Drought sensitivity of Norway spruce is higher than that of silver fir along an altitudinal gradient in southwestern Germany

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Abstract

For Central Europe, climate projections foresee an increase in temperature combined with decreasing summer precipitation, resulting in drier conditions during the growing season. This might negatively affect forest growth, especially at sites that are already water-limited, *i.e.*, at low elevation. At higher altitudes trees might profit from increasing temperatures. We analyzed variations in radial growth of silver fir (*Abies alba* Mill.) and Norway spruce (*Picea abies* (L.) Karst.) along an altitudinal gradient from 400 until 1140 m a.s.l. in the Black Forest, to assess climate responses with increasing elevation. Climate–growth relationships were analyzed retrospectively using tree-ring and climate data. In total, we sampled stem discs of 135 trees to build 27 species- and site-specific chronologies ($n_{fir} = 13$, $n_{spruce} = 14$). Our results indicate distinct differences in climate–growth relations between fir and spruce along the gradient. Growth of high-altitude fir was positively related to temperature from January till March. Growth of low-altitude fir and spruce at all elevations was positively related to precipitation and negatively to temperature during the growing season, particularly in July. A self-calibrating Palmer drought severity index (sc-PDSI) underlined summer drought sensitivity of these trees. Overall, we found that climatic control of tree growth changes over altitude for fir. For spruce, a remarkable synchrony in growth variation and climate response was shown, which indicates that this species is drought sensitive at all studied elevations. In a future warmer climate, the growth of low-altitude fir and spruce along the entire studied gradient may be negatively affected in the Black Forest, if an increased evaporative demand cannot be compensated by increased water supply.

1   Introduction

For Central Europe, increases in annual air temperature up to 4°C by the end of this century are predicted under climate change, whereby extremely high summer temperatures are expected to increase even more than average summer temperatures (Christensen *et al.*, 2007). As the amount of precipitation in summer is likely to decrease as well (Maracchi *et al.*, 2005), drought events will occur more frequently during the growing season. This might have negative consequences for tree growth and vitality. Major reductions in the productivity of European forests were already observed under the extremely warm and dry climate anomaly in 2003 (Ciais *et al.*, 2005). However, some trees may also benefit from a warmer climate, *e.g.*, at higher elevations, as these sites are primarily temperature-limited (Körner & Paulsen, 2004; Tranquillini, 1979). In the Swiss Alps, Jolly *et al.* (2005) analyzed both satellite-derived photosynthetic activity estimates and in situ forest growth measurements for 2003 and found growth enhancements at high elevations, while trees at low elevations suffered from drought. Similar altitudinal differences in growth responses to extremely warm and dry climate conditions have been found in the Swiss Lötschental (Neuwirth *et al.*, 2004), Swiss Valais (Lingg, 1986) and French Alps (Desplanque *et al.*, 1999).

Studies on climate–growth relationships along ecological gradients have shown that differences in growth responses between species are important to consider (*e.g.*, Affolter *et al.*, 2010; Graumlich, 1993; Scharnweber *et al.*, 2011). By comparing 10 coniferous species along altitudinal gradients in four different climatic regions, Kienast *et al.* (1987) found consistent tendencies in ring width and maximum density relating to altitude, although climate–growth relationships showed considerable variation between sites and species at the same altitudinal level.

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In this study, we analyzed radial growth of silver fir (*Abies alba* Mill.) and Norway spruce (*Picea abies* (L.) Karst.) along an altitudinal gradient in the Black Forest, southwestern Germany. Both species are highly abundant and economically important in this region. Previous studies on fir and spruce, *e.g.*, in the French Alps, revealed a drought sensitivity of both species at low elevation and southern exposed sites (Desplanque *et al.*, 1999; Rolland *et al.*, 2000). Further, Lebourgeois (2007) and Rolland *et al.* (1999) found that water supply in the previous year mainly influences current-year growth of fir, whereas for spruce, both previous and current summer precipitation and temperature were of major importance (Bouriaud & Popa, 2009). At high elevation, cold temperatures in winter and early spring were found to negatively affect growth of both tree species (Desplanque *et al.*, 1999; Rolland *et al.*, 2000), but fir was more sensitive to late frost and extremely low winter temperatures than spruce (Bouriaud & Popa, 2009; Frank & Esper, 2005; Gerecke, 1986; Lebourgeois, 2007; Lebourgeois *et al.*, 2010).

By comparing growth responses of silver fir and Norway spruce along an altitudinal gradient, this study aims at increasing the understanding on altitude- and species-specific effects of climatic factors on growth, which is necessary to assess the responses of tree growth to anticipated climate changes. Trees were sampled at southwest-exposed slopes of the Black Forest, as climatic conditions are more extreme here, with higher wind load and incident radiation.

2 Material and methods

2.1 Study area and site selection

The study area is located in the Black Forest, southwestern Germany (47°42'–48°06'N, 7°40'–8°00'E). Elevations range between ca. 300 m till almost 1500 m a.s.l. The actual upper treeline in the Black Forest is at about 1400 m a.s.l., whereas the forest line, where trees form closed-canopy forest, is at around 1200 m a.s.l. Along the gradient, natural forest types gradually change from submontane beech-oak-fir forest, to montane beech-fir-forest mixed with pine, to high-montane fir-spruce forest. Without human interventions, the share of Norway spruce would be small and restricted to the high-mountainous zones (Schlenker & Müller, 1978).

