

Sensitivity of French temperate coniferous forests to climate variability and extreme events (*Abies alba*, *Picea abies* and *Pinus sylvestris*)

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Abstract

Questions: (1) How do extreme climatic events and climate variability influence radial growth of conifers (silver fir, Norway spruce, Scots pine)? (2) How do elevation and soil water capacity (SWC) modulate sensitivity to climate?

Location: The sampled conifer stands are in France, in western lowland and mountain forests, at elevations from 400 to 1700 m, and an SWC from 50 to 190 mm.

Methods: We established stand chronologies for total ring width, earlywood and latewood width for the 33 studied stands (985 trees in total). Responses to climate were analysed using pointer years and bootstrapped response functions. Principal component analysis was applied to pointer years and response function coefficients in order to elucidate the ecological structure of the studied stands.

Results: Extreme winter frosts are responsible for greater growth reductions in silver fir than in Norway spruce, especially at the upper elevation, while Scots pine was the least sensitive species. Exceptional spring droughts caused a notable growth decrease, especially when local conditions were dry (altitude < 1000 m and SWC < 100 mm for silver fir, western lowlands for Scots pine). Earlywood of silver fir depended on previous September and November and current-year February temperature, after which current June and July water supply influenced latewood. Earlywood of Norway spruce was influenced by previous September temperature, after which current spring and summer droughts influenced both ring components. In Scots pine,

earlywood and latewood depended on the current summer water balance. Local conditions mainly modulated latewood formation.

Conclusions: If the climate becomes drier, low-elevation dry stands or trees growing in western lowlands may face problems, as their growth is highly dependent on soil moisture availability.

Keywords: Climate change; drought; extreme events; response function; tree ring.

Nomenclature: Tutin et al. (2001).

Introduction

In the past, many studies showed that exceptional droughts played a major role in increasing the mortality of forest trees, particularly among coniferous species such silver fir (Becker 1989; Bert & Becker 1990; Bert 1993; Thomas et al. 2002; Micaux 2008), Norway spruce (Becker et al. 1995) and Scots pine (Rebetez & Dobbertin 2004; Bigler et al. 2006; Pichler & Oberhuber 2007; Le Meignen & Micas 2008). Because of the steady warming observed throughout Europe, including France (Lebourgeois et al. 2001; Moisselin et al. 2002), questions are being raised concerning species-specific response patterns to climatic changes (Vennetier et al. 2005; Davi et al. 2006; Macias et al. 2006; Gärtner et al. 2008). Moreover, because climate change is likely to be very different between areas (Déqué 2007), a better understanding of the spatial variations of tree response patterns appears to be a key issue in forest management.

In France, the main distribution of silver fir, Norway spruce and Scots pine corresponds to mountainous regions (Alps, Pyrénées, Vosges, Jura, Massif Central), where mixed or pure stands cover a wide range of substrate, topographic and climatic conditions. The shade-tolerant silver fir is more frost- and drought-sensitive than Norway spruce, while the light-demanding pioneer Scots pine appears to be the most cold- and drought-resistant of the three species (Becker 1970; Guehl 1985; Ausse-nac 2000). Thus, silver fir stands are often dominant in eutrophic and humid contexts (northeast-facing

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or deep soils), and the presence of silver fir generally decreases with increasing altitude. At the upper level or on oligotrophic soils, silver fir is often replaced by Norway spruce or Scots pine on more xeric sites (shallow soils or southwest aspects) (Desplanque et al. 1998, 1999; Tardif et al. 2003; Pinto & Gégout 2005; Splechtna et al. 2005; Podlaski 2008).

