

Growth response of five co-occurring conifers to drought across a wide climatic gradient in Central Europe



Mathieu Lévesque^{a,b,*}, Andreas Rigling^a, Harald Bugmann^b, Pascale Weber^a, Peter Brang^a

^a WSL Swiss Federal Institute for Forest, Snow and Landscape Research, Zuercherstrasse 111, CH-8903 Birmensdorf, Switzerland

^b Swiss Federal Institute of Technology Zurich, Chair of Forest Ecology, CH-8092 Zurich, Switzerland

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ABSTRACT

Climate change projections indicate drier conditions and an increase in the frequency and duration of extreme drought events in the coming decades in Central Europe. However, it is not clear which tree species will be able to cope with drier climatic conditions and higher year-to-year climatic variability. We analyzed tree-growth responses of five co-occurring conifer species to past climatic variations and severe droughts across a wide climatic gradient in Central Europe, covering four distinct biogeographic regions: the northern Swiss Alps, the Swiss Plateau, the foothills of the Jura Mountains and the dry Central Alps. We studied three native tree species (*Larix decidua* Mill, *Picea abies* (L.) Karst. and *Pinus sylvestris* L.) and two non-native species (*Pinus nigra* Arn. and *Pseudotsuga menziesii* var. *menziesii* (Mirb.) Franco). Tree-ring width was measured for 770 trees from 14 sites and species-specific site chronologies were established. Response-function analysis, Principal Component Analysis (PCA), linear regressions and Superposed Epoch Analysis were used to assess the species-specific growth sensitivity to climate and severe drought along the gradient. Irrespective of the species and site conditions, high temperatures and low precipitation amounts in summer and autumn of the year prior growth significantly reduced tree growth. When evaporative demand, precipitation and soil water holding capacity were considered together, low water availability in current summer strongly reduced growth. Overall, the growth-climate relationships of the species were not or only slightly related to the site water balance per se. However, when all species-specific growth response coefficients were introduced into a PCA, a clear separation of the populations of the Central Alps (driest sites) became apparent. At these sites, soil water deficits in previous autumn and current spring strongly reduced radial growth, whereas at moist and wet sites on the Swiss Plateau, in the Jura Mountains and northern Alps summer drought impeded growth. Along the gradient, the native *P. abies*, *L. decidua* and *P. sylvestris* were the most sensitive species to drought, implying that their long-term performance and survival on nowadays dry sites can be compromised under a drier climate in Central Europe.

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1. Introduction

Consequences of global warming and reduced water availability on forest ecosystems are already visible worldwide (Allen et al., 2010). In Europe, prolonged water deficits and severe droughts have caused increasing rates of tree mortality, severe forest decline and vegetation shifts on dry sites and at the edge of species distribution ranges (Galiano et al., 2010; Rigling et al., 2013). These

phenomena will likely increase in magnitude in the coming years with the anticipated higher year-to-year climatic variability and long-term increase in aridity (Christensen et al., 2007), challenging forest management practices and compromising the provision of forest ecosystem goods and services (Elkin et al., 2013). Since anticipated drier climatic conditions may differ in magnitude between sites, priority should be given to understanding the sensitivity of tree species to drought along wide ecological gradients. This is becoming particularly critical as there is growing evidence of drought-induced growth declines at the range margins of species distribution (Andreu-Hayles et al., 2011; Lévesque et al., 2014), but also in the center of the species' ranges (Carnicer et al., 2011). At the same time, the search for alternative tree species that are drought tolerant, but also able to produce a sufficient amount of high

* Corresponding author at: Swiss Federal Institute for Forest, Snow and Landscape Research, Research Group Stand Dynamics and Silviculture, Zuercherstrasse 111, CH-8903 Birmensdorf, Switzerland. Tel.: +41 44 739 25 43.

E-mail address: mathieu.levesque@wsl.ch (M. Lévesque).

quality timber becomes essential for the elaboration of future adaptive forest management strategies (cf. Eilmann et al., 2013; Temperli et al., 2012).

Dendrochronological studies using tree-ring width are valuable to retrospectively analyze tree performance to past climatic conditions including droughts, as radial growth has a lower allocation priority in the short term than root and foliage formation (Kozłowski and Pallardy, 2002), making tree-ring width highly sensitive to climate variations (Fritts, 1976). By investigating tree growth responses to past climatic conditions and extreme drought events, the present sensitivity to climate of co-occurring tree species can be determined, and inferences can be drawn regarding their future performance. Tree response to drought depends on many environmental and site-related factors such as precipitation, temperature, topography and soil characteristics (Pasho et al., 2012; Weber et al., 2013). In regions with heterogeneous relief, topographic conditions and soil characteristics strongly influence and modulate tree-growth response to drought. Growth is most sensitive to drought at sites with low water holding capacity (Rigling et al., 2002; Weber et al., 2007) and on south and south-west aspects (Fekedulegn et al., 2003) where water deficits are exacerbated. Although drought sensitivity of tree species can vary markedly in space due to different ecological and climatic conditions, dendroecological analyses have rarely been conducted at large scales. Instead, they usually focus on a single or a few sites along a small ecological gradient. This is particularly true for Central Europe where the drought tolerance of co-occurring species has rarely been compared along wide ecological gradients (e.g. Zang, 2011). However, such analyses are highly relevant since recent findings indicate that co-occurring species with different life history strategies and contrasting responses to annual climate variability may reduce species-specific sensitivity to drought and enhance forest resilience to climate change (Drobyshev et al., 2013; Lebourgeois et al., 2013).

In this study, we analyzed tree-growth responses of five co-occurring conifer species to climatic variations (temperature, precipitation), soil moisture and to severe drought events across a wide climatic gradient in Central Europe. We studied three species that are native to Central Europe (*Larix decidua* Mill, *Picea abies* (L.) Karst. and *Pinus sylvestris* L.) and two non-native species (*Pinus nigra* Arn. and *Pseudotsuga menziesii* var. *menziesii* (Mirb.) Franco). *L. decidua* is a deciduous, pioneer and shade-intolerant species of mid to high altitudes, able to tolerate a high thermal amplitude (Ellenberg, 2009), but known to be somewhat sensitive to summer water deficits (Lévesque et al., 2013; Schuster and Oberhuber, 2013). *P. abies* is an intermediately shade-tolerant species, which is widely distributed across the Alps but has also been planted widely outside its natural range in Central Europe for economic reasons (Klimo et al., 2000). This species is quite sensitive to summer drought (Lebourgeois et al., 2010; Lévesque et al., 2013) and highly susceptible to bark beetle attacks during dry and hot summers (Wermelinger, 2004). *P. sylvestris* and *P. nigra* are light-demanding pioneer species, *P. sylvestris* being more drought sensitive (Lebourgeois et al., 2012; Martin-Benito et al., 2013). *P. sylvestris* occurs in a wide range of habitats from Spain to Siberia, and at elevations from sea level to 2600 m a.s.l. (Matias and Jump, 2012). *P. nigra* is native to the Mediterranean and Vienna basins, where summer droughts are frequent, and has been planted in Central Europe for ca. 130 years (Bürgi and Diez, 1986). This species is considered as a potential substitute for *P. sylvestris* under a drier climate in Central Europe (Thiel et al., 2012). *P. menziesii* (var. *menziesii*) is an intermediately shade-tolerant species native to western North America and was introduced to Europe in the mid 19th century. It is fast growing, produces high quality timber and is considered as a potential alternative to the more drought sensitive *P. abies* in Central Europe (Jansen et al., 2013).

The main objective of this study was to assess the growth sensitivity of five co-occurring conifers to climatic variability and severe droughts along a wide climatic gradient, with the goal of making inference about possible species responses to future increases in aridity in Central Europe. Specifically, the research questions were (1) How does tree growth response to temperature, precipitation and drought vary along a site moisture gradient? and (2) Do co-occurring species differ in their drought sensitivity along the gradient?

2. Materials and methods

2.1. Study area and sites

The study area is located in Switzerland and northern Italy and includes four distinct biogeographic regions: the northern Swiss Alps, the Swiss Plateau, the foothills of the Jura Mountains and the dry Central Alps (Table 1, Fig. 1). The order of the geographical regions corresponds to an ecological gradient of decreasing annual precipitation and increasing occurrence of summer drought. Within the study area, we selected 14 sites that met three criteria: (1) presence of at least one non-native species: *P. menziesii* or *P. nigra*, (2) co-occurrence of at least three of the five studied species, i.e., *P. abies*, *L. decidua*, *P. sylvestris*, *P. menziesii* and *P. nigra*, (3) even-aged stand with the presence of trees being at least 70 years old. Accordingly, 770 trees were sampled for dendroecological analysis (Table 2, Table S1). At each site, a soil profile was dug to determine soil type and soil properties. The physical and chemical properties of each soil horizon were recorded up to a depth of 1 m. The available water holding capacity of the soil between 0 and 100 cm depth was estimated using data on soil texture (content of sand, silt and clay), bulk density, content of coarse fragments (>2 mm) and depth of each of the recorded soil horizons according to AG Bodenkunde (1982).

