Climate–growth relationships at different stem heights in silver fir and Norway spruce

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Abstract

We investigated the effect of climate on variations in annual ring-area increment along the stem of dominant silver fir (*Abies alba* Mill.) and Norway spruce (*Picea abies* (L.) Karst.) trees in the Black Forest, southwestern Germany, to test the hypothesis that growth allocation changes as a result of climate fluctuations. Stem discs were taken at three different stem heights: 1.30, 11.50 and 16.70 m. For each site and stem height, average annual ring-area increment chronologies were computed. In addition, we calculated ratios between ring-area increment of the upper stem discs and the disc at breast height to compare growth variations along the stem. Pearson correlation coefficients revealed a highly similar growth pattern at different stem heights, where the two upper discs were most similar. Bootstrapped correlation coefficients between the ring-area increment chronologies, ratios, and monthly temperature, precipitation, and self-calibrated Palmer drought sensitivity index data were calculated to analyze differences in climate response. High temperatures in early summer were found to reduce growth of high-altitude fir in the upper stem parts, whereas high temperatures in summer limit growth of high-altitude fir and high-altitude spruce especially at breast height. For low-altitude trees, high temperatures as well as low precipitation amounts during summer were found to reduce growth at all stem heights, but more strongly at breast height. Growth at breast height seems to be biased, as it over- or underestimates annual ring-area increments along the stem (and thereby volume increment) particularly during warm and dry climate conditions.

1   Introduction

In dendrochronological analyses, increment cores or stem discs are traditionally extracted at breast height (1.30 m) because growth irregularities caused by strong taper at the stem base stabilize here, while the number of annual rings is still high (Schweingruber *et al.*, 1990). Furthermore, samples are easy to extract, and thus, breast height sampling became a conventional standard. The question whether radial growth at breast height can be used as a valuable proxy of the annual carbon sink and its fluctuations became increasingly important with the rising interest in trees' carbon storage and capture (*e.g.,* Bouriaud *et al.*, 2005b; Kerhoulas & Kane, 2012). Assuming that growth at breast height and its climatic signal are representative for growth at all positions along the stem can be considered a default approach. However, previous studies did not confirm its validity, since a reduced sensitivity to climate in the upper part of the stem was shown for European beech (*Fagus sylvatica* L.) (Bouriaud *et al.*, 2005b) and Norway spruce (*Picea abies* (L.) Karst.) (Bouriaud *et al.*, 2005a).

Stem form and growth allocation to different parts of the stem are influenced by many factors. Thinning, for example, causes maximum growth to move to the lower stem (Abetz, 1977; Assmann, 1961; Farrar, 1961; Holgèn *et al.*, 2003), shifting back to the upper stem after several years (*e.g.,* Myers, 1963; Peltola *et al.*, 2002; Tasissa & Burkhart, 1997). After stand closure, growth at breast height decreases, while stem volume increment continues to increase (LeBlanc, 1990).

Changes in stem form and taper are strongly related to crown size, which, in turn, depends on stand density (Muhairwe, 1994). In general, open-grown trees have a higher degree of taper compared with trees growing in closed stands (Kozlowski *et al.*, 1991), as a high exposure to wind in low-density stands causes growth to be allocated downwards

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for mechanical stabilization (Meng *et al.*, 2006; Mitchell, 2000; Telewski, 1995). Water availability was found to increase growth at the lower stem level as well (Wiklund *et al.*, 1995), whereas studies on the effect of fertilization pointed out to conflicting conclusions. Although Valinger (1992) and Wiklund *et al.* (1995) reported that fertilization caused growth to be allocated upwards along the stem in Scots pine (*Pinus sylvestris* L.) and Norway spruce, respectively, Spiecker (1991) found no effect of fertilization on stem form in Norway spruce and Thomson & Barclay (1984) found none in Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco). In middle and northern Sweden, thinning in combination with fertilization significantly increased growth of Scots pine at the base, but no effect on stem form or taper was found for Norway spruce (Karlsson, 2000).

Other studies investigated differences in intra-annual diameter increment at different stem heights (Kozlowski & Peterson, 1962; Künstle, 1994) or the climate response of radial growth and height growth of differently thinned trees (Mäkinen *et al.*, 2002b), but few studies analyzed climate–growth relationships of different stem portions or at different stem heights (Bouriaud *et al.*, 2005a,b; Chhin & Wang, 2005; Chhin *et al.*, 2010; Corona *et al.*, 1995; Kerhoulas & Kane, 2012). The aim of this study was to analyze whether differences exist in climate response of ring-area increment of silver fir (*Abies alba* Mill.) and Norway spruce at breast height in comparison with ring-area increment in upper parts of the stem, revealing possible changes in growth allocation as a result of climate. In addition, influences of altitude were considered by sampling at different altitudes.

2 Material and methods

2.1 Study sites, sampling and measurement

Our study material consists of mature trees from two high-altitude and two low-altitude fir sites and one high-altitude and one low-altitude site with both fir and spruce (KUHL and WALD, respectively) in the Black Forest region of southwestern Germany (Fig. 2.1). Sites were selected based on comparable soil conditions and a southwestern aspect to limit potential confounding factors. The difference between low- and high-altitude sites is more than 500 m. Further details on the sampling sites are provided in Table 1.
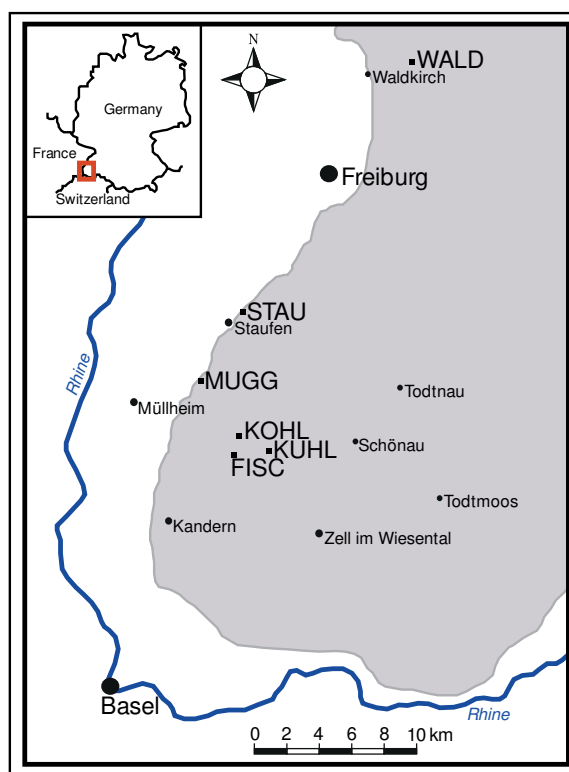