Study sites were selected in a two-step procedure that aimed at establishing a dataset typical for southwest-exposed closed-canopy fir and spruce stands along an altitudinal gradient. First, we made a pre-selection in ArcGis Desktop 10 based on digital forest classification and forest site data that were provided by the Regierungspräsidium Freiburg and Forest Research Institute of Baden-Württemberg, respectively. A final selection of 19 sites was made after field verification and was based on altitude, exposition and similarity in stand structure. In addition, data from five sites from a former research project were included (Table 1).

The predominant soil type is cambisol and the available soil water capacity (AWC) ranges from very low (<50 mm) to medium (90–140 mm) at the different sites.

2.2 Climate data

Site-specific climate data was obtained from spatially interpolated gridded data (1 km × 1 km) derived from the network of meteorological measurement stations of the German Weather Service, which is available from the Web-based Weather Request and Distribution System WebWerdis (http://www.dwd.de/webwerdis). Monthly temperature and precipitation data were extracted for the period 1950–2009. Distinct differences in baseline climate exist among the sites, as mean annual air temperature decreases and annual precipitation increases with elevation (Fig. 2.1). A warming trend can be observed for mean annual air temperature since the 1980's, whereas no trend is visible in the annual precipitation sum (Fig. 2.2).

For each site, a self-calibrating Palmer drought severity index (sc-PDSI) was calculated using an online available tool from the GreenLeaf Project (GreenLeaf, 2011) to test the combined effect of temperature and precipitation in terms of water availability on tree growth. The sc-PDSI is a variant of the original drought index by Palmer (1965) and improves upon PDSI by automatically calibrating climatic characteristics and duration factors based on historic climate data, making spatial comparisons more meaningfull (Wells *et al.*, 2004). Required input variables for the calculation are monthly temperature and precipitation, latitude and AWC. Values normally range between -4 (extreme drought) and $+4$ (extremely wet), while values near zero indicate average soil moisture conditions (Palmer, 1965).

2.3 Tree-ring data

Per site, we collected stem discs at breast height of five dominant or co-dominant spruce or fir trees from the stand interior with no visible signs of damage. On three sites, we sampled both fir and spruce trees. Stem discs were air-dried and sanded to highlight ring boundaries. Annual radial increment was measured in eight pre-defined directions,

Table 1: Site description and characteristics of sample trees (in order of increasing altitude). At site WALD, ADEL and KUHL both fir and spruce were collected, as indicated by the suffixes F and S, respectively

Site	Site nr	Altitude (m a.s.l.)	No. of trees	Time span (all trees)	Age (years)	DBH (cm)	Tree height (m)	Aspect (%)	Slope	AWC
Silver fir										
MUGG	1	400	5	1924–2010	103.2 (10.2)	59.1 (4.5)	29.1 (1.6)	SW	59	2, 3
BRIT	2	430	5	1954–2009	75.8 (13.3)	53.6 (6.1)	30.4 (1.7)	SSW	36	2, 3
WALDF	3a	430	5	1910–2010	109.8 (10.0)	70.0 (5.6)	30.9 (1.5)	SW	62	2, 3
STAU	4	430	5	1906–2010	123.6 (18.7)	51.7 (2.4)	27.0 (1.5)	WSW	38	1, 2
SULZ	5	450	5	1937–2009	84.0 (7.0)	66.8 (7.8)	33.3 (2.7)	SSW	37	2, 3
AU	6	520	5	1971–2010	42.8 (3.6)	43.5 (5.0)	25.2 (1.4)	WSW	43	2, 3
BURG	7	650	5	1909–2009	103.4 (2.1)	58.7 (4.5)	31.3 (2.5)	W	65	1, 2
ADELF	8a	750	5	1920–2010	93.2 (2.2)	66.9 (7.9)	35.0 (1.8)	S	41	1, 2
NEUE	9	800	5	1945–2010	71.0 (6.5)	57.9 (3.5)	31.9 (2.8)	S	67	1, 2
EGER	10	920	5	1973–2009	43.0 (4.5)	44.8 (2.2)	24.0 (3.6)	S	62	1, 2
KUHLF	11a	970	4	1913–2010	100.8 (3.2)	66.7 (9.7)	28.4 (1.9)	WSW	35	1, 2
FISC	12	985	5	1917–2010	96.6 (1.7)	60.4 (3.8)	27.7 (0.4)	WSW	28	2, 3
KOHL	13	1050	4	1921–2010	107.3 (17.1)	68.4 (9.1)	27.6 (1.8)	SW	70	2, 3
Norway spruce										
WALDS	3b	430	5	1931–2010	86.2 (7.3)	55.1 (2.4)	32.3 (0.6)	SW	61	2, 3
EHRE	14	470	5	1948–2006	62.2 (2.4)	31.3 (1.2)	27.4 (2.2)	WSW	57	2, 3
GUNT	15	500	5	1949–2009	62.4 (1.1)	52.3 (1.1)	30.8 (2.1)	SSW	64	2, 3
KLOS	16	530	5	1964–2010	49.6 (2.1)	43.4 (3.3)	27.8 (1.5)	SSW	71	1, 2
MUNS	17	640	5	1910–2009	102.2 (2.8)	48.2 (6.6)	29.8 (1.8)	SSW	74	2
DOTT	18	690	5	1948–2006	62.8 (4.1)	30.0 (0.6)	24.4 (2.0)	SW	62	1, 2
ADELS	8b	750	5	1940–2010	71.8 (0.8)	58.7 (5.4)	31.9 (6.4)	S	55	1, 2
MUNT	19	780	5	1920–2006	89.2 (1.5)	53.1 (0.4)	35.6 (2.3)	SSW	56	2
BLAU	20	960	5	1971–2009	47.4 (5.0)	41.6 (5.3)	27.2 (2.7)	S	39	1, 2
KUHLS	11b	970	5	1903–2010	112.4 (3.5)	53.3 (9.6)	28.9 (2.6)	WSW	41	1, 2
AFTE	21	1027	5	1966–2006	46.6 (3.4)	29.3 (1.4)	22.3 (0.6)	WSW	55	1, 2
BERN	22	1030	5	1966–2010	48.4 (4.4)	37.7 (2.8)	22.1 (0.5)	S	62	2, 3
SIRN	23	1040	5	1921–2010	94.6 (4.2)	54.4 (2.8)	28.5 (0.7)	SW	82	2, 3
TODT	24	1140	5	1902–2006	118.6 (15.3)	46.5 (7.6)	24.5 (2.8)	WSW	52	2, 3