2.2. Dendrochronological methods

At each site, between 11 and 15 healthy dominant or co-dominant trees per species were sampled by taking two increment cores per tree at ca. 50 cm height. Cores were mounted on wood supports and their surfaces were prepared using a core microtome (Gärtner and Nievergelt, 2010). Cambial age at sampling height was determined by estimating the number of missing rings between the first complete ring on the core and the pith according to the geometric method of Duncan (1989). The sampled trees were between 72 and 158 years old at coring height. Ring width was measured to the nearest 0.01 mm with a stereo microscope connected to a LINTAB digital positioning table and the software TSAP (Rinntech, Heidelberg, Germany). Individual tree-ring series were visually crossdated and verified statistically using COFECHA (Holmes, 1983). Cores that could not be correctly crossdated were removed from further analyses. For each tree, measurements from the two cores were averaged. Individual tree-ring width series were detrended to retain the high-to-mid frequency variability of growth using a 32 years cubic smoothing spline with a 50% frequency response using the package *dplR* (Bunn, 2008) within the R software (R Core Team, 2013). Individual standardized series were averaged per site using a biweight robust mean and standard chronologies were produced. To assess the signal strength of each chronology, inter-series correlations and expressed population signals were calculated (Wigley et al., 1984). The first order serial autocorrelation, which measures the influence of previous year's conditions on ring formation, and mean sensitivity, which quantifies the year-to-year variability in the width of consecutive tree rings (Fritts, 1976), were also calculated from the raw chronologies.

Table 1
Characteristics of the study sites.

Site	Site code	Biogeographic region	Species ^a	Latitude (N)	Longitude (E)	Elevation (m a.s.l.)	Aspect	Slope (%)	Water holding capacity (mm)	Mean annual temperature ^b (°C)	Mean annual precipitation sum ^b (mm)	Site water balance ^c (mm)
Schlanders	SC	Central Alps	Pn, Ld, Ps	46°38'02"	10°47'52"	1145	SW	45	128	7.0	493	-53
Aosta	AO	Central Alps	Pn, Pm, Ld, Ps, Pa	45°46'59"	7°32'52"	1150	SW	75	82	7.8	691	-43
Goppenstein	GO	Central Alps	Pm, Ld, Pa	46°21'35"	7°45'35"	1225	NW	70	84	6.3	931	-19
Crans	CR	Central Alps	Pn, Ld, Pa	46°17'20"	7°27'12"	1260	SW	27	186	6.0	954	-15
Steckhorn	ST	Swiss Plateau	Pn, Ld, Ps	47°39'36"	8°59'46"	535	W	20	82	8.7	932	-11
Yverdon-les-Bains	YB	Jura Mountains	Pn, Pm, Ld, Ps, Pa	46°52'10"	6°44'48"	570	SE	15	94	9.1	1071	-10
Stein am Rhein	SR	Swiss Plateau	Pm, Ld, Ps, Pa	47°41'44"	8°50'48"	615	SW	25	200	8.2	957	-6
Grenchen	GR	Jura Mountains	Pn, Ld, Ps, Pa	47°12'17"	7°23'59"	590	S	23	72	8.6	1169	3
Biel	BI	Jura Mountains	Pn, Pm, Ld, Ps, Pa	47°09'57"	7°16'06"	750	S	35	119	8.0	1240	12
Neuhaus	NE	Northern Swiss Alps	Pn, Ld, Ps, Pa	46°40'58"	7°48'32"	620	SW	61	59	8.7	1173	15
Merligen	ME	Northern Swiss Alps	Pn, Ps, Pa	46°42'20"	7°44'16"	750	NW	62	68	8.6	1170	19
Sargans	SA	Northern Swiss Alps	Pm, Ld, Ps	47°04'52"	9°28'09"	700	S	47	159	8.2	1275	30
Präfers	PF	Northern Swiss Alps	Pm, Ld, Pa	46°58'29"	9°29'30"	980	NW	65	90	6.8	1274	35
Balgach	BA	Swiss Plateau	Pn, Pm, Ld, Ps, Pa	47°24'45"	9°36'25"	600	SW	43	148	8.6	1296	43

^a Pn, *Pinus nigra*; Pm, *Pseudotsuga menziesii*; Ld, *Larix decidua*; Ps, *Pinus sylvestris*; Pa, *Picea abies*.

^b Averaged over the period 1941–2006.

^c The site water balance is calculated as the sum of precipitation minus potential evapotranspiration from April to September, averaged over the period 1941–2006. Potential evapotranspiration was estimated according to Thornthwaite (1948). Site water balance is positive when precipitation exceeds potential evapotranspiration and negative in the case of a moisture deficit. Sites are sorted from the driest to the wettest according to the site water balance values.

2.3. Climate data

For the sites located in Switzerland, we used spatially interpolated daily climatic data from the DAYMET model (Thornton et al., 1997). The model interpolates (100 m resolution) climate data from a wide range of nearby MeteoSwiss stations to each site based on a digital elevation model (100 m grid size). High-resolution daily temperature (mean, minimum and maximum) and total precipitation data were available for the period 1930–2006.

For the two sites in northern Italy, interpolated daily climatic data were not available, but data from several meteorological stations were available for the period 1930–2010. Climate data for the site in Aosta were obtained from the nearest station to the study site (5 km) located at the hydroelectric power station in Promiod Covalou (Department of Soil Conservation and Water Resources, Autonomous Region of Valle d'Aosta, Italy). Missing data were filled in by linear regression using data from the nearby stations of Saint-Christophe (13 km) and Brusson (15 km). For the site Schlanders, the nearest meteorological station was located 3 km away in Schlanders itself (Autonomous Province of Bozen, South Tyrol, Italy). For both Italian sites, temperature data were adjusted using lapse rates to account for the difference in altitude between the meteorological stations and the study sites (Rolland, 2003).

To estimate the site moisture gradient, a water balance index was calculated for each site as the sum of precipitation minus potential evapotranspiration from April to September, averaged over the period 1941–2006. Potential evapotranspiration was estimated according to Thornthwaite (1948). Site water balance is positive when precipitation exceeds potential evapotranspiration and negative in the case of a moisture deficit.

To test for the effect of water availability on tree growth, the self-calibrating Palmer Drought Severity Index (scPDSI), which is a measure of soil moisture, was calculated for each site according to Wells et al. (2004) using the PDSI program available online (<http://Greenleaf.unl.edu>). For the computation of the site-specific scPDSI, mean monthly temperature and precipitation sum, available water holding capacity of the soil and latitude are necessary. Values of scPDSI usually vary between -4 (extremely dry) and +4 (extremely wet), while values close to 0 indicate normal moisture conditions (Wells et al., 2004).

2.4. Statistical analysis

Growth-climate relationships were assessed with bootstrapped response functions using the standardized growth chronologies as dependent variables and monthly climatic indices (i.e., monthly mean temperature, precipitation sum and scPDSI) as independent variables. Response function analysis as introduced by Fritts et al. (1971) is a form of multiple regression analysis using the principal components of monthly climatic data to estimate indexed values of ring-width growth. The use of the principal components of the climatic predictors reduces the influence of collinearity among predictors on the regression models, whereas bootstrapping allows to test the significance and stability of the regression coefficients (Guiot, 1991). The statistical significance of the coefficient was assessed by calculating 95% confidence level based on 1000 bootstrapped resamples with the R package *bootRes* (Zang and Biondi, 2013). To determine the primary climatic factor and months influencing growth, monthly response coefficients were calculated for the year prior to ring formation (June to December) and the year of ring formation (January to September) for the common period 1941–2006 and introduced into a Principal Component Analysis (PCA). PCA is a multivariate analysis technique that aims at reducing data dimensionality while retaining as much of the original variation as possible (Everitt and Hothorn, 2011) and has been widely applied in dendroecological studies (e.g. Lebourgeois et al., 2010;

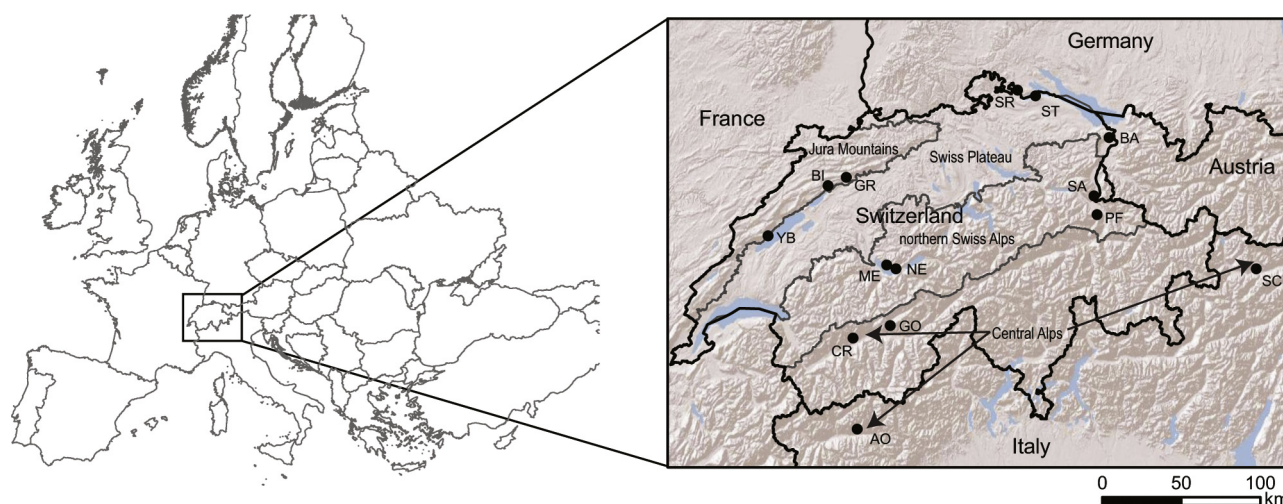


Fig. 1. Location of the study sites in Switzerland and northern Italy. The labels indicate the site code (See Table 1 for details). Base map reproduced with the permission of swissstopo (JA100118).