Figure 2.1: Location map of the study sites. Forest is highlighted in grey

Table 1: Description of study sites. *AWC* available soil water capacity: 1 = very low (<50 mm), 2 = low (50-90 mm), and 3 = medium (90-140 mm). Values in parentheses denote standard deviations

Species	Altitude class	Site	Altitude (m a.s.l.)	Latitude (°N)	Longitude (°E)	No. of trees	Age at breast height (years)	Diameter at breast height (cm)	Tree height (m)	Crown height (m)	AWC
Silver fir	Low	STAU	430	47.53	7.44	4	127.4 (19.4)	51.7 (2.1)	27.0 (1.5)	13.9 (2.8)	1, 2
		MUGG	400	47.49	7.41	4	100.3 (8.9)	59.1 (4.0)	29.1 (0.6)	17.2 (0.9)	2, 3
		WALDF	430	48.06	8.00	5	109.8 (10.0)	70.0 (5.6)	30.9 (1.5)	16.6 (4.3)	2, 3
	High	FISC	985	47.46	7.46	5	96.6 (1.7)	60.4 (3.8)	27.7 (0.4)	14.8 (1.3)	2, 3
		KOHL	1040	47.47	7.46	4	107.3 (17.1)	68.4 (9.1)	27.6 (1.8)	15.4 (0.9)	2, 3
		KUHLF	970	47.46	7.47	5	101.4 (3.1)	67.8 (8.8)	29.0 (2.1)	13.3 (1.8)	1, 2
Norway spruce	Low	WALDS	430	48.06	8.00	5	86.2 (7.3)	55.1 (2.4)	32.3 (0.6)	15.9 (2.7)	2, 3
	High	KUHLS	970	47.46	7.47	5	112.4 (3.5)	53.3 (9.6)	28.9 (2.6)	13.9 (1.6)	1, 2

Per site, stem discs of four or five dominant or co-dominant spruce or fir trees with no visible signs of damage were collected. Stem discs were extracted at three different stem heights: 1.30, 11.50 and 16.70 m (*cf.* Gerecke, 1988), hereafter referred to as D1, D2 and D3. D3 was generally situated in the crown. In the laboratory, discs were air-dried and sanded to highlight annual rings. Annual radial increment was measured with a precision of 0.01 mm in eight (D1) or four (D2 and D3) pre-defined directions using semi-automatic image analysis software (developed at the Institute for Forest Growth). Hence, the estimations of radial growth resulted from far more detailed measurements than usually done based on increment cores. Individual tree-ring series were calculated as quadratic means of the radii and cross-dated both visually and statistically (*Gleichläufigkeit*).

2.2 Chronology development

We transformed the radial growth series into ring-area increment series using

$$\pi(R_j^2 - R_{j-1}^2) \tag{1}$$

where R is the radius of the tree and j is the year of tree-ring formation. These ring-area increment series were standardized for further analysis. Ring-area increment exhibits an exponential shape with tree age. We therefore transformed the series to logarithmic values. The log-transformed ring-area increments in year $j - 1$ were expressed as a function of the log-transformed ring-area increment in year j. We fitted a linear regression line using the *regress* function in MATLAB V7.9.0 (R2009b) and residuals were calculated by subtracting the predicted values from the observed values. This kind of standardization, based on tree dimension in the year prior to growth, has been proven to provide a sound climate signal (Bouriaud *et al.*, 2005b; Le Goff & Ottorini, 1993). A cubic smoothing spline with 50% frequency cut-off at 10 years was fitted to each residual chronology to retain high-frequency variations (Cook & Peters, 1981) using MATLAB's Spline Toolbox function *csaps* (V3.3.7) in combination with the spline smoothing parameter function *splinep* (presented courtesy of J.L. Dupouey). Residuals were calculated and series were then averaged per site using an arithmetic mean. This procedure resulted in site-specific ring-area increment chronologies for the different stem heights, hereafter referred to as RAI1, RAI2 and RAI3.

The average correlation between chronologies, the inter-series correlation (IC) (Fritts, 1976), was calculated for each site and stem height over the common overlap period 1970–2008 to reveal the strength of the common signal among the trees. The confidence of the chronologies was evaluated by the expressed population signal (EPS) (Wigley *et al.*, 1984). Expressed population values were calculated with the *wigley1* function (presented courtesy of D. Meko).

2.3 Growth variations

We calculated Pearson correlation coefficients between the ring-area increment chronologies to assess the stability of the growth signal at different stem heights. To analyze growth variations along the stem, we calculated ratios of ring-area increments for each tree as

$$\frac{RAI_{i,j,k}}{RAI1_{i,j}} \tag{2}$$

where RAI1 is the ring-area increment at 1.30 m and i denotes the ith tree, j the jth year and k one of the two upper stem heights (11.50 or 16.70 m) (Bouriaud *et al.*, 2005b). The ratios were standardized similar to the ring-area increment series using cubic smoothing splines with 50% frequency cut-off at 10 years. Residuals were calculated as

for ring-area increment chronologies and averaged per site. The produced ratios are referred to as R2 (11.50 m) and R3 (16.70 m).

Additionally, we divided the ratios in drought-event years 1976, 2003 and 2006 and in the normal year 1999 by the average ratio over the 5 preceding years to quantitatively compare the growth increase or reduction at 11.50 or 16.70 m relative to breast height under extreme and normal climate conditions.