Previous dendroecological analyses have provided some information on the influence of climatic factors on radial growth of silver fir and Norway spruce. These studies concerned either a small spatial scale in a high-elevation alpine valley (1380–1950 m) where both species were analysed (Desplanque et al. 1998) or a broad-scale analysis on silver fir stands in the Vosges (Becker 1989) and Jura Mountains (Bert & Becker 1990). In the alpine valley, the interspecific comparison revealed that silver fir was more thermophile and had higher sensitivity to climate along an altitudinal gradient than Norway spruce (Desplanque et al. 1998). In the Vosges and the Jura Mountains, the analyses provided an average response of silver fir to summer drought and winter frost, but without taking into account ecological variability of the sampled stands. Thus, the influence of contrasting site conditions on the response pattern is still largely unknown for this species (Lebourgeois 2007). Concerning Scots pine, the effect of climate on its growth is poorly documented in France, and studies have mainly been conducted in Mediterranean areas (Tessier 1989; Vennetier et al. 2005).

We used eight, 11 and 14 managed mature stands of Norway spruce, silver fir and Scots pine, respectively, from the French Permanent Plot Network for the Monitoring of Forest Ecosystems (RENECOFOR) to study patterns of climatic response and assess the influence of various ecological conditions on tree climate response. The starting hypothesis was that species-specific ecophysiological traits should lead to significant differences in climate/growth relationships, and that contrasting site conditions (altitude, soil water capacity) should modulate these species-specific relationships. The calculation of response functions over sufficiently long period provides readily accessible information about the average linear response between tree rings and climate variables (Guiot 1991). As a disadvantage, however, such an approach is unable to provide evidence about less frequent and time-dependent growth limiting factors. As recurrent forest declines demonstrate that extreme events are among the most important factors triggering carbon balance dysfunction and tree mortality, particular attention was given to abrupt changes in growth pattern through analysis of “pointer years”

(Schweingruber et al. 1990). Extreme values in tree-ring width series are a powerful tool to provide quantitative information on tree reaction thresholds to extreme climatic events (Desplanque et al. 1999). We hypothesized that extreme values in tree-ring width series follow particular patterns in comparison with the mean climatic response. Even if the onset, rate and duration of stem wood production can only be precisely assessed by monitoring intra-annual cambial activity and xylem cell formation (Rossi et al. 2009), analysis of early- and latewood widths as separate variables of ring growth provide useful information about the key periods and climatic factors influencing tree-ring structure (Lebourgeois 2000; Miina 2000). Such an analysis appears important because technological properties of wood partly depend on total ring density, which depends on the proportion of earlywood to latewood width and earlywood to latewood density. Moreover, some studies have shown that the effects of long-term environmental changes affect the two ring components differently (Lebourgeois & Becker 1996). Thus, for each species and site, growth responses to climate were separately assessed on each ring component.

Materials and Methods

Study area and sites

The 33 studied stands were sampled between 42°5' and 49°2'N and 1°5'W and 7°4'E (Fig. 1). In each stand, between 28 and 30 dominant trees were sampled to give a total of 985 trees. The coniferous forests are composed of pure, naturally regenerated even-aged stands (silver fir and half of Norway spruce stands) and plantations (most Scots pine stands). Site types were characterized using the species composition of the ground vegetation and soil chemical and physical properties. Soil water capacity (SWC) was calculated according to textural properties, depth and coarse element percentage, together with the rooting characteristics observed for each soil horizon. Soil depth averaged 110 cm unless physical or pedological constraints to root penetration occurred. Soil types varied from Cambisol (Hypereutric) with low SWC (50 mm) to deep Cambisol (Hypereutric) with high SWC (190 mm) (International Soil Classification) (Table 1). Six Norway spruce stands were sampled at the intermediate altitude (mean: 1142 m) in the eastern part of France with a mainly humid and cold climate (Table 1). The two other sites (71 and 63) correspond to drier conditions with milder winters. Levels