Table 2

Tree characteristics and time series statistics of ring width for the period 1941–2006.^a

Species	No. of sites	No. of trees	Age	DBH (cm)	Height (m)	Width (mm)	MS	AC1
<i>Pinus nigra</i>	10	149	109 (19)	49.2 (8.6)	26.2 (5.4)	1.68 (0.44)	0.21	0.65
<i>Pseudotsuga menziesii</i>	8	115	93 (9)	70.2 (14.1)	36.4 (7.8)	3.40 (0.95)	0.19	0.61
<i>Larix decidua</i>	13	187	99 (18)	46.1 (9.7)	28.6 (6.0)	2.00 (0.66)	0.29	0.62
<i>Pinus sylvestris</i>	11	163	109 (23)	43.3 (7.8)	25.5 (6.2)	1.38 (0.65)	0.23	0.73
<i>Picea abies</i>	11	156	103 (22)	47.8 (9.2)	30.2 (6.0)	2.39 (0.83)	0.23	0.67

^a Mean values with standard deviation in parentheses. Mean sensitivity (MS) and first order autocorrelation (AC1) were calculated from raw tree-ring chronologies.

Tessier, 1989; Weber et al., 2007). Subsequently, growth-climate relationships were computed for six seasons (previous summer, June to August of the previous year; previous autumn, September to November of the previous year; winter, December to February; spring, March to May, summer, June to August; and growing season, April to August). To test the effect of site moisture on growth sensitivity of each species along the climatic gradient, linear regressions between seasonal growth-response coefficients and site water balance were used.

Superposed Epoch Analysis was used to determine the growth sensitivity and to test the significance of growth reductions to extreme drought events among species and along the site moisture gradient (Orwig and Abrams, 1997). Superposed Epoch Analysis is a nonparametric randomization test to evaluate radial growth departures from mean values to events such as droughts (Lough and Fritts, 1987). For each site, we selected the three driest years based on the lowest scPDSI values for the period 1941–2006 (Fig. 2), and the extreme drought year 2003. Departures from tree-ring indexed values during these drought years and for 3 years before and after the drought years were averaged and tested against 1000 randomly selected sets of 7 years to estimate the confidence interval ($P < 0.05$). Response functions and Superposed Epoch analyses were performed on standardized chronologies (autocorrelation retained) for taking into account the influence of prior growth and climate on growth responses.

3. Results

3.1. Climatic conditions and trends

For the period 1941–2006, mean annual temperature at the study sites ranged from 6.0 to 9.1 °C, and mean annual precipitation sum from 493 to 1296 mm (Table 1). At all sites, mean annual temperature rose slightly over the period 1941–2006 and increased

strongly after ca. 1980 (Fig. S1). Over the period 1980–2006, mean annual temperature increased by 0.5 to 1.5 °C and was significant at 11 of the 14 study sites (Table S1). For the period 1941–2006, a slight increase in annual precipitation was observed, whereas precipitation tended to decrease or remained constant after ca. 1980 (Table S1, Fig. S1). This increase in temperature and decrease in precipitation led to a reduction in water availability and soil moisture at all sites, except in Schlanders, over the period 1980–2006, as indicated by the decreasing trend in scPDSI values (Table S1, Fig. 2).

3.2. Characteristics of sampled trees and tree-ring chronologies

Mean diameter at breast height of the sampled trees ranged from 24.7 to 84.4 cm, and height from 9.5 to 43.3 m, with *P. sylvestris* having the smallest and shortest individuals, and *P. menziesii* having the largest and tallest individuals (Table S2). Mean radial growth ranged from 0.55 to 5.25 mm/year, with the lowest radial increment recorded for *P. sylvestris* and the highest for *P. menziesii*. Mean sensitivity varied between 0.15 and 0.52, and varied depending on site moisture conditions and species. Tree-ring chronologies had higher mean sensitivity values on dry than on moist sites (Table S2). The highest mean sensitivity values were found for *L. decidua* (mean 0.29), followed by *P. abies* and *P. sylvestris* (mean 0.23). First order autocorrelation ranged between 0.31 and 0.81 (Table S2) with *P. sylvestris* (mean 0.73) and *P. abies* (mean 0.67) having the highest values (Table 2).

3.3. Effect of temperature, precipitation, drought and site moisture conditions on radial growth of co-occurring species

PCAs from response coefficients between standardized tree-ring width chronologies and monthly temperature, precipitation and scPDSI revealed that the influence of climate on radial growth varied between species and sites (Fig. 3). While species responded

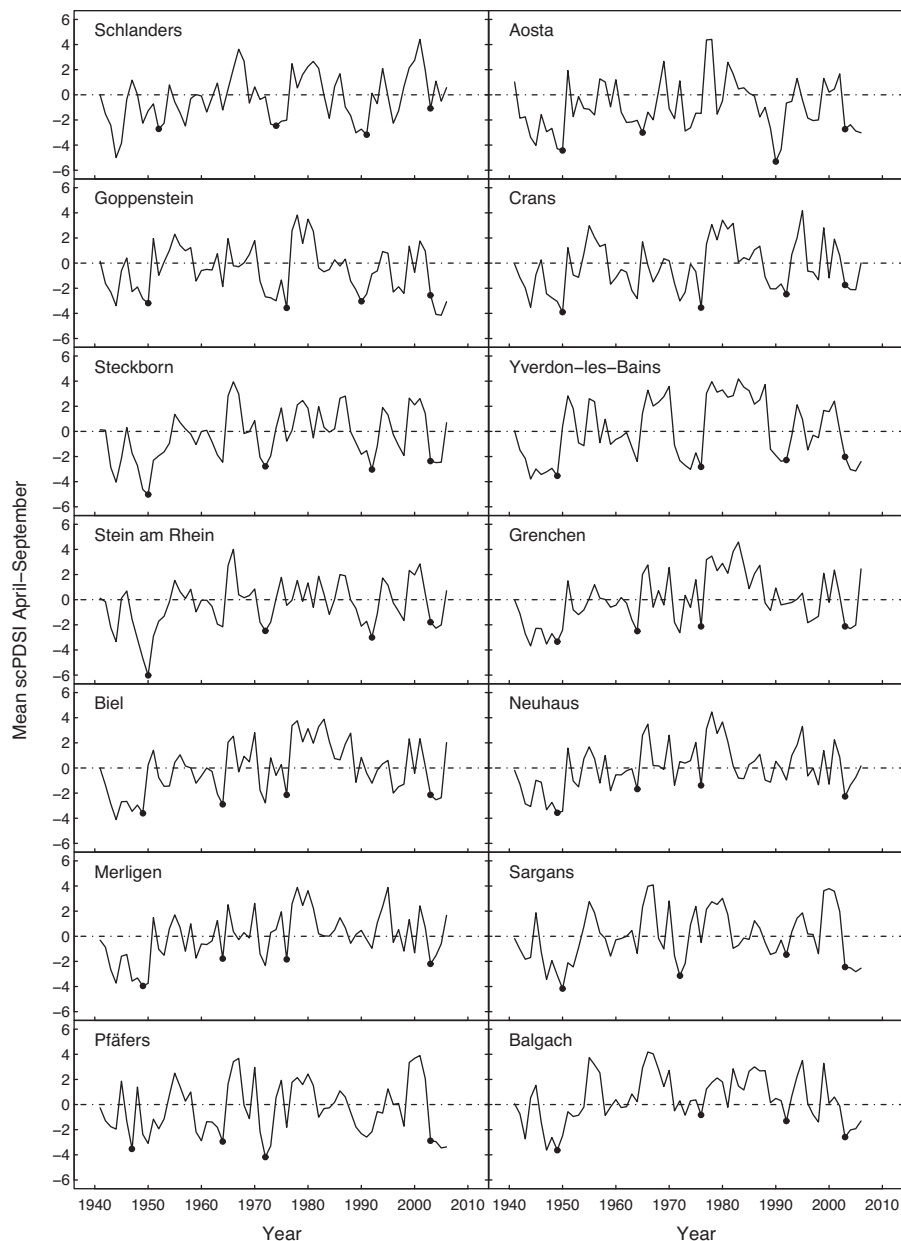


Fig. 2. Time series of mean self-calibrating Palmer drought severity index (scPDSI) during the growing season (April to September) for the period 1941–2006 at the study sites. Black dots denote the dry years used in the Superposed Epoch Analysis.

differently to monthly temperature (Fig. 3c), no distinct growth responses to monthly precipitation and scPDSI were found between the species (Fig. 3f, i). Still, the ordination of the first two components resulted in a seasonal grouping of monthly climatic variables, particularly precipitation and scPDSI. To further reduce the dimensionality of the dataset and to find growth-response patterns common to all species and sites, growth-climate relationships were then calculated for each season. When growth-climate relationships were analyzed at the seasonal scale, the importance of previous year climatic conditions (temperature and precipitation) on radial growth of the species became apparent (Fig. 4). Irrespective of the species, high temperatures in the summer and autumn of the year prior growth significantly reduced tree growth as indicated by the negative relationships between tree-ring width and temperature (Fig. 4). Similarly, low precipitation amounts in the summer prior growth impeded growth. When temperature (evaporative demand), precipitation and soil characteristics (water

holding capacity) were considered together by the computation of the scPDSI, water availability in current summer appeared to be critical for tree growth.