2.4 Climate–growth relationships

The German Weather Service provided a gridded climate surface (1 km x 1 km) from which we extracted site-specific monthly air temperature and precipitation data for the period 1900–2009. For each site, a self-calibrating Palmer drought severity index (sc-PDSI) was calculated using a tool from the GreenLeaf Project (GreenLeaf, 2011), to test the combined effect of temperature and precipitation. Required input variables for the calculation are temperature, precipitation, latitude and available soil water capacity (AWC). The monthly temperature, precipitation and sc-PDSI data were used to analyze climate–growth relationships for the ring-area increment chronologies (RAI1, RAI2 and RAI3) and for the ratios (R2 and R3). The climate factors mainly responsible for the growth variations found were determined by calculating bootstrapped correlation coefficients over the common overlap period of all discs, which was 1970–2008, using the software package DENDROCLIM2002 (Biondi & Waikul, 2004). In these analyses, we considered monthly climate data from January to September of the current year. Previous-year climate data customarily included (October to December) were checked but not presented here, as no clear signals were found.

3 Results

3.1 Chronology characteristics

Over the period 1970–2008 average annual radial increment was lowest in D2 for all sites (Table 2) except STAU. Average ring-area increment decreased from D1 to D3, except for site MUGG where average ring-area increment was higher for D3 than for D2. The coefficient of variation (CV; ratio of the standard deviation to the mean) decreased with stem height, suggesting a higher sensitivity of ring-area growth in the lower stem. The CV of the ring-area ratios was highest for R3 at all sites (Table 3), indicating more variation in growth pattern between D1 and D3, than between D1 and D2 or D2 and D3. For all sites, IC values were high and EPS values exceeded the critical value of 0.85 proposed by Wigley *et al.* (1984), indicating strong common signals.

3.2 Growth variation along the stem

The ring-area increment chronologies for the three different stem heights are presented in Fig. 3.1. Growth variation at the different tree heights was highly correlated (Table 4). In most cases, the strongest correlations were found between RAI2 and RAI3, whereas RAI1 and RAI3 displayed the lowest correlation, regardless of sites and species.

3.3 Climate response

First, we analyzed the relation between monthly temperature and precipitation and the ring-area increment chronologies. The correlation patterns at different sites were quite similar for a given altitude band. At high-altitude sites (Fig. 3.2), high winter temperature was found to favor growth. Further, we found a positive tendency of temperature in May and August for fir. Precipitation in May reduced growth of high-altitude trees, while June precipitation had a positive effect, both only significant for KUHLF.

At low-altitude sites (Fig. 3.2), tree-growth series showed a negative correlation with temperature in June and July. Precipitation in February and July positively influenced growth at several low-altitude sites, whereas June precipitation favored growth at all of these sites. The integrative parameter sc-PDSI indicates a high drought sensitivity of low-altitude sites, except for WALDF (Fig. 3.3). Results on high-altitude sites are not shown, as they did not indicate significant and clear patterns.

Second, the climate response of the ratios was analyzed. For the high-altitude fir trees (Fig. 3.4) R2 was negatively correlated with temperature in April and May. This suggests a higher relative reduction of growth at 11.50 m compared with breast height under high temperatures in these months. For all sites (both high and low altitude), temperature in June and/or July showed a positive effect on R2 and R3, indicating a stronger decrease in growth at breast height under high summer temperatures. No clear effects of precipitation on the ratios of high-altitude trees could be found. But for the low-altitude fir at WALD, favorable summer conditions relatively favors growth at breast height, as suggested

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Table 2: Average radial increment (*RI*) and average ring-area increment (*Mean*) for the period 1970–2008. Sampling heights are: D1 – 1.30 m, D2 – 11.50 m, D3 – 16.70 m. *SD* standard deviation, *CV* coefficient of variation, *IC* inter-series correlation, *EPS* expressed population signal

Species	Altitude class	Site	Sample height	RI (mm)	Ring-area increment Mean (mm^2)	SD (mm^2)	CV (%)	IC	EPS
Silver fir	Low	STAU	D1	2.76	3237	1584	49	0.810	0.945
			D2	2.91	2110	855	41	0.805	0.943
			D3	3.66	1566	887	57	0.800	0.941
		MUGG	D1	3.14	3302	1827	55	0.854	0.959
			D2	2.43	1752	729	42	0.801	0.942
			D3	3.12	2041	745	36	0.812	0.945
		WALDF	D1	3.90	6452	3096	48	0.752	0.938
			D2	2.25	2439	953	39	0.757	0.940
			D3	2.44	2162	710	33	0.781	0.947
	High	FISC	D1	3.26	4401	2387	54	0.745	0.936
			D2	2.20	2009	908	45	0.731	0.931
			D3	2.73	1784	550	31	0.785	0.948
		KOHL	D1	2.81	4693	2052	44	0.694	0.901
			D2	2.27	2514	914	36	0.713	0.909
			D3	3.14	2478	648	26	0.766	0.929
		KUHLF	D1	3.03	4857	2323	48	0.730	0.931
			D2	2.56	2592	908	35	0.735	0.933
			D3	3.42	2391	640	27	0.783	0.948
Norway spruce	Low	WALDS	D1	2.98	3560	1240	35	0.783	0.974
			D2	2.49	2132	601	28	0.782	0.947
			D3	2.74	1727	501	29	0.745	0.936
	High	KUHLS	D1	2.47	3022	855	28	0.808	0.955
			D2	1.97	1753	455	26	0.750	0.938
			D3	2.22	1484	357	24	0.688	0.917

Table 3: Average ratio and standard deviation (*SD*) of the ratios for the period 1970–2008. *R2* is the ratio between RAI2 and RAI1, *R3* is the ratio between RAI3 and RAI1. *CV* coefficient of variation

Species	Altitude class	Site	Series	Ratio	SD	CV (%)
Silver fir	Low	STAU	R2	0.68	0.20	29
			R3	0.55	0.21	39
		MUGG	R2	0.61	0.16	26
			R3	0.63	0.27	42
		WALDF	R2	0.43	0.14	32
			R3	0.40	0.13	33
	High	FISC	R2	0.50	0.11	22
			R3	0.50	0.17	35
		KOHL	R2	0.71	0.33	46
			R3	0.68	0.39	57
		KUHLF	R2	0.47	0.11	24
			R3	0.39	0.10	25
Norway spruce	Low	WALDS	R2	0.63	0.12	19
			R3	0.52	0.12	24
	High	KUHLS	R2	0.60	0.10	16
			R3	0.51	0.11	21