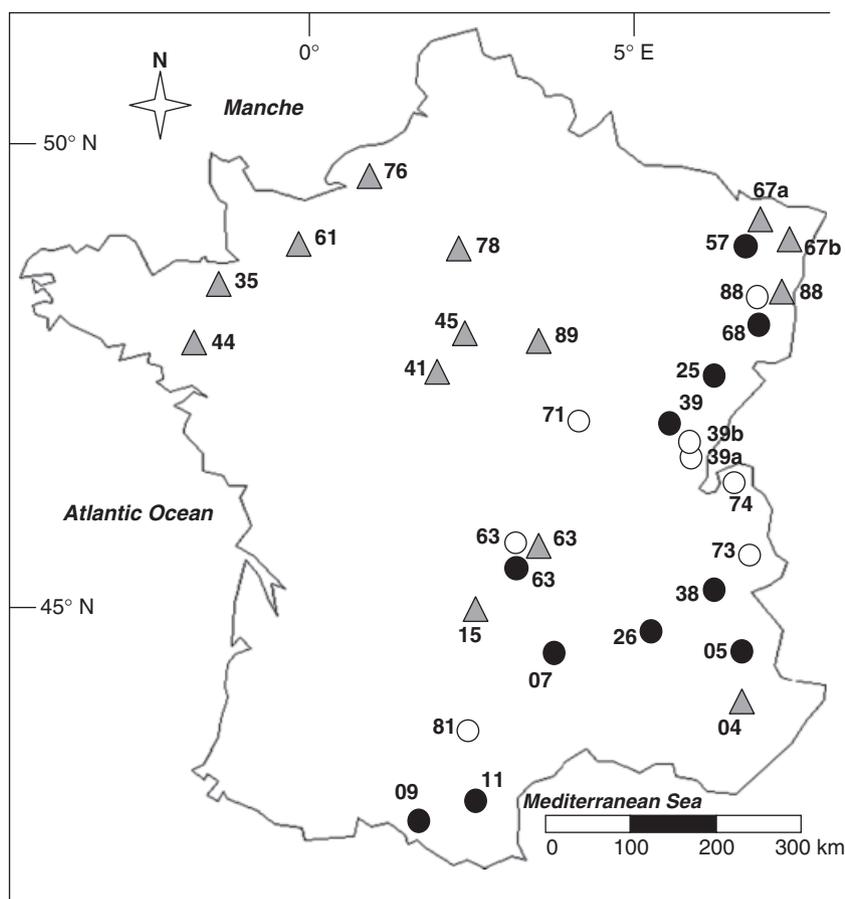


Fig. 1. Geographical location of the 33 coniferous stands of the French network RENECOFOR. Grey triangle = Scots pine; black circle = Silver fir; open circle = Norway spruce. Each number indicates the administrative French department in which sampling was done.

of SWC also separate a group of dry stands (39a, 81 and 88; mean: 76 mm) from a group of humid sites (mean: 127 mm). Eight silver fir stands also correspond to intermediate altitude (mean: 1125 m), with a humid and cold climate and rather a high SWC (mean: 120 mm). The three other silver fir stands (39, 57, 68) correspond to low-altitude (571 m) and dry stands (71 mm) (Table 1). Scots pine stands were mainly sampled in lowlands on mesic-acidic soils in the northern part of France, along a longitudinal gradient from west to east (Fig. 1). For about 60% of these stands, the climate is rather dry (total precipitation between 650 and 750 mm), with mild winters and warm summers. The other sites correspond to more humid conditions (800 to 1600 mm), with colder winters and fresher summers.

Ring-width measurement and analysis

In 1995, trees were cored to the pith with an incremental borer at breast height (one core per tree). Earlywood, latewood and total ring widths of 71 091

tree rings were measured under a stereomicroscope with a precision of 0.01 mm (Becker 1989). Early- and latewood were defined according to qualitative aspects (darkening). The individual ring-width series were cross-dated carefully after progressively detecting regional pointer years (Schweingruber et al. 1990). Pointer years were defined as those calendar years when at least 75% of the tree rings presented the same sign of change: at least 10% narrower or wider than the previous year (Becker 1989; Lebourgeois 2007). Absolute dating was checked with the COFECHA v6.06P program (Holmes 1983). The mean sensitivity (MS) and the first-order autocorrelation coefficient (AC) were calculated for each tree and averaged per stand. MS is a measure of year-to-year variability, and AC assesses the influence of the previous year growth upon the current-year growth (Fritts 1976). Computation of tree-ring chronologies was performed using the program ARSTAN v6.05P (Cook 1985). A double-detrending process, based on an initial negative exponential curve or a linear regression line, followed by fitting a