Along the moisture gradient, the growth of *P. nigra* was significantly more sensitive to precipitation amount on dry than moist sites, whereas its growth sensitivity to temperature and water availability (scPDSI) was not related to site moisture conditions (Fig. 5). Of all the investigated species, *P. menziesii* showed the lowest growth sensitivity to previous summer temperature and precipitation, particularly at sites having low water balance. Still, *P. menziesii* did not show any relationships between its growth response to climate and site moisture conditions. Similarly, the growth sensitivity of *L. decidua* was not significantly related to site moisture conditions, but was the highest at sites where the annual water balance was close to zero. *P. sylvestris* showed significantly higher growth sensitivity to previous autumn temperature on wet than on dry sites. Along the site moisture gradient, the

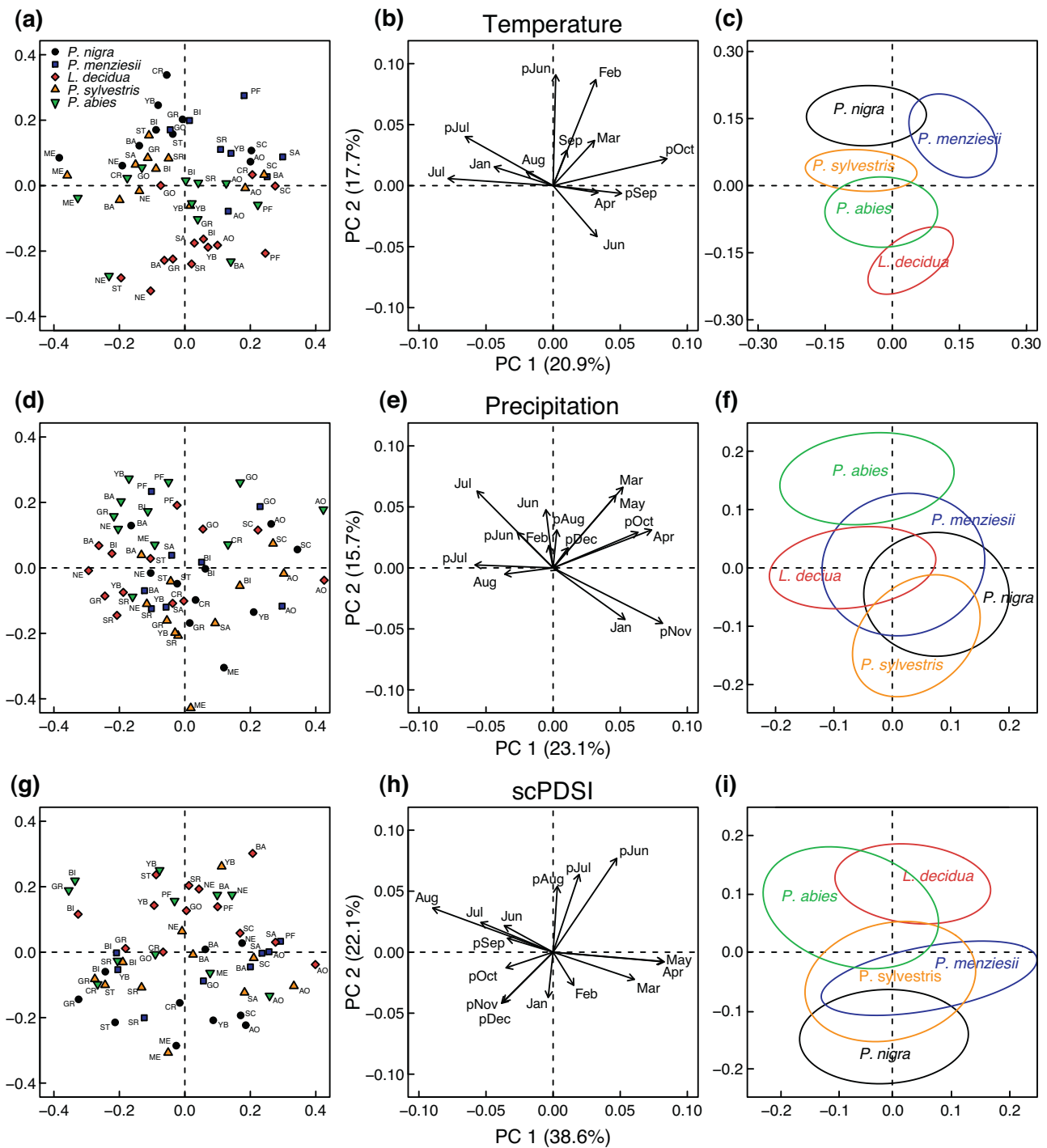


Fig. 3. Principal Component Analysis of the bootstrapped response coefficients between the standardized ring-width chronologies of the species and the monthly mean temperatures (a–c), precipitation sums (d–f) and self-calibrating Palmer drought severity index (scPDSI, g–i). Responses are grouped according to species. Significant temperature (b), precipitation (e) and scPDSI (h) vectors are shown. Differences between groups are depicted with ellipses showing the 95% confidence interval. Groups and climatic vectors pointing in the same direction indicate a high positive correlation, whereas vectors and groups in opposite direction indicate a high negative correlation. Vectors and groups in perpendicular direction indicate no or marginal correlation.

growth sensitivity of *P. abies* to previous summer temperature and precipitation amount was significantly higher on wet than on dry sites. On moist sites, *P. abies* and *L. decidua* were the species showing the highest sensitivity to drought as indicated by the high response coefficients. Overall, the results clearly showed that the growth sensitivity of the species to past climatic conditions was not or only slightly related to site moisture conditions since only a few significant relationships between response coefficients and site

water balance were found (Fig. 5). However, when all the species-specific responses were introduced into a PCA, a clear separation of the populations located in the Central Alps (driest sites) became apparent (Fig. 6). Trees in the Central Alps were most sensitive to precipitation amount in previous autumn and current spring. In contrast, conifers growing in the northern Swiss Alps, on the Swiss Plateau and the foothills of the Jura Mountains responded mostly to current or prior summer water availability (Fig. 6).

