norway spruce and European larch at their dry distribution limits in the Central Alps (<1200 m a.s.l.) are already at their physiological limits

and may undergo severe growth decline if the climate develops as projected for the dry inner-Alps over the coming decades. Indeed, the small environmental niche breadth and range of these two species in the dry inner-Alps may limit their adaptation to future environmental conditions. Thus, the projected decrease in water availability in these regions (Christensen et al., 2007; CH2011, 2011) will likely pose severe threats to these two species, triggering major changes in forest composition and the provision of ecosystem goods and services such as biodiversity, timber production, and protection against gravitational hazards (Elkin et al., 2013). Such impacts from ongoing changes in the climate are already evident at low elevations (<1000 m a.s.l.) in several inner-Alpine valleys where shifts in species composition are occurring at unprecedented speed, possibly compromising the provision of ecosystem services (Rigling et al., 2013). At moist sites located at low elevation (<750 m a.s.l.) in Central Europe, an increase in the frequency, duration, and intensity of summer drought will certainly decrease soil water availability and negatively affect tree growth and fitness. Furthermore, summer drought can promote the development of forest pests and pathogens (Desprez-Loustau et al., 2006; Rouault et al., 2006), with less vigorous trees being more susceptible to be attacked by biotic disturbance agents (Gaylord et al., 2013). Therefore, the performance or even the survival of species vulnerable to bark beetle attack, such as Norway spruce, can be compromised under a warmer and drier climate in the lowlands of Central Europe. As the results of this study are solely based on two sites, generalization of the results in a global context needs to be done with some cautions, and further studies are needed before to draw general conclusion. Lastly, the $\delta^{13}C$ and $\delta^{18}O$ of all species were more sensitive to water deficits than the radial growth variables, indicating that the former proxies yield valuable physiological information that would otherwise remain undetected with standard radial growth analysis.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Raw $\delta^{13}C$ chronologies, corrected $\delta^{13}C$ chronologies for changes in atmospheric $\delta^{13}C$ and corrected chronologies after correcting the $\delta^{13}C$ values for changes in atmospheric $\delta^{13}C$ and CO_2 concentrations at the xeric site in Aosta.

Figure S2. Raw $\delta^{13}C$ chronologies, corrected $\delta^{13}C$ chronologies for changes in atmospheric $\delta^{13}C$ and corrected chronologies after correcting the $\delta^{13}C$ values for changes in atmospheric $\delta^{13}C$ and CO_2 concentrations at the mesic site in Biel.

Table S1. Correlations found for the $\delta^{13}C$ series corrected only for changes in atmospheric $\delta^{13}C$ vs. those found after correcting for changes in atmospheric $\delta^{13}C$ and CO_2.