Table 1. Characteristics of the 33 studied stands. Age in 1994 (mean (SD)/max). DBH = Diameter at breast height. JJA = June–July–August. SWC = Soil water capacity (in mm) calculated according to textural properties, depth and coarse element percentages, together with the rooting characteristics observed for each soil horizon. Climatic means from 1961 to 1990. Stands were sorted according to altitude (Norway spruce and silver fir) or longitude (Scots pine). See Fig. 1 for stand location.

Site	Latitude	Longitude	Alt. (m)	Slope (%)	Aspect	SWC (mm)	Soil type (WRB 2006)	pH (0–10 cm)	No. of trees	Age (years)	Height (m)	DBH (cm)	N (n ha ⁻¹)	Precipitation (mm)		Temperature (°C)		
														Year	JJA	Year	JJA	
<i>Norway spruce</i>																		
73	45°35'12"N	6°47'23"E	1700	40	NW	118	Cambisol (Hyperdystric)	4.5	29	185 (12)/209	22 (2.6)	45 (4.4)	499	971	223	9	-0.2	18.2
39b	46°31'00"N	6°03'44"E	1210	8	W	109	Folic Umbrisol (Hypereutric)	5.3	30	106 (6)/262	23.6 (2.2)	44 (5.1)	746	2054	491	4.9	0.1	13.1
74	46°13'42"N	6°20'58"E	1200	20	W	130	Haplic Luvisol	5.6	30	73 (5)/85	29.9 (1.4)	56 (6)	369	970	239	9.8	1	19.3
39a	46°34'47"N	5°52'37"E	970	10	SE	65	Cambisol (Hypereutric)	5.3	30	58 (3)/69	30.2 (2.5)	45 (4)	414	2054	491	4.9	0.1	13.1
63	45°45'20"N	2°57'58"E	950	0	-	130	Cambisol (Eutric)	4.4	30	28 (1)/31	20.2 (1)	30 (3.5)	924	591	189	10.9	3.1	19.3
81	43°26'31"N	2°26'05"E	820	24	N	75	Entic Podzol	4.2	30	42 (3)/49	22.8 (1.6)	40 (3.5)	401	1411	214	8.9	1.8	16.9
88	48°14'02"N	7°06'14"E	660	20	SW	88	Cambisol (Hyperdystric)	4.1	30	88 (2)/92	34.8 (2.3)	52 (4.4)	401	1696	369	7.8	0.7	16.3
71	47°00'33"N	4°07'06"E	600	20	SE	149	Entic Podzol	4.2	30	48 (2)/50	27 (1.2)	41 (3.7)	460	813	189	10.3	2.8	18.3
<i>Silver fir</i>																		
5	44°29'25"N	6°27'33"E	1360	30	NE	190	Cambisol (Hypereutric)	6.0	30	99 (14)/152	28.3 (2.7)	50 (7.1)	375	716	167	10	1.2	19.3
7	44°42'36"N	3°57'57"E	1300	20	W	92	Entic Podzol	4.1	30	80 (3)/86	25.7 (1.5)	58 (5.8)	315	1103	228	5.8	-1.6	14.4
26	44°56'53"N	5°19'50"E	1150	7	W	110	Cambisol (Hypereutric)	5.3	30	120 (17)/157	22.4 (2.9)	56 (6.9)	225	1523	314	8	0.2	16.7
38	45°25'17"N	6°07'53"E	1100	35	E	100	Cambisol (Hyperdystric)	4.3	30	94 (28)/162	27.9 (2)	47 (7.9)	386	970	226	10.8	1.8	19.7
9	42°51'52"N	1°20'43"E	1100	66	NW	80	Entic Podzol	4.1	29	168 (4)/183	25.1 (3)	44 (4.1)	427	1610	346	11.8	5.1	19.4