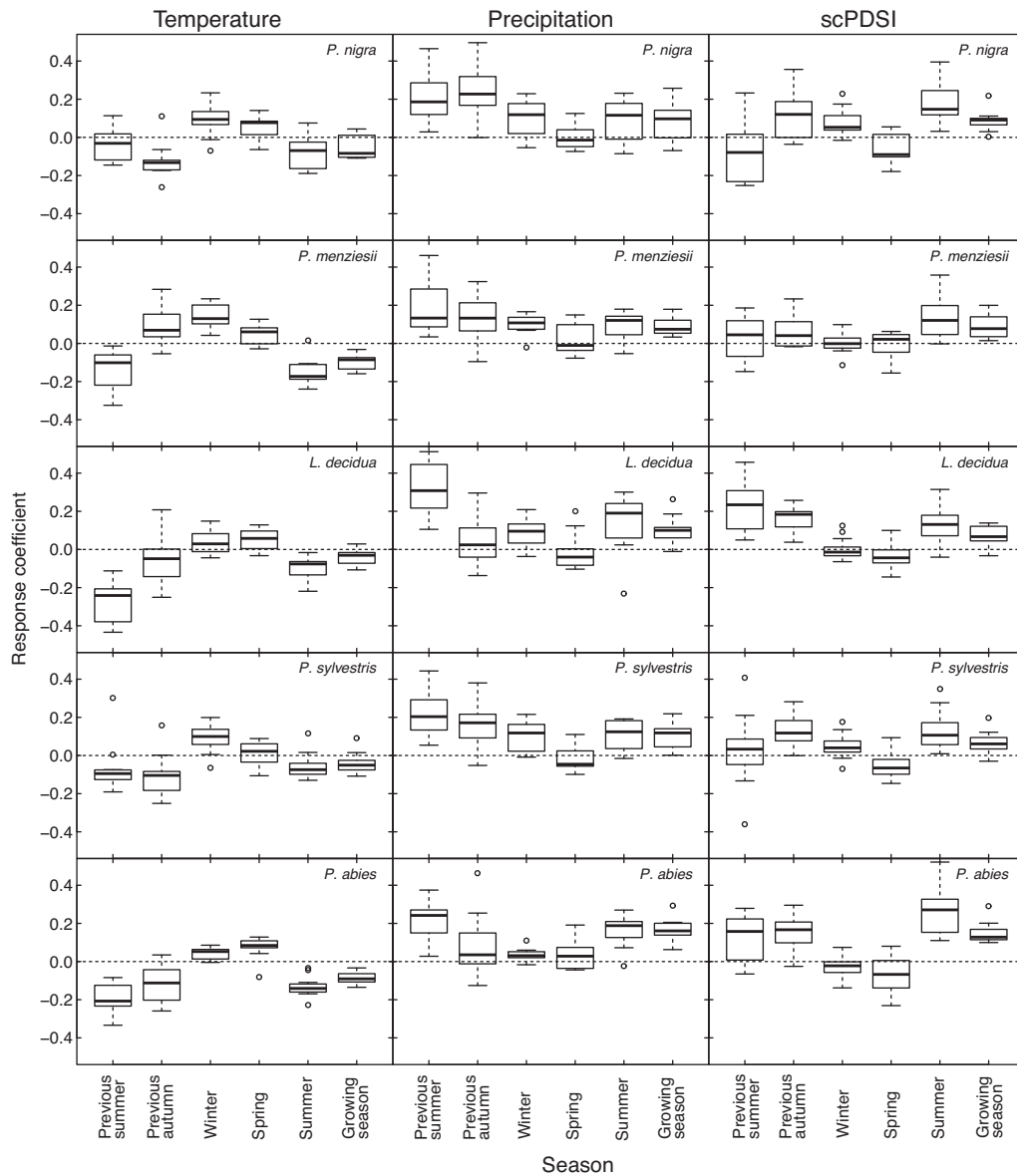


Fig. 4. Boxplots of the bootstrapped response coefficients computed between the standardized chronologies of the species and the mean temperatures, precipitation sums and mean self-calibrating Palmer Drought Severity Indices (scPDSI) aggregated over six seasons (previous summer=July to August of the previous year, previous autumn=September to November of the previous year, winter=December to February, spring=March to May, summer=June to August, and growing season=April to August).

3.4. Species-specific response to extreme dry years

Superposed Epoch Analysis of growth departures in extremely dry years revealed species-specific differences in radial growth reductions during severe drought events, with *L. decidua* and *P. abies* showing the strongest reductions during such years (Fig. 7). Tree-ring widths of these two species significantly declined (up to ca. –50%) during extreme drought years at the driest sites. Further, *P. abies* and *L. decidua* had the highest number of significant negative growth departures. Growth of *P. menziesii* was not significantly influenced by drought, except at two dry sites in the Central Alps (AO and GO). Similarly, growth of *P. nigra* and *P. sylvestris* was little affected by severe drought and only showed significant growth reductions at a few sites. All species showed significant growth reductions during the drought events in at least one of the driest sites, but the growth of most species recovered to their pre-drought growth levels one or two years after the drought events.

4. Discussion

4.1. Site-specific growth responses to water availability

Our results highlight a high variability of growth responses to temperature, precipitation and water availability (scPDSI) between species and sites, and depended on the biogeographic regions. Trees located in the Central Alps (dry conditions) showed lower radial growth rates and higher mean sensitivity than trees on more mesic sites. At dry sites, summer water availability was not critical for radial growth, whereas dry conditions in previous autumn and current spring strongly impeded tree growth. Water deficits in spring can strongly reduce tree growth in dry valleys of the Central Alps because it is during this period of the year that most radial growth occurs before the start of the summer drought period (Eilmann et al., 2011; Swidrak et al., 2013). Summers in inner-Alpine valleys are usually very dry, so one strategy that trees have to cope

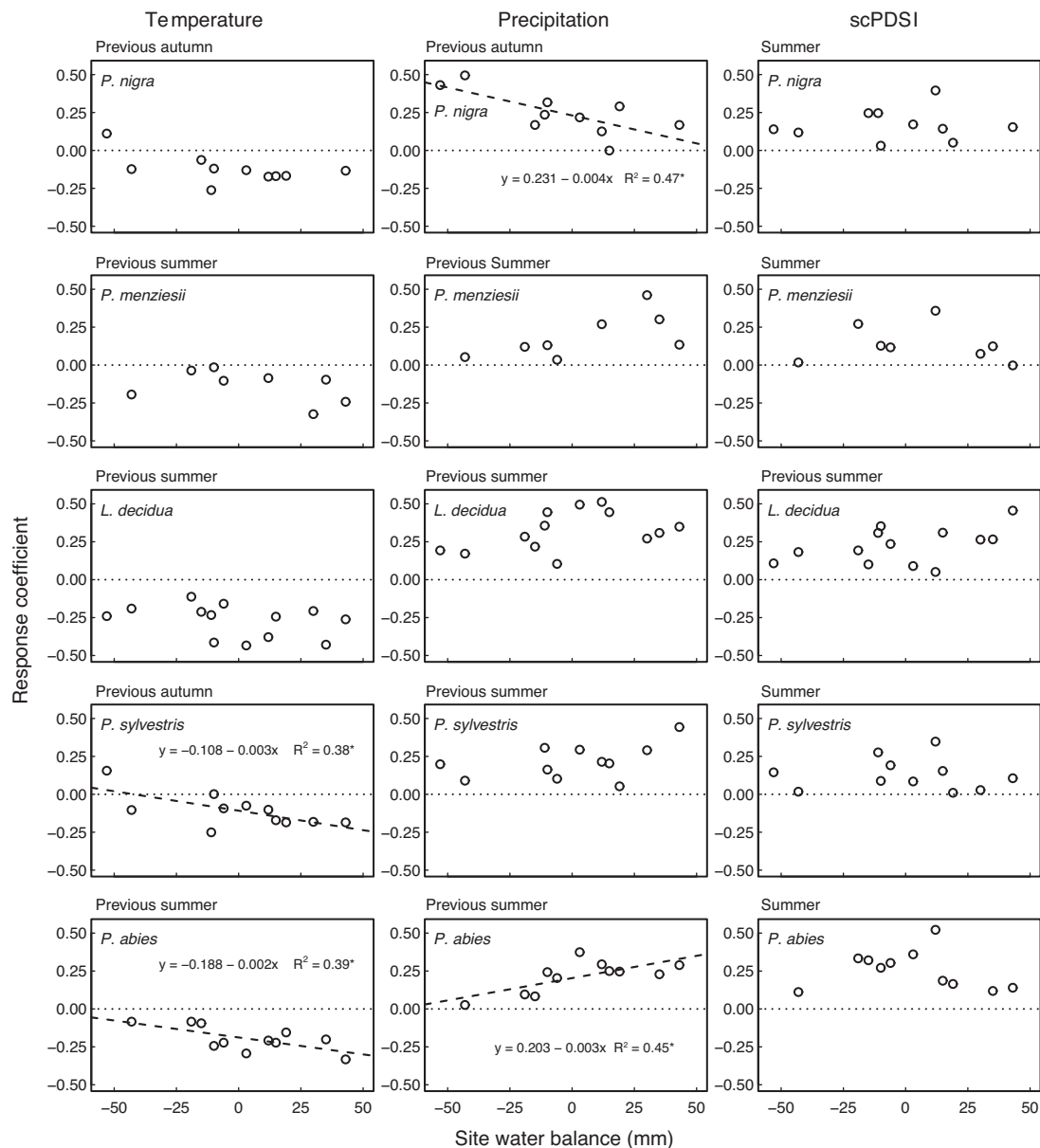


Fig. 5. Relationships between bootstrapped response coefficients of the species and site water balance. Response coefficients were computed between standardized chronologies of the species and seasonal temperatures, precipitation sums and mean self-calibrating Palmer Drought Severity Index (scPDSI). For each species and climatic variable, only the season for which the highest coefficient in absolute term was reached is displayed. Regression lines (dashed) are only shown for significant relationships.

with this period is to restrict their cambial activity and tracheid production to spring and early summer, when conditions are more favorable (Eilmann et al., 2011).

In contrast to the responses found at the dry sites in the Central Alps, tree radial growth at the moist and wet sites (Swiss Plateau, Jura Mountains and northern Swiss Alps) responded strongly to summer climatic conditions. Under moist conditions, growth can occur during the entire growing season as long as water deficits are not severe enough to induce stomatal closure (L vesque et al., 2013). When conditions become too dry to satisfy the high water demand of the canopy, the safest strategy that large and tall trees have to maintain a functional hydraulic system is to reduce or even stop stomatal conductance. This reduces water loss, as well as carbon uptake, which is then reflected in reduced tree-ring growth during dry summer periods at mesic sites (L vesque et al., 2013). This is in line with the high susceptibility to summer drought of

various conifer species reported recently from mesic forests in north-eastern Spain (Pasho et al., 2011) and France (Lebourgeois et al., 2010). Overall, the strong coupling between summer water availability and tree growth under moist conditions suggests that trees at moist sites may be more sensitive to severe summer droughts than their counterparts at dry and wet sites in the Alps. However, there is also evidence that many tree species have narrow hydraulic safety margins regardless of site water availability, making trees at dry, moist and wet sites similarly vulnerable to drought (Choat et al., 2012). In such situations, changes in drought seasonality or increases in drought severity and duration may be detrimental for tree survival (Andregg et al., 2013), especially for species with weak stomatal control of water loss, i.e., *L. decidua* (Leo et al., 2013), and species with shallow rooting system, such as *P. abies*, having limited access to deep soil water sources (Schmid and Kazda, 2002).