Table 4: Correlations between standardized ring-area increment chronologies (RAI) at different stem heights of silver fir and Norway spruce. All correlations are significant at P < 0.0001

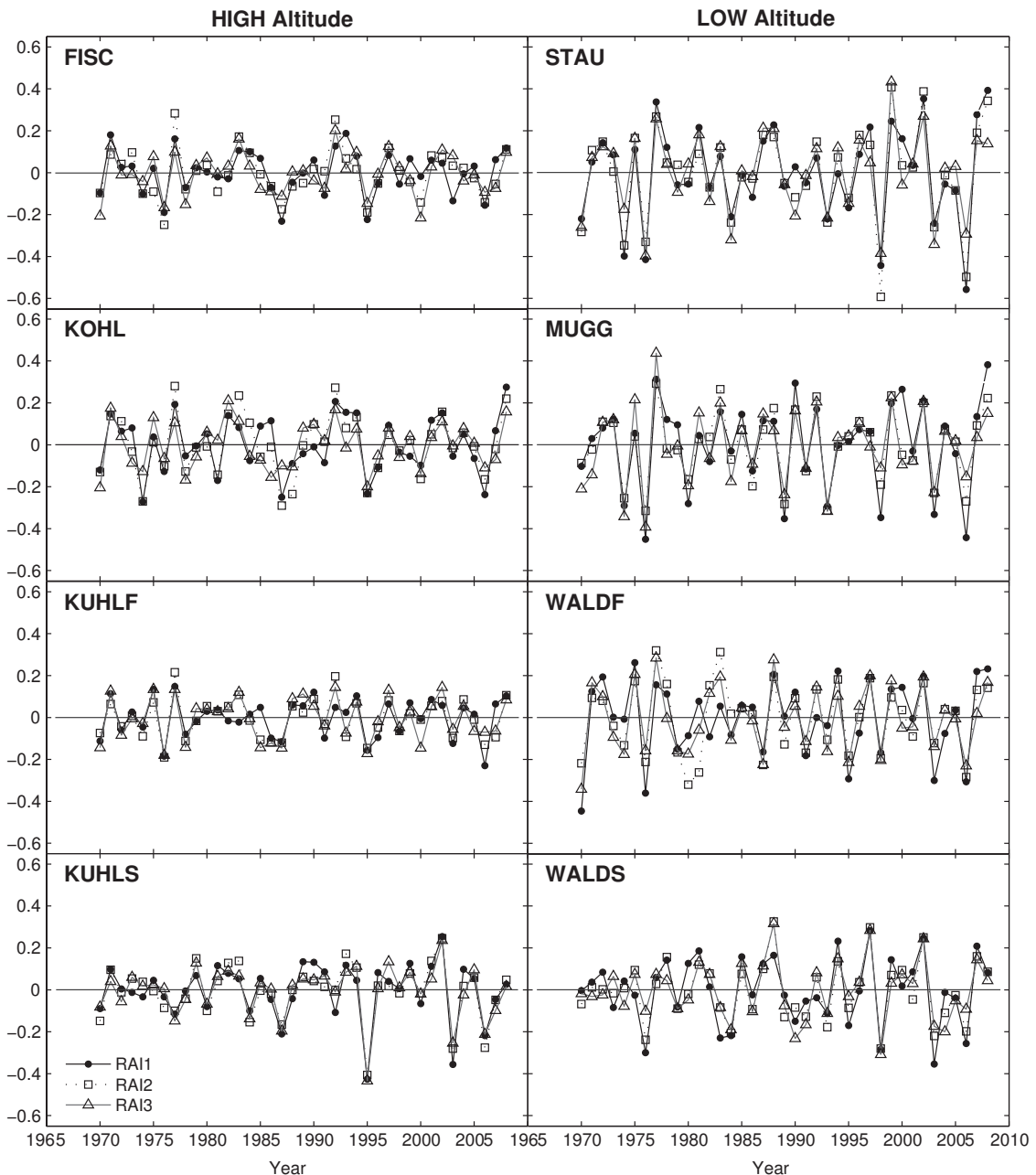| Species	Altitude class	Site	RAI1 vs. RAI2	RAI1 vs. RAI3	RAI2 vs. RAI3
Silver fir	Low	STAU	0.95	0.86	0.92
		MUGG	0.90	0.82	0.91
		WALDF	0.74	0.80	0.90
	High	FISC	0.78	0.65	0.79
		KOHL	0.85	0.66	0.80
		KUHLF	0.77	0.72	0.89
Norway spruce	Low	WALDS	0.87	0.78	0.92
	High	KUHLS	0.91	0.91	0.94

Figure 3.1: Ring-area increment chronologies for the three different stem heights over the period 1970–2008. Chronologies are presented for all sites separately

by the negative effect of precipitation in June and July on R2 and R3. Spruce behaved in a very comparable manner to fir. A stronger correlation between June–July temperatures, June–July precipitation, and breast height is also visible in Fig. 3.2, especially for WALDS. The correlations between the ratios and the sc-PDSI (Fig. 3.5) support the findings presented in Fig. 3.4, displaying positive correlations in spring and negative in summer, thus suggesting that water availability favors successively upper stem growth in spring and breast height in summer, although not being significant at $P < 0.05$. Hence, ratios were more strongly correlated with temperatures and precipitation than with the sc-PDSI.