Age age at breast height, *DBH* diameter at breast height, *Aspect* exposition of study site: S = south, W = west, *AWC* available soil water capacity: 1 = very low (<50 mm), 2 = low (50–90 mm), 3 = medium (90–140 mm). Values in parentheses denote standard deviations
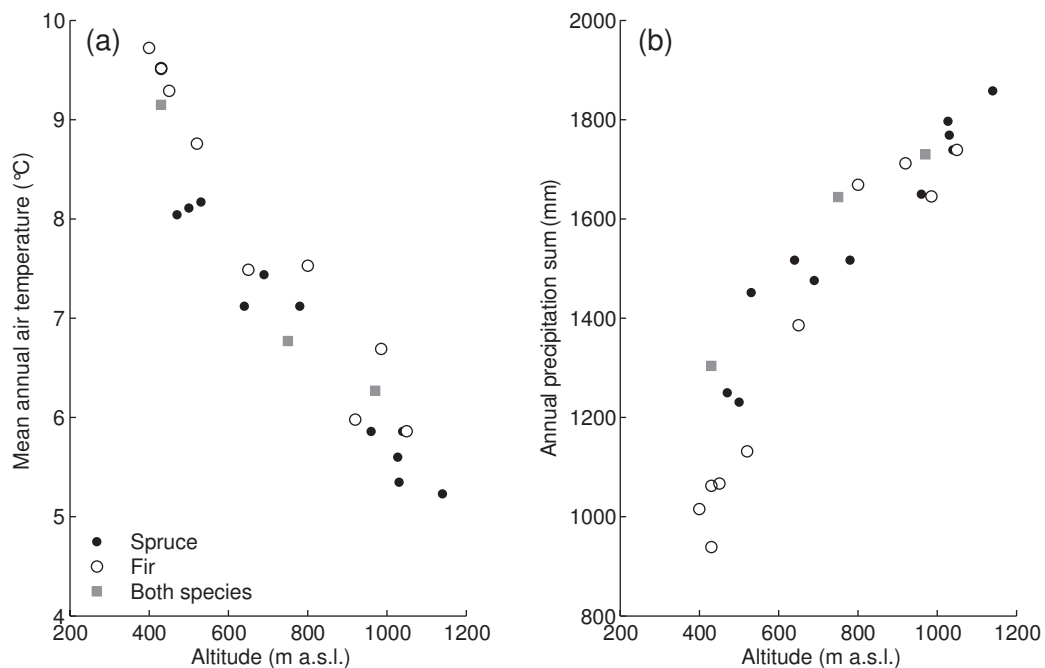

Figure 2.1: (a) Mean annual air temperature and (b) total annual precipitation at the study sites during the climate normal period 1961–1990 versus altitude
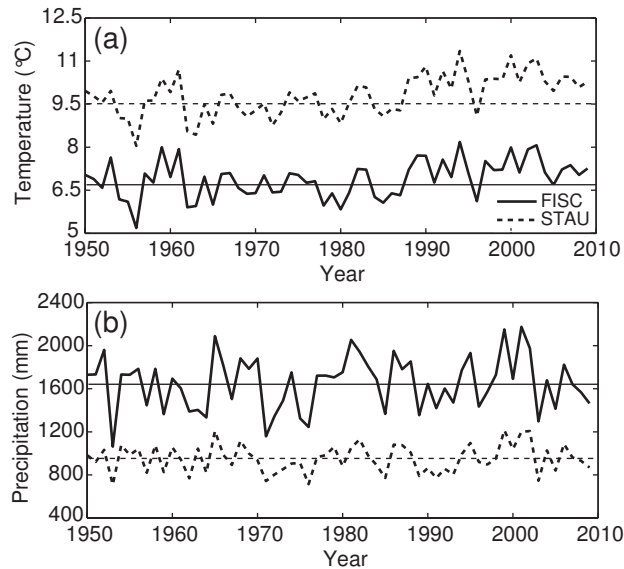
Figure 2.2: Time series of (a) mean annual air temperature and (b) total annual precipitation of a high-altitude site (FISC) and a low-altitude site (STAU) for the period 1950–2009, horizontal lines denote average values of the climate normal period 1961–1990

using semi-automatic image analysis software (developed at the Institute for Forest Growth). For each tree, the annual radial increment was calculated as the quadratic mean of the eight measurements. The tree-ring series were cross-dated visually and tested statistically (*Gleichläufigkeit*). Each series was detrended by fitting a cubic smoothing spline with 50% frequency cut-off at 30 years, in order to remove long-term trends and to retain high-frequency variability (Cook & Peters, 1981), using MATLAB's V7.9.0 (R2009b) Spline Toolbox function *csaps* (V3.3.7) in combination with the spline smoothing parameter function *splinep* (presented courtesy of J.L. Dupouey). Indices were calculated dividing the observed by the predicted values. Chronologies were constructed per site and tree species (in total 27 chronologies), and inter-series correlations (IC), mean sensitivities (MS) and first-order autocorrelations (AC) were calculated over the common overlap period 1974–2006. The IC is the average correlation coefficient between the series, MS is the average relative difference in radial increment between consecutive years and AC assesses the average relation between subsequent values within the time series (Fritts, 1976). The confidence of the chronologies was evaluated by the expressed population signal (EPS), which indicates the degree to which the particular sample chronology portrays a hypothetically perfect chronology (Wigley *et al.*, 1984). EPS values were calculated with the *wigley1* function (presented courtesy of D. Meko). All computations were carried out using MATLAB (V7.9.0, R2009b).