63	45°26'51"N	3°31'39"E	1040	25	SW	125	Cambisol (Hyperdystric)	4.0	29	100 (14)/225	26.8 (2.7)	53 (6.4)	358	591	189	10.9	3.1	19.3
25	46°58'34"N	6°27'42"E	1000	10	NW	120	Cambisol (Hypereutric)	5.3	30	81 (32)/153	25.6 (1.7)	48 (4.7)	432	1469	391	7.5	-0.6	15.8
11	42°52'02"N	2°06'04"E	950	40	N	140	Cambisol (Hypereutric)	5.4	30	80 (3)/85	29.2 (1.9)	50 (6.2)	523	934	181	8.9	2.5	16.7
68	47°56'01"N	7°07'31"E	680	45	NW	60	Cambisol (Dystric)	5.0	30	104 (6)/114	29.3 (2)	53 (5.9)	322	1566	336	8.1	-0.3	16.8
39	46°50'33"N	5°47'18"E	560	7	SE	50	Cambisol (Hypereutric)	5.2	30	41 (3)/47	23.6 (1.2)	40 (3.6)	702	1222	284	10.6	2.3	19.5
57	48°36'36"N	7°08'02"E	400	20	NW	103	Cambisol (Hyperdystric)	4.2	30	54 (4)/60	27.5 (1.5)	39 (5)	410	859	231	9	1.2	17.8
<i>Scots pine</i>																		
61	48°36'54"N	0°30'25"W	260	4	-	120	Cambisol (Dystric)	4.1	30	43 (2)/46	22.6 (1.6)	38 (4.3)	443	735	137	10.4	3.8	17.7
76	49°27'14"N	0°44'53"E	70	0	-	100	Haplic Podzol	3.9	29	43 (3)/49	24.2 (1.1)	33 (3.5)	521	778	171	9.9	3.2	17.1
35	48°12'04"N	1°33'17"W	80	0	-	150	Haplic Luvisol	3.9	30	41 (10)/56	17.2 (1.9)	32 (4.1)	408	626	127	11.4	5.1	18.3
78	48°41'37"N	1°43'58"E	170	3	-	70	Entic Podzol	4.1	30	43 (2)/45	21.4 (1.2)	33 (2.5)	765	673	164	10.3	3	18
44	47°32'24"N	1°48'05"W	38	0	-	170	Haplic Luvisol	4.0	30	56 (3)/60	19.9 (1.5)	35 (4)	559	787	136	11.8	5.3	19
41	47°39'14"N	2°05'41"E	140	0	-	100	Entic Podzol	4.2	30	39 (1)/40	20.3 (1)	29 (2)	685	637	145	10.6	3.1	18.5
45	47°49'12"N	2°26'04"E	145	0	-	140	Haplic Planosol	4.1	30	53 (3)/61	20.7 (0.9)	33 (3)	468	637	145	10.6	3.1	18.5
89	47°56'57"N	3°43'05"E	120	0	-	100	Entic Podzol	3.8	30	58 (9)/76	26.9 (1.4)	41 (5.5)	396	657	165	10.8	2.8	19.1
15	44°51'40"N	3°03'30"E	1000	5	-	85	Cambisol (Hyperdystric)	4.7	30	60 (2)/64	22 (1.2)	36 (2.8)	623	1567	287	7.3	0.5	15.1
63	45°24'21"N	3°41'44"E	750	25	NW	75	Cambisol (Dystric)	4.9	30	93 (15)/143	24.6 (1.5)	39 (3.8)	361	591	189	10.9	3.1	19.3
4	44°01'30"N	6°40'16"E	1670	20	S	50	Cambisol (Eutric)	5.0	30	69 (17)/121	17 (1.6)	38 (5)	997	736	163	12.4	4	21.9
67a	48°51'01"N	7°42'39"E	175	0	-	80	Entic Podzol	4.0	30	65 (6)/70	24.6 (1.7)	35 (4.8)	388	1243	273	8.8	1.3	17.3
67b	48°55'53"N	7°26'40"E	290	5	-	60	Entic Podzol	4.0	30	64 (2)/68	25.9 (1.9)	39 (4)	492	859	231	9	1.2	17.8
88	48°13'17"N	6°41'45"E	500	2	-	60	Entic Podzol	4.1	30	66 (4)/76	24.4 (2)	41 (5.5)	284	1112	274	9.1	1.4	17.5