To quantify the consequences of differences in climate sensitivity among stem heights pointed out by the correlations, we compared the relative growth reduction at 11.50 and 16.70 m relative to breast height for selected years. As displayed in Fig. 3.6, index values in years with high temperatures and low precipitation amounts (1976, 2003 and 2006) are generally higher compared with index values in a climatically normal year (1999). For 1999, median values are below 1 in almost all cases, indicating relatively more growth at breast height. In the other years, however, index values are mostly beyond 1, hence showing a stronger reduction of growth at breast height, with higher values for the comparison between D3 and D1. The index reaches on average values of $1.1-1.5$, indicating a relative growth reduction of $10\%-50\%$ at breast height compared with higher parts of the stem. Altitude seems not to alter this trend, but generally, higher index values for low-altitude sites suggest more extreme growing conditions at these sites.
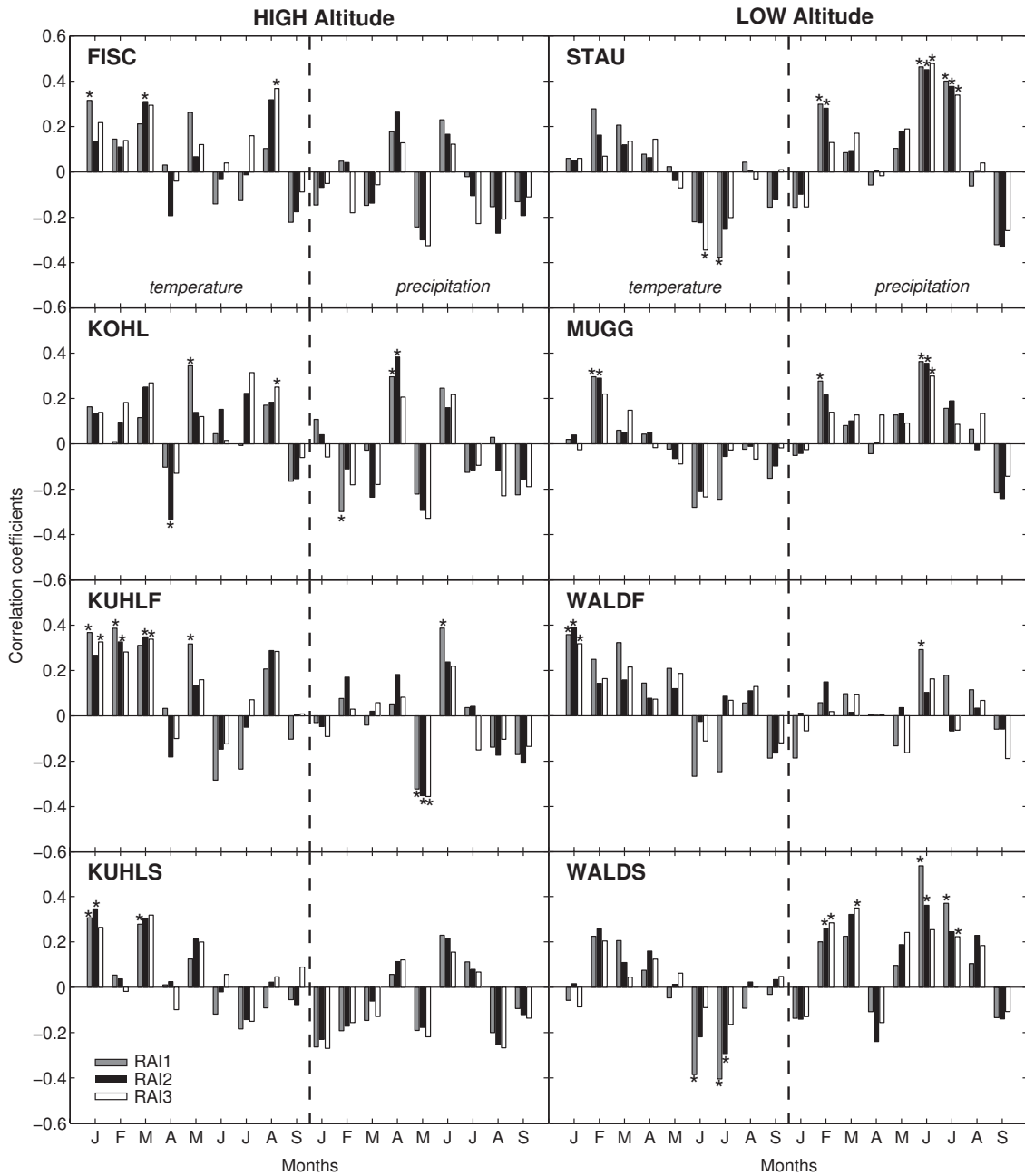
Figure 3.2: Bootstrapped correlation coefficients between the ring-area increment chronologies (RAI1, RAI2 and RAI3) and monthly temperature and precipitation data of the different sites for January to September of the current year (*significant correlations (P < 0.05))

4 Discussion and conclusion

The comparison between climate–growth relationships for ring-area increment at three positions along the stem for silver fir and Norway spruce at different altitudes in the Black Forest showed that breast-height series are not comparably sensitive to climate than upper series and that growth allocation was most influenced by temperature. In hot summers, reduction of growth was univocally larger at breast height than in upper parts of the stem. Although having less replication for Norway spruce than for silver fir, our results showed a similar behavior for both species. Growth allocation to different parts of the stem may be influenced by many factors, such as silvicultural practices (*e.g.,* Kozlowski *et al.*, 1991; Larson, 1963) and wind (*e.g.,* Meng *et al.*, 2006; Telewski, 1995). However, a uniform climate response for high-altitude stands, as well as for low-altitude stands, suggests no strong influences of these factors on our chronologies. We sampled trees in different plots to avoid bias and used a flexible spline of 10 years to remove most of the low-frequency variation. High IC and EPS values underline a strong common signal and a
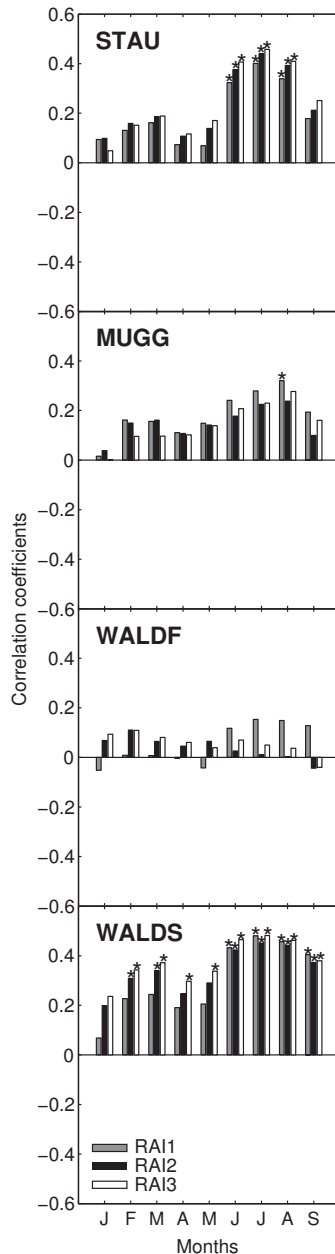
Figure 3.3: Bootstrapped correlation coefficients between the ring-area increment chronologies (RAI1, RAI2 and RAI3) and monthly sc-PDSI data of the different sites for January to September of the current year (*significant correlations (P < 0.05))