2.4 Statistical analysis

We calculated Pearson correlation coefficients between site chronologies and plotted them as a function of altitudinal distance, to analyze whether sites at the same altitude have more growth variation in common compared to sites that are further apart. Principal component analysis (PCA) was performed to investigate common growth signals in the site chronologies. Principal component scores represent the common growth variation, whereas the component loadings indicate the association of chronologies with the component.

Climate factors mainly responsible for the variation in annual radial increment were determined by bootstrapped correlation analysis. Coefficients were calculated between site chronologies and monthly climate data for the period 1974–2006 using the software package DENDROCLIM2002 (Biondi & Waikul, 2004). Monthly temperature, precipitation and sc-PDSI data over a 15-month window were considered, from June of the previous year to August of the current year. In addition, seasonal temperature means and precipitation sums of April – August, May – August and June – August of the current year were included, hereafter referred to as season I, II and III.

3 Results

3.1 Chronology characteristics and growth variations

For the period 1974–2006, the IC of the sites varies from 0.593 to 0.887 (Table 2), indicating strong common signals between trees from the same site. For both species, sites at lower altitudes have the largest MS values, suggesting a higher climate-sensitivity of these trees. All chronologies show EPS values exceeding the threshold of 0.85 as proposed by Wigley *et al.* (1984), meaning that the chronologies can be considered representative for tree growth at the sites.

Table 2: Chronology statistics of tree-ring series (in order of increasing altitude). Statistics refer to the maximum common overlap period 1974–2006

Site	RI (SD)	IC	MS	AC	EPS
Silver fir					
MUGG	3.63 (1.18)	0.729	0.294	0.298	0.931
BRIT	4.17 (1.46)	0.883	0.198	0.406	0.974
WALDF	4.02 (1.67)	0.696	0.256	0.150	0.920
STAU	2.67 (1.19)	0.838	0.290	0.272	0.963
SULZ	4.99 (1.86)	0.654	0.227	0.227	0.905
AU	4.91 (1.21)	0.764	0.224	-0.115	0.942
BURG	3.14 (1.10)	0.690	0.221	-0.024	0.917
ADELF	3.79 (1.14)	0.670	0.159	0.187	0.910
NEUE	4.36 (1.01)	0.672	0.156	0.209	0.911
EGER	5.05 (1.09)	0.627	0.155	0.328	0.894
KUHLF	3.55 (0.87)	0.633	0.145	0.290	0.873
FISC	3.22 (1.37)	0.692	0.156	0.523	0.918
KOHL	2.93 (1.42)	0.593	0.185	0.483	0.854
Norway spruce					
WALDS	3.16 (1.16)	0.775	0.235	0.215	0.945
EHRE	1.92 (0.58)	0.786	0.200	0.328	0.948
GUNT	3.97 (1.31)	0.666	0.200	0.376	0.909
KLOS	3.66 (1.01)	0.688	0.193	0.270	0.917
MUNS	2.17 (0.69)	0.887	0.184	0.521	0.975
DOTT	1.93 (0.56)	0.595	0.193	0.266	0.880
ADELS	3.30 (0.89)	0.685	0.192	0.356	0.916
MUNT	2.17 (0.69)	0.790	0.229	0.311	0.950
BLAU	3.85 (0.99)	0.816	0.201	0.363	0.957
KUHLS	2.48 (0.63)	0.726	0.185	0.231	0.930
AFTE	2.75 (0.70)	0.761	0.120	0.426	0.941
BERN	3.52 (1.28)	0.836	0.157	0.572	0.962
SIRN	2.54 (0.55)	0.788	0.164	0.322	0.949
TODT	1.77 (0.65)	0.884	0.193	0.582	0.974

RI radial increment (mm) with standard deviation (*SD*), *IC* inter-series correlation, *MS* mean sensitivity, *AC* first-order autocorrelation, *EPS* expressed population signal

Pearson correlation coefficients between site chronologies were plotted as a function of distance in altitude between sites (Fig. 3.1). For silver fir, the strength of the correlation significantly decreases with increasing distance, whereas the correlation coefficients for Norway spruce are higher and decrease only slightly with increasing altitudinal distance. To reveal common patterns in the 27 site chronologies a PCA was performed. Three low-altitude fir sites (STAU, BRIT, MUGG) and the spruce sites have the highest loadings on the first principal component (PC1), which explains 55.6% of the total variance (Fig. 3.2a). The scores of PC1 show the common growth variation of the chronologies, with pronounced growth depressions in the dry years 1976, 2003 and 2006 (Fig. 3.2b).