cubic smoothing spline with a frequency-response cut-off set at two-thirds of the length of each series was applied. Dividing the observed values by the predicted values produced a residual series of dimensionless ring-width indices. The residual series were then averaged using a bi-weighted robust mean to create stand chronologies (Cook & Peters 1981).

Climate data and statistical analysis

Meteorological data were gathered from 27 meteorological stations of the French National Climatic Network (Météo-France). The locations were carefully screened to be as representative as possible for the stand weather conditions. Thus, the distance between stands and meteorological stations averaged 15 km. For altitude, the difference was < 100 m for 65% of the cases, and averaged 260 m. Monthly means of minimum and maximum temperature (T_{\min} , T_{\max}) and precipitation (P) were calculated for each year of the 1949–1994 period (common period of the analysis). Bootstrapped confidence intervals were used to estimate the significance of response function coefficients (Guiot 1991) with the software package DENDROCLIM2002 (Biondi & Waikul 2004). This software computes the statistical significance of the coefficients by calculating 95% quantile limits based on 1000 bootstrap re-samples of the data. Response functions were calculated for each tree-ring variable (earlywood, latewood and total ring width) using stand chronologies. Climatic parameters were considered from September of the previous year to August of the current year. Analyses were performed using 12 monthly precipitations and 12 maximum or minimum monthly temperatures ($P-T_{\min}$ and $P-T_{\max}$). Pointer years and response function coefficients were introduced into principal component analysis (PCA) using the statistical software Splus[®] 2000 to elucidate the ecological structure of the stands.

Results

Ring widths averaged more than 2.2 mm in most stands (Table 2), but ring widths of about 1.0 mm were observed for the high-elevation old Norway spruce and silver fir stands (Ns73 and Sf09). For each species, earlywood represented between 60% and 70% of the total ring (data not shown). The values of MS were higher for latewood width than for total and earlywood widths, suggesting a greater sensitivity to climate of the latewood component. In contrast, first-order ACs were higher in

earlywood, indicating its strong dependence on previous year growth. Scots pine had the greatest values of MS for all ring components, whereas silver fir and Norway spruce presented similar lower values.

Response to extreme events

For the period 1949–1994, the number of pointer years ranged from 4 to 30, with a mean value of 14 for each species. The mean number of positive and negative years was similar between species (7), with average relative growth variations of about +38% and –24%, respectively. For each species, the number of pointer years and the relative growth variation increased with increasing mean sensitivity (data not shown).

PCA axes 1 and 2 explained 27.4% and 13.2% of the total variance (Fig. 2a). On the first component axis, the main structuring years were 1976, 1949, 1991 and 1989 in the positive direction and 1977 in the negative direction (Fig. 2b). On the second component axis, the discriminant years were 1956, 1962, 1986, 1964 and 1969 (group 2). The first group characterizes exceptional droughts. At stands with a significant growth reduction, rainfall from late spring to early summer (May to July) was at least 40–50% lower than the long-term mean for 1961–90. Among these dry years, a common widespread growth decrease was only observed in 1976 (Table 3), which is known to have been one of the most important droughts in many regions throughout Europe (Bréda et al. 2004). In 1976, the rainfall deficit from May to July averaged –60% in comparison to normal conditions. The second group corresponds to extreme winter frosts. For example, mean minimum temperatures in February for the two coldest years (1986 and 1956) averaged –9.6°C (–0.5 to –20.2°C), which correspond to a mean deviation of –7.6°C (–1.6 to –13.7°C) compared to the long-term monthly mean.