high quality of ring-area increment chronologies obtained. The number of rings in D3 restricted the length of the observation period to 39 years. Although a longer observation period could have resulted in clearer climatic signals, we identified major climatic constraints for growth of these trees.

Pearson correlation coefficients showed that growth variation at different stem heights was highly correlated (Table 4). Consequently, climate–growth relationships for the individual ring-area increment chronologies (RAI1, RAI2 and RAI3) were also highly similar (Fig. 3.2). Although the strength of the correlation differed occasionally, the direction of the correlation (positive or negative) was the same. In general, high-altitude trees were found to be more susceptible for cold temperatures from January until March, being in accordance with findings of other studies at high elevation (*e.g.,* Frank & Esper, 2005; Savva *et al.*, 2006). Especially silver fir is known to be sensitive to frost (*e.g.,* Gerecke, 1988; Lebourgeois *et al.*, 2010; Rolland *et al.*, 1999). Further, both fir and spruce negatively reacted to high temperatures and/or low precipitation amounts during summer, especially at low altitudes. This is consistent with other studies on these species (*e.g.,* Desplanque *et al.*, 1999; Mäkinen *et al.*, 2002a; Rolland *et al.*, 2000), highlighting their drought sensitivity.

To analyze under which climate conditions allocation patterns changed, we calculated ratios between growth in the upper stem discs and growth at breast height. Bootstrapped correlation analyses between the ratios and monthly cli-
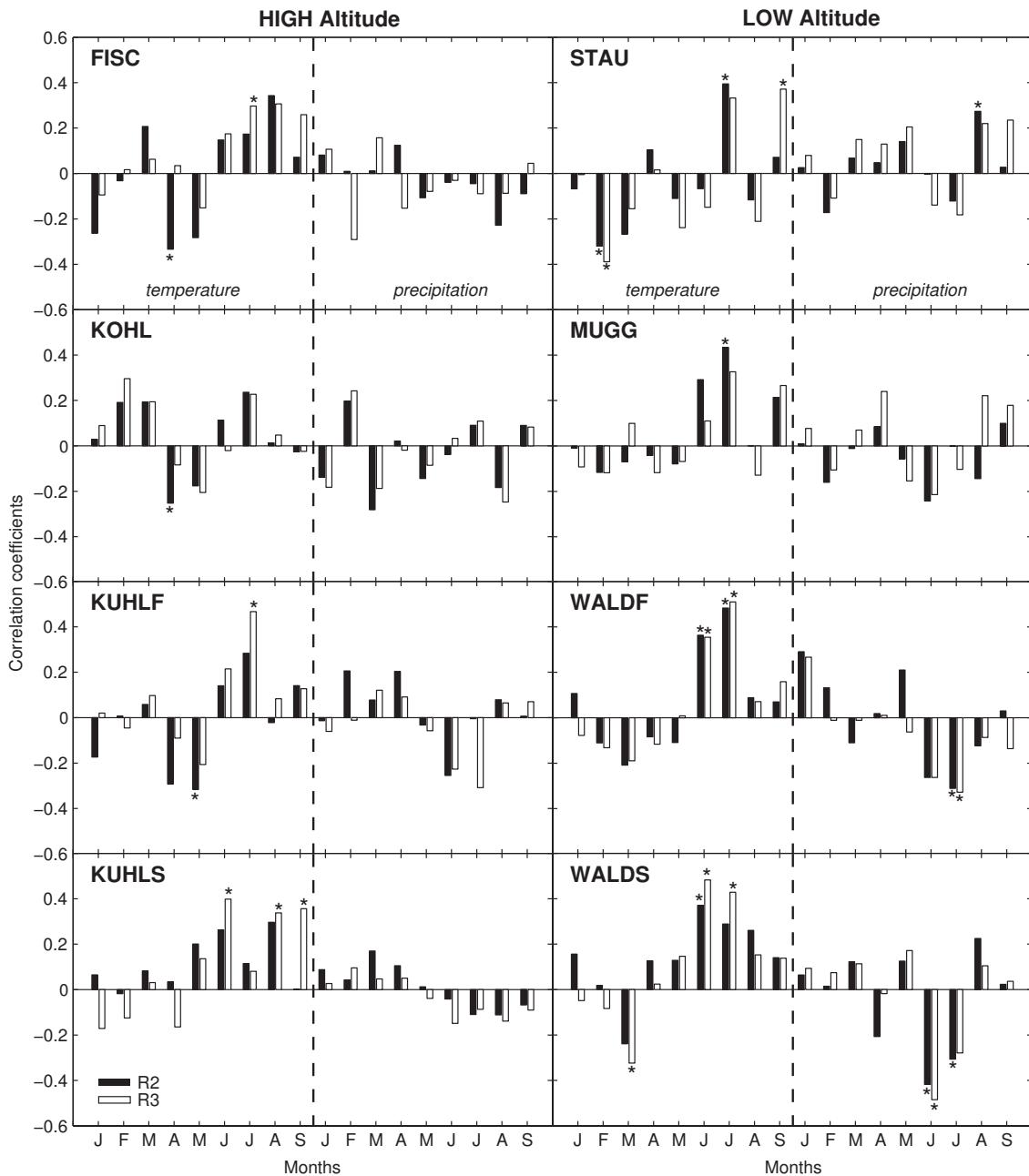
Figure 3.4: Bootstrapped correlation coefficients between the ratios (R2 and R3) and monthly temperature and precipitation data of the different sites for January till September of the current year (*significant correlations (P < 0.05))