3.2 Climate–growth relationships

Bootstrapped correlation analyses between site chronologies of fir (see Fig. S1) and spruce (Fig. S2) and monthly temperature, precipitation and sc-PDSI revealed altitude- and species-specific differences in climate–growth relationships. Growth of fir at sites above 900 m a.s.l. is reduced under low temperatures from January till March, as indicated by significant positive correlations with temperature in these months (Fig. S1). For the highest site, also seasonal temperatures (I, II, III) are found to have a positive effect on growth, whereas at lower elevations radial growth is negatively related to temperature and positively to precipitation during the growing season. For low-altitude sites, significant
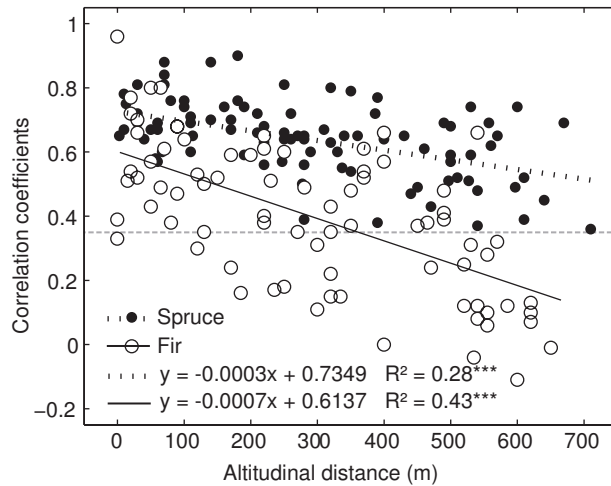
Figure 3.1: Pearson correlation coefficients between site chronologies as a function of altitudinal distance. The horizontal dotted line denotes the 95% confidence limit. Asterisks indicate significance levels of linear regressions, ***$P < 0.001$
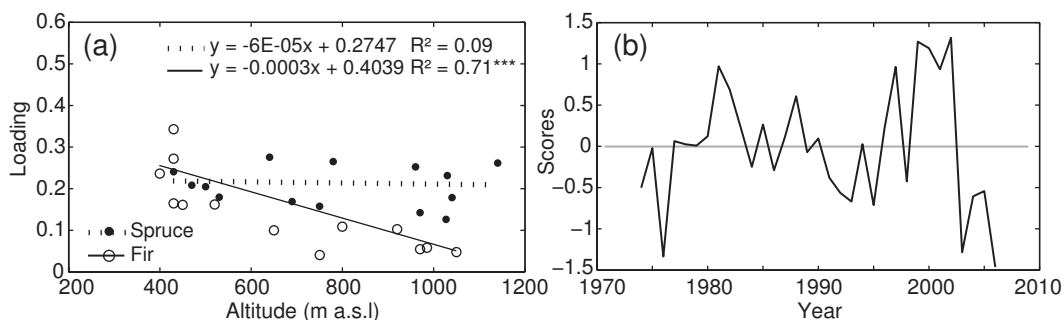

Figure 3.2: (a) Loadings and (b) scores of the first principal component of the 27 site chronologies. PC1 explains 55.6% of the total variance. Lines indicate linear regressions

correlations with sc-PDSI assume a high drought sensitivity of these trees. Further, a positive correlation with precipitation in February, suggests a favorable effect on water availability at the subsequent beginning of the growing season. However, a positive effect of temperature (*cf.* high-altitude sites) may be suggested as well, as high precipitation amounts in winter as usually accompanied by relatively high temperatures (low-pressure area).

Similar to high-altitude fir, high-altitude spruce shows significant positive correlations with March temperature at higher elevations (Fig. S2). Over the entire altitudinal range, negative correlations with previous and current-year July temperatures are found, indicating that growth of spruce is negatively affected by high summer temperatures independent of altitude. Strong positive correlations with current-year June and July precipitation as well as with seasonal precipitation (I, II, III), however, suggest that especially low-altitude spruce suffers under summer drought. This is substantiated by the strong correlations with sc-PDSI for these trees. But, also at higher elevations spruce seems still sensitive to drought, as illustrated by correlation coefficients for sc-PDSI in July plotted over altitude (Fig. 3.3). Although the strength of the correlations decreases with altitude for both species, they are generally higher for spruce than for fir, indicating higher summer drought sensitivity for spruce over the whole altitudinal range. Further, for fir a switch between more precipitation-controlled growth towards more temperature-controlled growth can be observed around 800–900 m a.s.l.

4 Discussion

Our aim was to provide insight into climate factors controlling radial growth of silver fir and Norway spruce along an altitudinal gradient in southwestern Germany. We constructed 27 chronologies by measuring radial growth from stem discs of five dominant or co-dominant trees per site. The number of sampled trees contrasts with, *e.g.*, Mérian & Lebourgeois (2011), who suggested using a total number of 15–20 trees per stand. However, as radial growth of our trees was measured on stem discs in eight pre-defined directions, radial growth estimates resulted from more
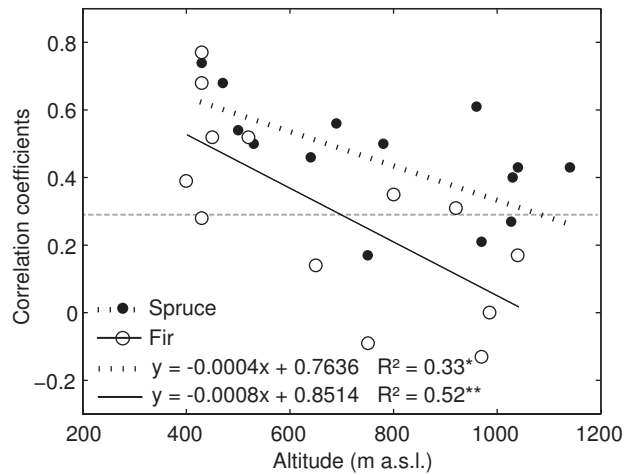
Figure 3.3: Bootstrapped correlation coefficients between standardized chronologies of spruce and fir and sc-PDSI in July as a function of altitude. The horizontal dotted line denotes the 95% confidence limit. Asterisks indicate significance levels of linear regressions, *P < 0.05, **P < 0.01

detailed measurements than estimates of ring width based on only one core per tree (*cf.* van der Maaten-Theunissen & Bouriaud, 2012). The reliability of the obtained site chronologies is substantiated by high inter-series correlations and high EPS values (Table 2) that are well above the critical threshold.