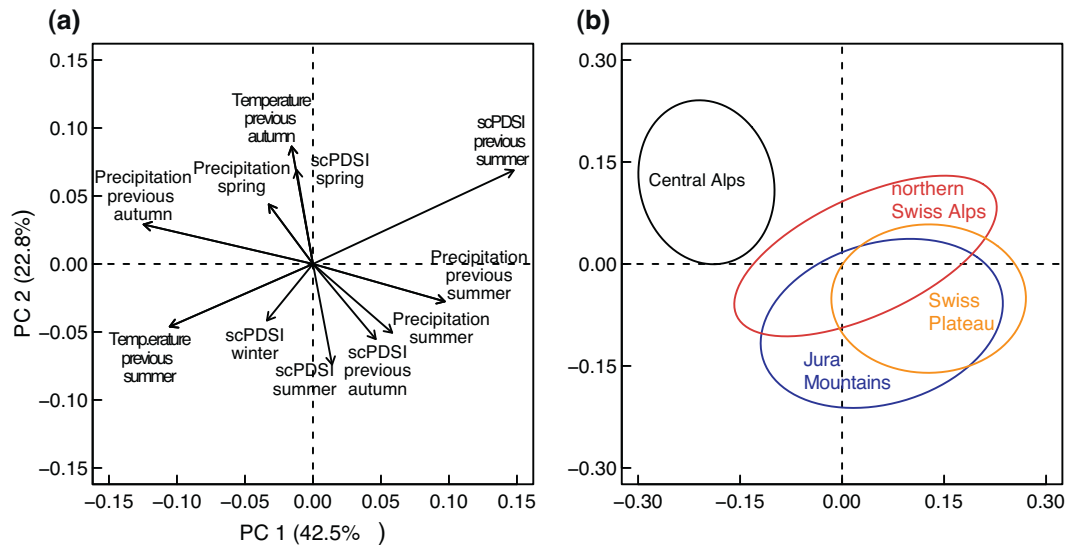


Fig. 6. Principal Component Analysis showing the influence of seasonal temperatures, precipitation sums and self-calibrating Palmer drought severity index (scPDSI) on mean growth responses of trees between the biogeographic regions. Significant temperature, precipitation and scPDSI vectors are shown in (a). Differences between biogeographic regions are depicted with ellipses showing the 95% confidence interval (b). Groups and climatic vectors pointing in the same direction indicate a high positive correlation, whereas vectors and groups in opposite direction indicate a high negative correlation. Vectors and groups in perpendicular direction indicate no or marginal correlation.

4.2. Species-specific growth responses to water availability and severe droughts

Across the four biogeographic regions, *P. abies* and *L. decidua* were the most sensitive species to drought. Growth of *L. decidua* and *P. abies* depended considerably on summer water availability. *L. decidua* was very sensitive to previous summer water availability, whereas current summer drought impeded growth of *P. abies*. Bud development and foliage formation of *L. decidua* depend almost entirely on carbon reserves that are strongly influenced by the climatic conditions prior the actual vegetation period (Swidrak et al., 2013). Mild and moist weather conditions during the previous summer can enhance carbohydrates storage, fine root elongation and bud formation (Weber et al., 2007), which, in return, promote radial growth. Even if previous year's conditions are highly favorable for growth, drought during the vegetation period may be detrimental for *L. decidua* due to its deciduous character which forces it to be photosynthetically active during the driest period of the year (Lévesque et al., 2013). Dry summer periods can also strongly reduce photosynthesis, stomatal conductance, carbohydrate transfer and growth of *P. abies* (Zweifel et al., 2009), hence making radial growth of this species very sensitive to summer water availability. *L. decidua* and *P. abies* were also the species that showed the strongest and highest number of significant growth reductions during extremely dry years along the gradient. Severe summer drought, such as the one that occurred in 2003, can reduce photosynthesis, growth and vigor of these species for more than 3 years (Fig. S2). Prolonged recovery time and reduced tree vigor can increase the susceptibility of these species to be attacked by pest and pathogens (Jactel et al., 2012). Ultimately, severe heat stress and drought can lead to dieback of species that are physiologically and anatomically maladapted to drought such as *P. abies* (Hentschel et al., 2014). Therefore, the long-term performance or even the survival of *P. abies*, a species highly susceptible to cavitation (Hentschel et al., 2014) and bark beetle attack (Wermelinger, 2004), and *L. decidua*, a species prone to larch budmoth outbreaks (Büntgen et al., 2009) and with inefficient stomatal control (Leo et al., 2013), can be compromised under a drier climate at today's dry sites in Central Europe.

Of all the investigated species, *P. sylvestris* showed an intermediate response in its drought tolerance along the ecological gradient. In general, growth of *P. sylvestris* was mainly influenced by previous summer precipitation amount and current summer water deficits. Favorable weather conditions in previous summer can improve carbon uptake and the amount of stored carbohydrates in *P. sylvestris* trees (Eilmann et al., 2010), enhance bud and foliage formation for the following growing season, and subsequently photosynthetic capacity and radial growth (Weber et al., 2007). The importance of previous year conditions is also supported by the high autocorrelation values (0.73) found for *P. sylvestris*. This lag effect can thus hinder the response of *P. sylvestris* to current spring moisture conditions. Under dry summer conditions, *P. sylvestris* shows a drought avoidance strategy and closes its stomata at an early stage to reduce the risk of hydraulic failure (Irvine et al., 1998; Zweifel et al., 2009), but this simultaneously limits its assimilation rate, hence its growth (Eilmann et al., 2010). Overall, our results and those from previous studies (Bigler et al., 2006; Michelot et al., 2012; Weber et al., 2007) indicate that the capacity of *P. sylvestris* to withstand periodic and severe water stress on currently dry sites is limited and suggest that this species may be unable to cope with prolonged and frequent dry conditions.

In contrast to the native *P. abies*, *L. decidua* and *P. sylvestris*, radial growth of the non-native *P. nigra* and *P. menziesii* was less affected by climatic variability and water deficits. Both species were able to maintain high radial increments and had the lowest mean sensitivity values. In addition, few chronologies of *P. nigra* and *P. menziesii* responded significantly to temperature, precipitation and scPDSI along the gradient (data not shown). *P. nigra* and *P. menziesii* have a drought avoidance strategy and maintain effective stomatal control to reduce transpirational water loss under summer dry conditions, whereas they maximize their carbon uptake when soil moisture conditions are favorable (Lassoie and Salo, 1981; Lebourgeois et al., 1998). This enables these species to maintain a positive carbon balance even under dry conditions, making them little sensitive to drought along the ecological gradient. Growth reductions in *P. nigra* and *P. menziesii* during extremely dry years were rare and occurred solely at the driest sites. However, both species were able to recover to or even exceed their pre-drought growth levels in