mate data revealed reduced growth in the upper stem of high-altitude fir trees under high temperatures in April and/or May (Fig. 3.4). For lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. latifolia Engelm.), Chhin *et al.* (2010) also found growth-limiting effects of hot and dry conditions in early summer higher up the stem. During early summer, active crown and foliage growth occurs and the upper stem has a higher priority for carbon allocation (Fritts, 1976). However, unfavorable conditions during this period, *i.e.*, high temperatures, will increase respiration, decreasing the net amount of carbon available for growth in the upper stem (Chhin *et al.*, 2010; Gower *et al.*, 1995; Lacointe, 2000). For low-altitude trees, correlation coefficients for the two ratios R2 and R3 indicated a higher relative reduction in growth at breast height when June and/or July were hot and dry (Figs. 3.4 and 3.6), whereas R2 and R3 of high-altitude trees only showed a negative effect of high temperatures in these months (Fig. 3.4). Other studies found similar reductions of growth at breast height under warm and dry summer conditions in European beech (Bouriaud *et al.*, 2005b) and latewood production of loblolly pine (*Pinus taeda* L.) (Smith and Wilsie, 1961 cited in Dougherty *et al.*, 1994; Zahner, 1968). Sevanto *et al.* (2003) observed comparable top growth in Scots pine in 2001 and 2002, whereas growth at the base was reduced during the dry early summer of 2002. Also Künstle (1994) found a reduction in diameter growth of Norway spruce at 1.90 m compared with 6.20 m under extreme drought in 1991. On the other hand, high water availability, as simulated by an irrigation experiment with spruce, had a positive effect on growth at breast height
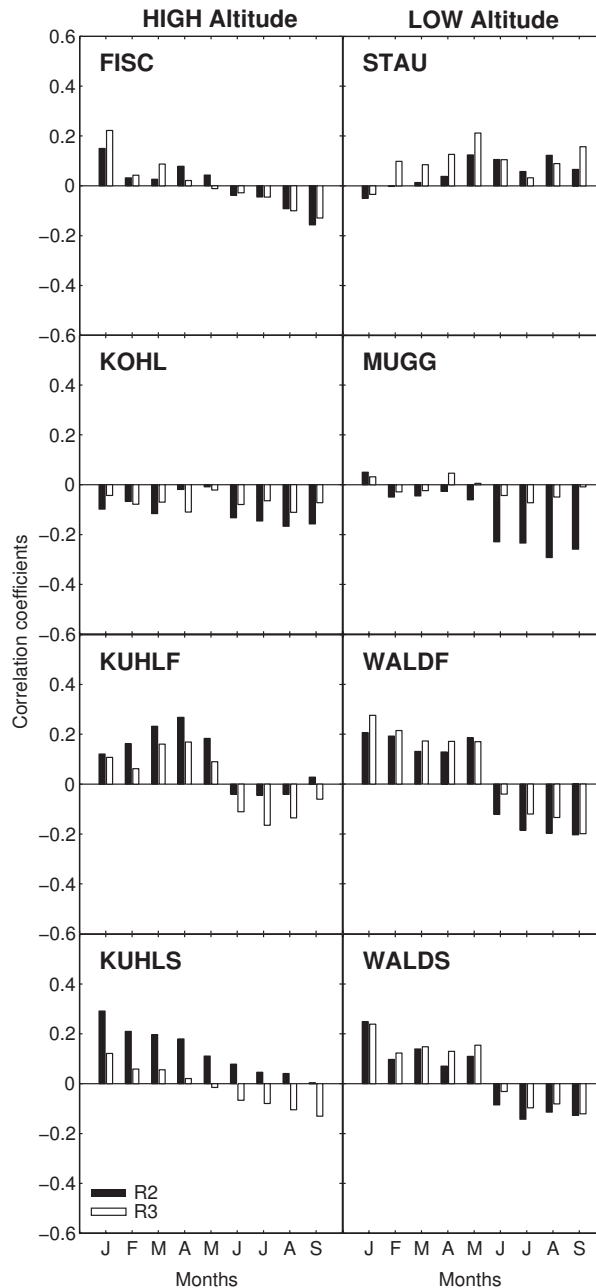
Figure 3.5: Bootstrapped correlation coefficients between the ratios (R2 and R3) and monthly sc-PDSI data of the different sites for January till September of the current year

(Wiklund *et al.*, 1995). All of these findings are consistent with patterns of carbon allocation. During summer, assimilates are largely directed to the lower stem and roots (Gower *et al.*, 1995), but growth tends to shift upward under unfavorable conditions (Larson, 1963). Then, assimilates that are produced in the leaves will be used for respiration first, and relatively small amounts may be left for diameter growth (Fritts, 1976). From these assimilates, the upper stem, being close to the crown, will profit most, as the distance between carbon sinks and sources is also a major factor in the allocation of assimilates (Lacointe, 2000; Woodruff & Meinzer, 2011). Besides, dry conditions were found to reduce phloem transport at the base of loblolly pine, thereby reducing latewood production (Zahner, 1968). The proximity to sources could help maintaining a greater supply in periods of reduced availability such as droughts, hence explaining a better relative growth in upper parts of the stem.