The analyzed tree-ring dataset contains variation in stand age among the study sites (Table 1). Although tree age might influence growth responses of trees to climate (*cf.* Carrer & Urbinati, 2004; Szeicz & MacDonald, 1994), a limited number of relatively young stands that met our selection criteria (see section 2.1) hampered a separate analysis of trees belonging to different age classes. Hence, we analyzed climate–growth relationships for each study site individually (Figs. S1 and S2). The number of annual rings of the youngest trees restricted the common overlap period for these analyses to 33 years, but we were nevertheless able to identify major climatic constraints. As both younger and older stands displayed similarly directed climate responses over the altitudinal gradient, it is suggested that the identified climate limitations with altitude are of major importance for the area.

For spruce, our results indicate a high similarity in growth responses along the altitudinal gradient (Figs. 3.1 and 3.2). Similar to our study, Meining *et al.* (2004) observed reduced stem growth of Norway spruce in the extreme year 2003 at 10 permanent monitoring plots in southwestern Germany (from 510 m to 1020 m a.s.l.), irrespective of elevation (*cf.* scores of PC1 in Fig. 3.2b). Other studies found that fir and spruce from different altitudes share less variation in growth (Lingg, 1986; Wilson & Hopfmüller, 2001), but an effect of fir was strongest for fir in our study (Fig. 3.1). Generally stronger correlation coefficients between chronologies of spruce might relate to a stronger climate signal captured by this species. We could elucidate altitude-dependent and species-specific growth patterns with results from the bootstrapped correlation analysis.

For growth of spruce, we observed strong correlations with both previous- and current-year climate conditions (Fig. S2). Of the previous-year conditions, negative effects of July temperature were strongest and present for almost all sites along the altitudinal gradient. The existence of such lagged climate effects on growth of spruce are known (*e.g.*, Kahle, 1996), and might be related to reduced growth rate and increased respiration losses under high temperatures that reduce the amount of carbohydrate reserves available for needle expansion and growth initiation at the beginning of the next growing season (Bouriaud & Popa, 2009).

During the current season, both high temperatures and low precipitation amounts in July were found to constrain growth of spruce (Fig. S2). This was substantiated by results for sc-PDSI. Although the strength of the correlation between growth and sc-PDSI decreased with altitude, spruce at high elevation was still found susceptible for water limitation (Figs. 3.3 and S2). This was unexpected because of the relatively high amounts of precipitation at these sites, but consistent with other studies in the same region (Kahle, 1994; Spiecker, 1991a) and in other mountainous regions like in Saxony, eastern Germany (Neumann & Röhle, 2001).

Low-altitude fir sites displayed a negative correlation with temperature and a positive correlation with precipitation in current June/July (Fig. S1). Together with the high correlations with sc-PDSI for these months (Figs. S1 and 3.3), it indicates water availability in mid summer as a major factor constraining growth of these trees. The importance of water availability for tree growth at low elevations is supported by previous studies (*e.g.*, Affolter *et al.*, 2010; Büntgen *et al.*, 2007; Dittmar & Elling, 1999; Mäkinen *et al.*, 2002; Neuwirth *et al.*, 2004). For fir above 900 m a.s.l., we found a significant positive effect of above-average temperatures from January till March (Fig. S1) on growth. As

warming in winter can initiate winter photosynthesis in fir (Guehl, 1985), this could improve carbohydrate storage and growth in the following growing season (Lebourgeois, 2007). Besides, higher temperatures in spring allow an early start of cambial activity (Deslauriers *et al.*, 2008; Kozlowski & Pallardy, 1997; Rossi *et al.*, 2007) thereby advancing tree-ring development. Positive correlations with precipitation in February for low-altitude sites might point at a favorable effect of above-average winter temperatures on growth as well, as high precipitation amounts in winter are often associated with relatively warm air (low-pressure area). Also for other regions, positive effects of winter temperature on fir growth have been reported (*e.g.*, Bouriaud & Popa, 2009; Frank & Esper, 2005; Lebourgeois *et al.*, 2010; Rolland *et al.*, 1999).

In our study, we did not observe a consistent correlation between water availability in summer and radial growth of high-elevation fir, whereas previous studies in the Black Forest found close relations with the climatic water balance during the growing season (*e.g.*, Kahle, 1996; Spiecker, 1991a,b). Especially in the dry year 1976, growth of high-altitude fir was strongly reduced (Spiecker, 1991b). Probably, this growth reduction relates to preconditioning of tree vigor. Pichler & Oberhuber (2007) reported that drought-exposed forest trees react less sensitive when a dry year is preceded by sufficiently wet years. In contrast to 2003, a year in which the growth of high-altitude fir was much less reduced compared to spruce and low-altitude fir, the year 1976 was preceded by several dry years. Hence, it is likely that this preconditioning in 1976 has negatively affected growth of these trees (*cf.* Becker, 1989). In Bavaria, sulphur dioxide (SO_2) emissions were further suggested as an important influencing factor for the observed growth depression of fir (Elling *et al.*, 2009). For the Black Forest, possible effects of SO_2 are less likely as concentrations were (and are) much lower compared to those observed in Bavaria (Beilke & Uhse, 1999). A moderate drought sensitivity of fir is as well found in dendroecological studies in other regions (*e.g.*, Bouriaud & Popa, 2009; Zang *et al.*, 2011).