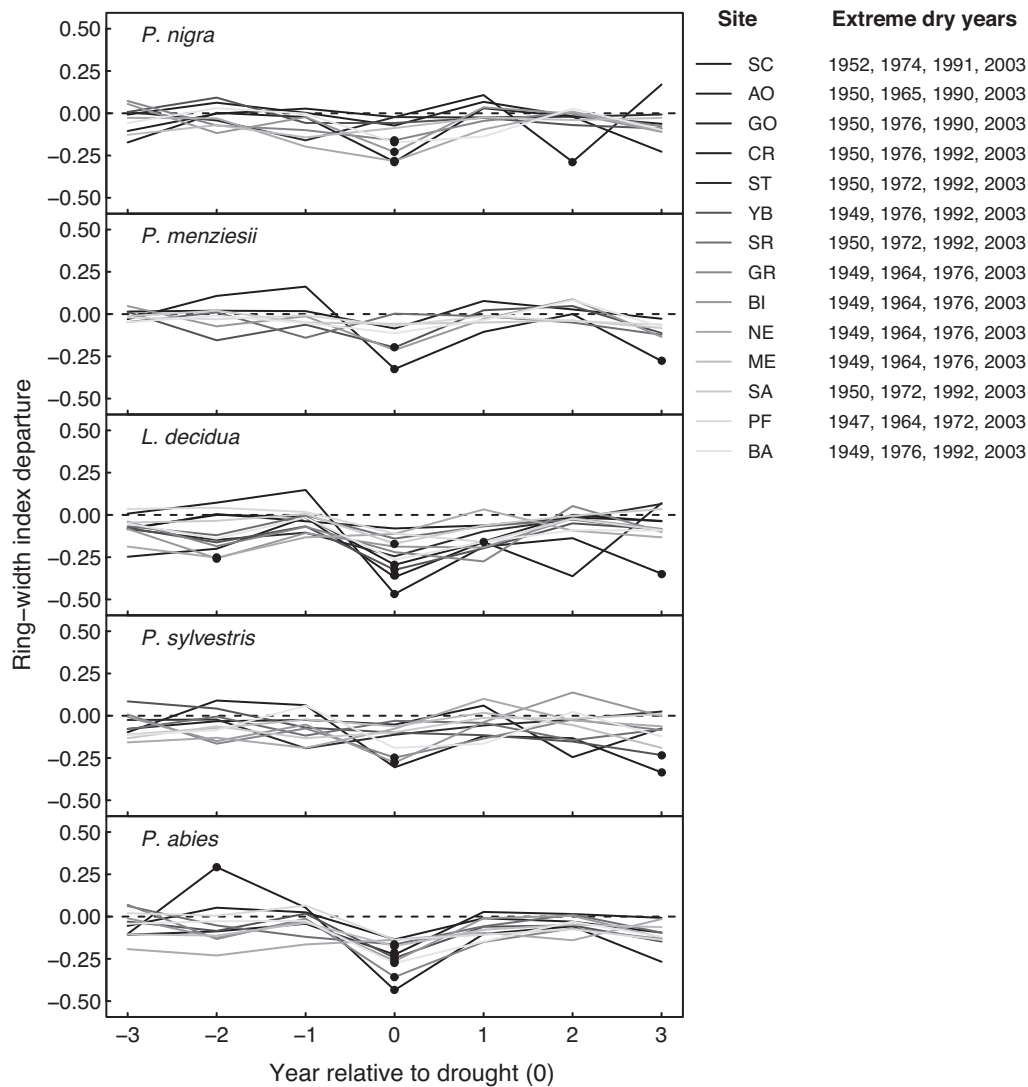


Fig. 7. Superposed Epoch Analysis showing negative and positive tree growth departures (standard chronologies with autocorrelation retained) for the drought year (0) and 3 years before and after the drought year. Black dots indicate significant ($P < 0.05$) growth departures from 1000 random simulations. Extreme dry years correspond to the three driest years with the lowest scPDSI values and the extreme drought year 2003 (Fig. 2).

the year following the events, indicating their high ability to offset drought-induced growth declines. This fast recovery implies a strong coupling between carbon assimilation and radial growth for these species (L evesque et al., 2013). The high recovery capacity of *P. menziesii* and *P. nigra* and their ability to withstand dry periods reported here agree with the results of Eilmann and Rigling (2012) from the dry inner-Alps. Although some studies suggest that *P. menziesii* is somehow sensitive to severe summer drought (e.g., Jansen et al., 2013; Sergent et al., 2013), our results indicate that this species was only slightly affected by water deficits in summer and severe droughts. Furthermore, *P. menziesii* was the most productive species along the gradient, even at the driest sites in the Central Alps. These characteristics make *P. menziesii* (var. *menziesii*) and *P. nigra* interesting alternative species to the more drought sensitive *P. abies* and *P. sylvestris* at dry sites in Central Europe.

Overall, our results indicate that the long-term performance or even the survival of the native *P. abies*, *L. decidua* and *P. sylvestris* at dry sites in Central Europe will likely be compromised if the climate becomes drier. Prolonged drought conditions can deplete stored carbohydrates, reduce growth and recovery (McDowell et al., 2008), diminish resistance to insects and pathogens agents, and may ultimately lead to tree mortality (Bigler et al., 2006; Gaylord et al.,

2013). Particularly, the expected increase in frequency and duration of summer droughts (CH2011, 2011) is likely to pose severe threats to species with small environmental niche breadth and range (Morin and Lechowicz, 2013) such as *P. abies* and *L. decidua* in the dry-inner Alps.

5. Conclusion

We assessed the growth sensitivity of five co-occurring conifers to climatic variability and severe drought along a wide ecological gradient covering four distinct biogeographic regions in Central Europe. Our study highlights that conifer responses to climatic variability and drought were not uniform and varied between species, regions and drought seasonality. At dry sites located in the Central Alps, water availability prior and at the beginning of the vegetation period was critical for tree growth, whereas summer water availability was important at moist sites on the Swiss Plateau, at the foothills of the Jura Mountains and on wet sites in the northern Swiss Alps. Summer water deficits significantly impeded growth of *P. abies* and *L. decidua* along the ecological gradient, and both species were very sensitive to severe summer droughts. Surprisingly, our results revealed that the growth sensitivity of the species

was little related to site water balance per se. This suggests that other environmental factors (e.g., soil characteristics, topography) significantly affect growth and may buffer the sensitivity of trees to climatic variability at the site level.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.agrformet.2014.06.001>.

References

- Allen, C.D., et al., 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *For. Ecol. Manage.* 259 (4), 660–684.
- Anderegg, L.D.L., Anderegg, W.R.L., Abatzoglou, J., Hausladen, A.M., Berry, J.A., 2013. Drought characteristics' role in widespread aspen forest mortality across Colorado, USA. *Global Change Biol.* 19 (5), 1526–1537.
- Andreu-Hayles, L., et al., 2011. Long tree-ring chronologies reveal 20th century increases in water-use efficiency but no enhancement of tree growth at five Iberian pine forests. *Global Change Biol.* 17 (6), 2095–2112.
- Bigler, C., Bräker, O.U., Bugmann, H., Dobbertin, M., Rigling, A., 2006. Drought as an inciting mortality factor in Scots pine stands of the Valais, Switzerland. *Ecosystems* 9 (3), 330–343.
- Bodenkunde, A.G., 1982. *Bodenkundliche Kartieranleitung*. Schweizerbart, Stuttgart, 331 pp.
- Bunn, A.G., 2008. A dendrochronology program library in R (dplR). *Dendrochronologia* 26 (2), 115–124.
- Büntgen, U., et al., 2009. Three centuries of insect outbreaks across the European Alps. *New Phytol.* 182 (4), 929–941.
- Bürgi, A., Diez, C., 1986. Übersicht über den Exotenanbau in der Schweiz aufgrund einer Umfrage vom Herbst/Winter 1984/85. *Schweizerische Zeitschrift für Forstwesen* 137, 833–851.
- Carnicer, J., et al., 2011. Widespread crown condition decline, food web disruption, and amplified tree mortality with increased climate change-type drought. *Proc. Natl. Acad. Sci. U S A* 108 (4), 1474–1478.
- Choat, B., et al., 2012. Global convergence in the vulnerability of forests to drought. *Nature* 491 (7426), 752–755.
- Christensen, J.H., et al., 2007. Regional climate projections. In: Solomon, S. (Ed.), *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, United Kingdom/New York, NY, USA.
- R Development Core Team, 2013. *R: A Language and Environment for Statistical Computing*. Foundation for Statistical Computing, Vienna, Austria.
- Drobyshev, I., Gewehr, S., Berninger, F., Bergeron, Y., 2013. Species specific growth responses of black spruce and trembling aspen may enhance resilience of boreal forest to climate change. *J. Ecol.* 101 (1), 231–242.
- Duncan, R., 1989. An evaluation of errors in tree age estimates based on increment cores in kahikatea (*Dacrydium dacrydioides*). *N Z Nat. Sci.* 16 (3), 1–37.
- Eilmann, B., Rigling, A., 2012. Tree-growth analyses to estimate tree species' drought tolerance. *Tree Physiol.* 32 (2), 178–187.
- Eilmann, B., et al., 2010. Fast response of Scots pine to improved water availability reflected in tree-ring width and $\delta^{13}C$. *Plant Cell Environ.* 33 (8), 1351–1360.
- Eilmann, B., Zweifel, R., Buchmann, N., Graf Pannatier, E., Rigling, A., 2011. Drought alters timing, quantity, and quality of wood formation in Scots pine. *J. Exp. Bot.* 62 (8), 2763–2771.
- Eilmann, B., et al., 2013. Origin matters! Difference in drought tolerance and productivity of coastal Douglas-fir (*Pseudotsuga menziesii* (Mirb.)) provenances. *Forest Ecol. Manage.* 302, 133–143.
- Elkin, C., et al., 2013. A 2 °C warmer world is not safe for ecosystem services in the European Alps. *Global Change Biol.* 19 (6), 1827–1840.
- Ellenberg, H., 2009. *Vegetation Ecology of Central Europe*. Cambridge University Press, Cambridge.
- Everitt, B., Hothorn, T., 2011. *An Introduction to Applied Multivariate Analysis with R*. Springer, New York/Dordrecht/Heidelberg/London, pp. 274.
- Fekedulegn, D., Hicks, R.R., Colbert, J.J., 2003. Influence of topographic aspect, precipitation and drought on radial growth of four major tree species in an Appalachian watershed. *For. Ecol. Manage.* 177 (1–3), 409–425.
- Fritts, H.C., 1976. *Tree Rings and Climate*. Academic Press, London, 567 pp.
- Fritts, H.C., Blasing, T.J., Hayden, B.P., Kutzbach, J.E., 1971. Multivariate techniques for specifying tree-growth and climate relationships and for reconstructing anomalies in paleoclimate. *J. Appl. Meteorol.* 10 (5), 845–864.
- Galiano, L., Martínez-Vilalta, J., Lloret, F., 2010. Drought-induced multifactor decline of Scots pine in the Pyrenees and potential vegetation change by the expansion of co-occurring oak species. *Ecosystems* 13 (7), 978–991.
- Gärtner, H., Nievergelt, D., 2010. The core-microtome: a new tool for surface preparation on cores and time series analysis of varying cell parameters. *Dendrochronologia* 28 (2), 85–92.
- Gaylord, M.L., et al., 2013. Drought predisposes piñon-juniper woodlands to insect attacks and mortality. *New Phytol.* 198 (2), 567–578.
- Guiot, J., 1991. The bootstrapped response function. *Tree-Ring Bull.* 51, 39–41.
- Hentschel, R., et al., 2014. Norway spruce physiological and anatomical predisposition to dieback. *For. Ecol. Manage.* 322, 27–36.
- Holmes, R.L., 1983. Computer-assisted quality control in tree-ring dating and measurement. *Tree-Ring Bull.* 43 (1), 69–78.
- Irvine, J., Perks, M.P., Magnani, F., Grace, J., 1998. The response of *Pinus sylvestris* to drought: stomatal control of transpiration and hydraulic conductance. *Tree Physiol.* 18 (6), 393–402.
- Jactel, H., et al., 2012. Drought effects on damage by forest insects and pathogens: a meta-analysis. *Global Change Biol.* 18 (1), 267–276.
- Jansen, K., Sohr, J., Kohnle, U., Ensminger, I., Gessler, A., 2013. Tree ring isotopic composition, radial increment and height growth reveal provenance-specific reactions of Douglas-fir towards environmental parameters. *Trees-Struct. Funct.* 27 (1), 37–52.
- Klimo, E., Hager, H., Kulhavý, J., 2000. Spruce Monocultures in Central Europe – Problems and Prospects, 33. European Forest Institute, Joensuu, Finland.
- Kozłowski, T., Pallardy, S., 2002. Acclimation and adaptive responses of woody plants to environmental stresses. *Bot. Rev.* 68 (2), 270–334.
- Lassioe, J.P., Salo, D.J., 1981. Physiological-response of large Douglas-fir to natural and induced soil-water deficits. *Can. J. For. Res.* 11 (1), 139–144.
- Lebourgeois, F., Levy, G., Aussenac, G., Clerc, B., Willm, F., 1998. Influence of soil drying on leaf water potential, photosynthesis, stomatal conductance and growth in two black pine varieties. *Ann. For. Sci.* 55 (3), 287–299.
- Lebourgeois, F., Rathgeber, C.B.K., Ulrich, E., 2010. Sensitivity of French temperate coniferous forests to climate variability and extreme events (*Abies alba*, *Picea abies* and *Pinus sylvestris*). *J. Veg. Sci.* 21 (2), 364–376.
- Lebourgeois, F., Mérian, P., Courdier, F., Ladier, J., Dreyfus, P., 2012. Instability of climate signal in tree-ring width in Mediterranean mountains: a multi-species analysis. *Trees – Struct. Funct.* 26 (3), 715–729.
- Lebourgeois, F., Gomez, N., Pinto, P., Mérian, P., 2013. Mixed stands reduce *Abies alba* tree-ring sensitivity to summer drought in the Vosges mountains, western Europe. *For. Ecol. Manage.* 303, 61–71.
- Leo, M., et al., 2013. Evaluating the effect of plant water availability on inner alpine coniferous trees based on sap flow measurements. *Eur. J. For. Res.*, <http://dx.doi.org/10.1007/s10342-013-0697-y>.
- Lévesque, M., et al., 2013. Drought response of five conifer species under contrasting water availability suggests high vulnerability of Norway spruce and European larch. *Global Change Biol.* 19 (10), 3184–3199.
- Lévesque, M., Siegwolf, R., Saurer, M., Eilmann, B., Rigling, A., 2014. Increased water-use efficiency does not lead to enhanced tree growth under xeric and mesic conditions. *New Phytol.* 203 (1), 94–109.
- Lough, J., Fritts, H., 1987. An assessment of the possible effects of volcanic eruptions on North American climate using tree-ring data, 1602 to 1900 AD. *Climatic Change* 10 (3), 219–239.
- Martin-Benito, D., Beekman, H., Cañellas, I., 2013. Influence of drought on tree rings and tracheid features of *Pinus nigra* and *Pinus sylvestris* in a mesic Mediterranean forest. *Eur. J. For. Res.* 132 (1), 33–45.
- Matías, L., Jump, A.S., 2012. Interactions between growth, demography and biotic interactions in determining species range limits in a warming world: the case of *Pinus sylvestris*. *For. Ecol. Manage.* 282, 10–22.
- McDowell, N., et al., 2008. Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb to drought? *New Phytol.* 178 (4), 719–739.
- Michelot, A., Bréda, N., Damesin, C., Dufréne, E., 2012. Differing growth responses to climatic variations and soil water deficits of *Fagus sylvatica*, *Quercus petraea* and *Pinus sylvestris* in a temperate forest. *For. Ecol. Manage.* 265, 161–171.
- Morin, X., Lechowicz, M.J., 2013. Niche breadth and range area in North American trees. *Ecography* 36 (3), 300–312.
- Orwig, D.A., Abrams, M.D., 1997. Variation in radial growth responses to drought among species, site, and canopy strata. *Trees-Struct. Funct.* 11 (8), 474–484.
- Pasho, E., Camarero, J.J., de Luis, M., Vicente-Serrano, S.M., 2011. Impacts of drought at different time scales on forest growth across a wide climatic gradient in north-eastern Spain. *Agric. For. Meteorol.* 151 (12), 1800–1811.