Other explanations for the relative lower reduction in growth at the upper stem under dry summer conditions include a time lag in growth between the upper and lower parts of the stem. The upper part may start earlier, therefore being less affected by drought events during summer (Bouriaud *et al.*, 2005b)). Although we did not measure growth initiation and cessation along the stem, our results indicate differences between the upper and lower stem regions. However, the progression of cambial activity initiation and ending is still under debate. Earlier work described cambial reactivation in relation to bud break (Ladefoged, 1952; Moser *et al.*, 2010; Priestley, 1930; Wareing, 1951). Several studies
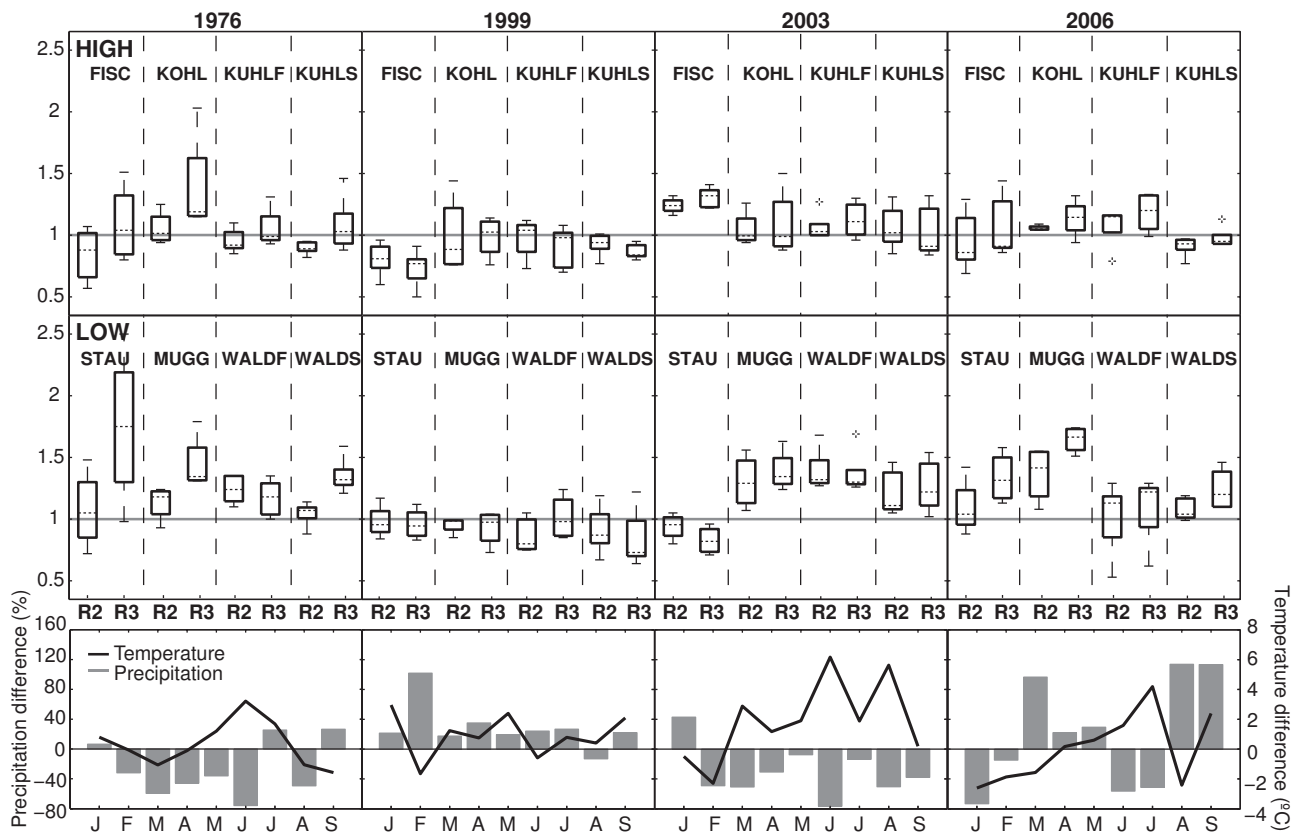
Figure 3.6: Boxplots for selected event years presenting index values for ratios between D2 and D1 and between D3 and D1 as relative to the average ratio over the 5 preceding years. Boxplots are presented for high- and low-altitude study sites. Outliers are indicated by "+". Climate conditions are presented as a diversion from climate conditions during the period 1961–1990

affirmed that cambial reactivation and cell division start close to buds and subsequently spread in a basipetal direction (Funada *et al.*, 2002; Ladefoged, 1952; Zimmermann & Brown, 1971). This was confirmed for diffuse-porous species, whereas simultaneous reactivation seems common in ring-porous species (Lachaud *et al.*, 1999). In conifers, cambial reactivation was found to occur before shoot and needle growth (Rossi *et al.*, 2009). Sundberg *et al.* (1991) found no clear pattern or direction of cambial onset in Scots pine, and also, Anfodillo *et al.* (2012) observed first enlarging cells almost simultaneously along the stem of a Norway spruce tree. Similarly, Bouriaud *et al.* (2005a) observed no difference in onset of growth initiation among stem heights in Norway spruce. Cessation of cambial growth is controlled by the exhaustion of soil moisture, growth substances or assimilates (Fritts, 1976; Zimmermann & Brown, 1971). Riding & Little (1986) found a downward progression of cessation, whereas others suggested that the process would begin at the base of the tree and from there proceed to the top of the crown (Kozlowski & Pallardy, 1997; Vaganov *et al.*, 2006; Zimmermann & Brown, 1971). Hence, the hypothesis and relative contribution of a lag in growth among stem heights remains arguable. Further physiological studies would be required to reveal the factors driving the observed differences in growth among stem heights, which potentially involve a broad range of mechanisms from water potential gradients to carbon allocation.

Our study shows that patterns of growth distribution along the stem of silver fir and Norway spruce are influenced by climate. Climate–growth relationships indicate a stronger limitation of growth in the upper stem of high-altitude fir trees when early summer conditions are hot, whereas high temperatures in mid- to late summer cause growth to be allocated upwards in both high-altitude fir and high-altitude spruce. In low-altitude trees, both high temperatures and low precipitation amounts in summer limit growth, especially at breast height. Growth at breast height therefore seems to be biased, as it over- or underestimates annual ring-area increments along the stem (and thereby volume increment) under the described environmental constraints. These findings also suggest a dynamic pattern of carbon allocation along the stem being affected by climate. This may have implications for carbon models but also for carbon balance studies, which use growth at breast height as a proxy for the annual stem carbon storage. More studies on differences in timing of growth and wood formation at different positions along the stem will be necessary to explain and eventually model the variability in growth revealed in this study.

11

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