Although numerous studies along altitudinal gradients report positive effects of increased summer temperature on tree growth at high elevation (*e.g.*, Dittmar & Elling, 1999; Frank & Esper, 2005; Leal *et al.*, 2007; Savva *et al.*, 2006), this was not consistent with our study. It may be suggested that our high-elevation sample sites are not as close to the upper tree line as sites in these other studies. This is in accordance with the observation of Fritts *et al.* (1965) that climatic control of growth increases towards the limits of tree growth. Trees growing on more favorable sites do not respond as strongly to temperature as trees on temperature-limited sites (*e.g.*, Čejkova & Kolář, 2009; Wilson & Hopfmüller, 2001).

Further, trees at high elevation are generally not water-limited, but when temperatures are high, the importance of water availability increases here as well (*e.g.*, Carrer *et al.*, 1998; Tranquillini, 1964). In the northeastern Italian Alps, Anfodillo *et al.* (1998) demonstrated for three coniferous species that even moderate changes in water deficit might reduce transpiration in trees adapted to moist conditions. Norway spruce and Stone pine (*Pinus cembra* L.) were found more susceptible for water shortage than the deep rooting European larch (*Larix decidua* Mill.). On long-term forest research plots in Switzerland, Zingg & Bürgi (2008) observed a higher drought susceptibility of spruce compared to fir. Fir has, like larch, a deep taproot that allows reaching deeper water reserves, whereas spruce typically develops a superficial root system (Larcher, 1995). Therefore, growth of spruce may be more negatively affected when an increase in temperatures is not followed by an increase in water supply. In the Swiss Alps, late-summer drought stress of subalpine spruce has already increased since ~1900 following the recent warming trend (Büntgen *et al.*, 2006).

5   Conclusion

We observed differences in growth patterns and climate response of silver fir and Norway spruce at southwest-exposed sites along an altitudinal gradient in the Black Forest. Overall, we identified water availability as a major growth-limiting factor for fir at low altitudes and spruce along our altitudinal gradient. In a future warmer climate, with more frequent and severe summer droughts (Beniston, 2004), growth and vitality, especially of spruce, will be at risk, when an increased evaporative demand cannot be compensated by water supply. As adaptation measure forest conversion has to be considered (*cf.* Baumgarten *et al.*, 2005). However, uncertainty remains on future growth responses of both species, as climate change may subject these trees to extreme climatic conditions they were not exposed to before.