- Pasho, E., Camarero, J.J., de Luis, M., Vicente-Serrano, S.M., 2012. Factors driving growth responses to drought in Mediterranean forests. *Eur. J. For. Res.* 131 (6), 1797–1807.
- Rigling, A., Bräker, O., Schneiter, G., Schweingruber, F.H., 2002. Intra-annual tree-ring parameters indicating differences in drought stress of *Pinus sylvestris* forests within the Erico-Pinion in the Valais (Switzerland). *Plant Ecol.* 163 (1), 105–121.
- Rigling, A., et al., 2013. Driving factors of a vegetation shift from Scots pine to pubescent oak in dry Alpine forests. *Global Change Biol.* 19 (1), 229–240.
- Rolland, C., 2003. Spatial and seasonal variations of air temperature lapse rates in Alpine regions. *J. Climate* 16 (7), 1032–1046.
- CH2011, 2011. Swiss Climate Change Scenarios CH2011. C2SM, MeteoSwiss, ETH, NCCR Climate, and OcCC, Zurich, Switzerland, 88 pp.
- Schmid, I., Kazda, M., 2002. Root distribution of Norway spruce in monospecific and mixed stands on different soils. *Forest Ecol. Manage.* 159 (1–2), 37–47.
- Schuster, R., Oberhuber, W., 2013. Drought sensitivity of three co-occurring conifers within a dry inner Alpine environment. *Trees-Struct. Funct.* 27 (1), 61–69.
- Sergent, A.-S., Rozenberg, P., Bréda, N., 2013. Douglas-fir is vulnerable to exceptional and recurrent drought episodes and recovers less well on less fertile sites. *Ann. For. Sci.*, <http://dx.doi.org/10.1007/s13595-012-0220-5>.
- Swidrak, I., Schuster, R., Oberhuber, W., 2013. Comparing growth phenology of co-occurring deciduous and evergreen conifers exposed to drought. *Flora* 208, 609–617.
- Temperli, C., Bugmann, H., Elkin, C., 2012. Adaptive management for competing forest goods and services under climate change. *Ecol. Appl.* 22 (8), 2065–2077.
- Tessier, L., 1989. Spatio-temporal analysis of climate-tree ring relationships. *New Phytol.* 111 (3), 517–529.
- Thiel, D., et al., 2012. Uniform drought and warming responses in *Pinus nigra* provenances despite specific overall performances. *Forest Ecol. Manage.* 270 (0), 200–208.
- Thorntwaite, C., 1948. An approach toward a rational classification of climate. *Geogr. Rev.* 38 (1), 55–94.
- Thornton, P.E., Running, S.W., White, M.A., 1997. Generating surfaces of daily meteorological variables over large regions of complex terrain. *J. Hydrol.* 190 (3–4), 214–251.
- Weber, P., Bugmann, H., Rigling, A., 2007. Radial growth responses to drought of *Pinus sylvestris* and *Quercus pubescens* in an inner-Alpine dry valley. *J. Veg. Sci.* 18 (6), 777–792.
- Weber, P., Bugmann, H., Pluess, A.R., Walthert, L., Rigling, A., 2013. Drought response and changing mean sensitivity of European beech close to the dry distribution limit. *Trees-Struct. Funct.* 27 (1), 171–181.
- Wells, N., Goddard, S., Hayes, M., 2004. A self-calibrating Palmer drought severity index. *J. Climate* 17, 2335–2351.
- Wermelinger, B., 2004. Ecology and management of the spruce bark beetle *Ips typographus* – a review of recent research. *For. Ecol. Manage.* 202 (1–3), 67–82.
- Wigley, T.M.L., Briffa, K.R., Jones, P.D., 1984. On the average value of correlated time series, with applications in dendroclimatology and hydrometeorology. *J. Climate Appl. Meteorol.* 23 (2), 201–213.
- Zang, C., (Ph.D. thesis) 2011. Growth Reactions of Temperate Forest Trees to Summer Drought – a Multispecies Tree-ring Network Approach. Chair of Ecoclimatology, Technische Universität München, München, 164 pp.
- Zang, C., Biondi, F., 2013. Dendroclimatic calibration in R: the bootRes package for response and correlation function analysis. *Dendrochronologia* 31 (1), 68–74.
- Zweifel, R., Rigling, A., Dobbertin, M., 2009. Species-specific stomatal response of trees to drought – a link to vegetation dynamics? *J. Veg. Sci.* 20 (3), 442–454.