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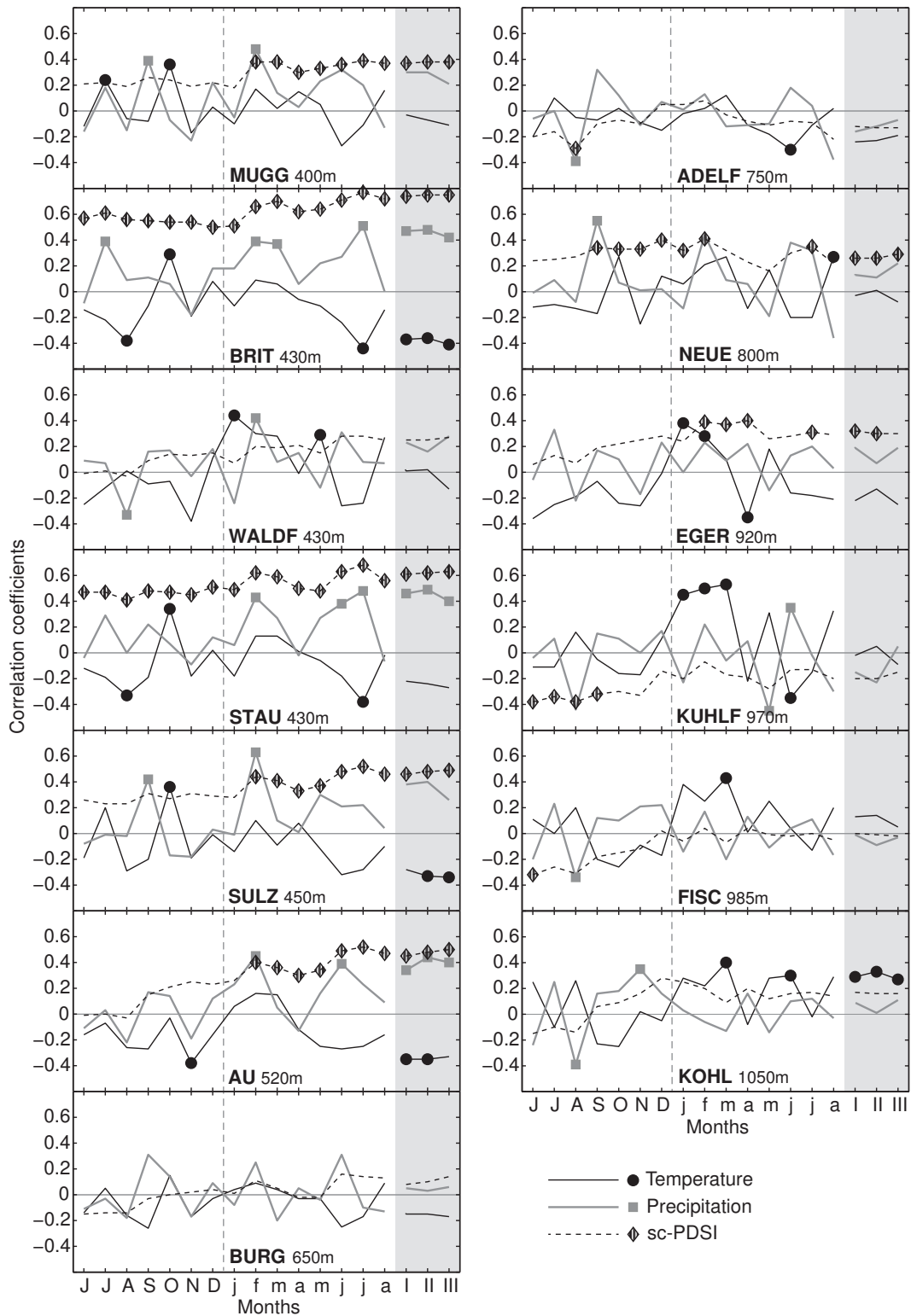
Figure S1: Bootstrapped correlation coefficients between annual radial growth of fir and monthly temperature, precipitation and sc-PDSI from previous June till current August. Seasonal means are averaged over: I = April-August, II = May-August, III = June-August. Symbols indicate significant correlations at P < 0.05. Sites are ranked in order of increasing altitude (from MUGG to KOHL)
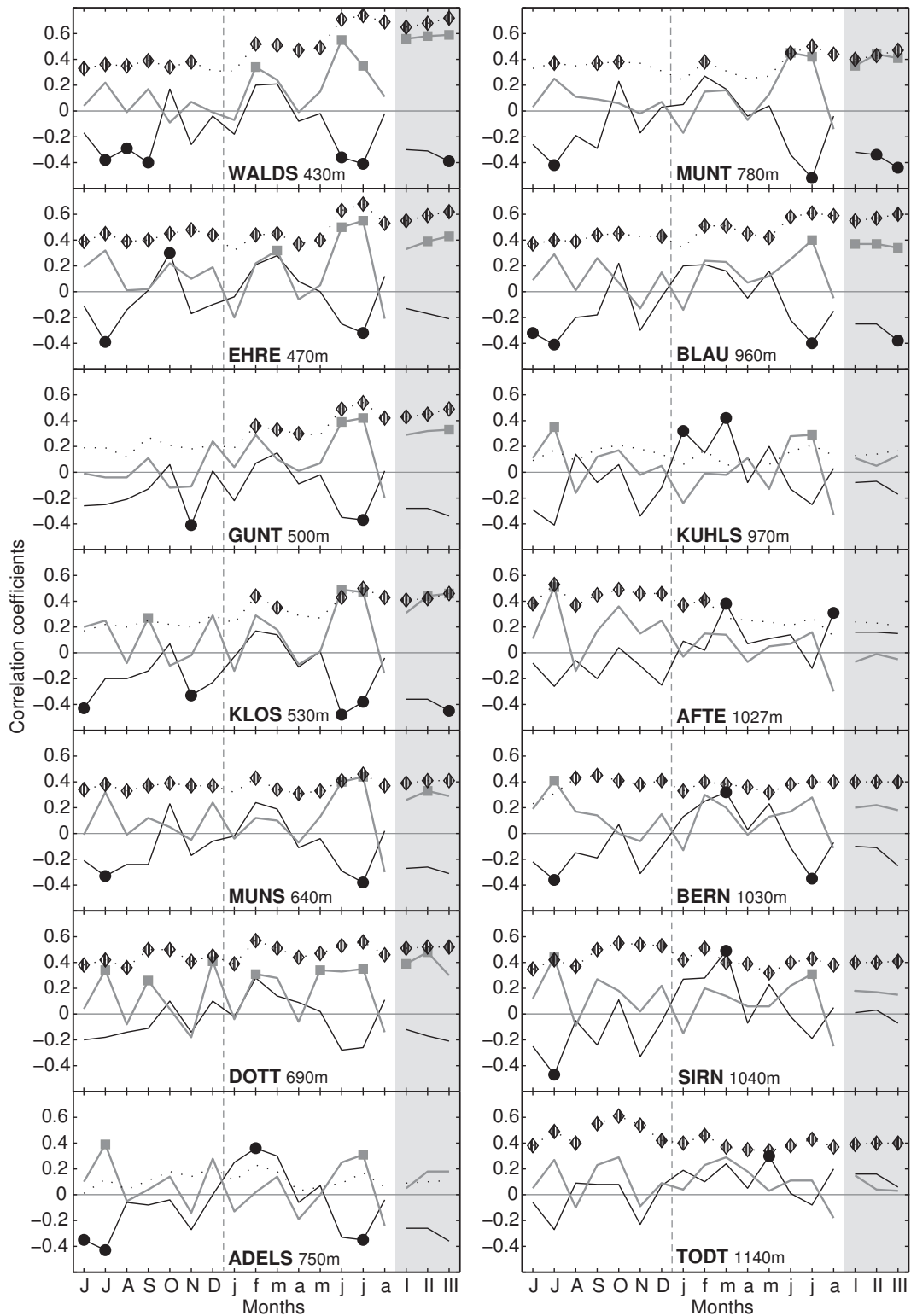
Figure S2: Bootstrapped correlation coefficients between annual radial growth of spruce and monthly temperature, precipitation and sc-PDSI (see legend Fig. S1) from previous June till current August. Seasonal means are averaged over: I = April-August, II = May-August, III = June-August. Symbols indicate significant correlations at P < 0.05. Sites are ranked in order of increasing altitude (from WALDS to TODT)