Finally, the ordination of the first two principal components resulted in a nearly complete separation of silver fir, Norway spruce and Scots pine (Fig. 2a and Table 1). Silver fir chronologies were grouped according to the response to winter frost, but the PCA split the response into a subgroup of low-altitude dry or mesic sites (< 1000 m), for which growth variations were less pronounced for frost years but more important after drought. For the effect of altitude and frost years, mean growth reduction increased with increasing altitude, from –26% to –36% between 1000 and 1400 m. Norway spruce is an intermediate group related to both frost and drought responses. Scots pine chron-

Table 2. Chronology statistics of unfiltered tree-ring series for each species. IC = series intercorrelation. WR = ring width in mm. MS = mean sensitivity (MS). AC = first-order autocorrelation coefficient. Stands were sorted according to altitude (Norway spruce and silver fir) or longitude (Scots pine). See Table 1 for details.

Site	Common interval	Total ring				Earlywood				Latewood			
		IC	WR	AC	MS	IC	WR	AC	MS	IC	WR	AC	MS
<i>Norway spruce</i>													
73	1946–1994	0.572	1.11 (0.32)	0.639	0.173	0.494	0.81 (0.24)	0.552	0.209	0.369	0.30 (0.13)	0.44	0.307
39b	1946–1994	0.662	1.47 (0.37)	0.566	0.177	0.664	1.10 (0.31)	0.518	0.211	0.3	0.36 (0.11)	0.359	0.238
74	1946–1994	0.598	2.76 (1.20)	0.826	0.184	0.561	2.05 (0.99)	0.808	0.221	0.355	0.71 (0.34)	0.568	0.279
39a	1946–1994	0.671	3.11 (1.0)	0.61	0.214	0.612	2.34 (0.86)	0.589	0.246	0.451	0.77 (0.31)	0.389	0.314
63	1968–1994	0.662	5.28 (1.74)	0.795	0.168	0.498	3.53 (1.59)	0.771	0.229	0.404	1.75 (0.66)	0.353	0.317
81	1953–1994	0.532	4.54 (1.80)	0.779	0.189	0.488	3.26 (1.57)	0.715	0.259	0.187	1.28 (0.58)	0.492	0.295
88	1946–1994	0.475	2.20 (0.84)	0.651	0.235	0.438	1.46 (0.65)	0.548	0.296	0.322	0.74 (0.31)	0.493	0.316
71	1950–1994	0.784	4.02 (2)	0.765	0.264	0.724	3.16 (1.78)	0.752	0.291	0.634	0.86 (0.46)	0.408	0.418
	Mean:	0.62		0.704	0.201	0.56		0.657	0.245	0.377		0.438	0.311
<i>Silver fir</i>													
5	1946–1994	0.654	2.53 (0.73)	0.694	0.165	0.468	1.44 (0.44)	0.585	0.208	0.495	1.09 (0.42)	0.553	0.264
7	1946–1994	0.753	2.93 (0.91)	0.67	0.18	0.7	1.93 (0.68)	0.651	0.211	0.607	1.00 (0.37)	0.517	0.258
26	1946–1994	0.728	2.17 (0.86)	0.657	0.238	0.611	1.16 (0.49)	0.588	0.284	0.635	1.0 (0.47)	0.535	0.304
38	1946–1994	0.607	3.61 (1.55)	0.788	0.205	0.429	1.72 (0.87)	0.711	0.257	0.471	1.88 (0.96)	0.691	0.289
9	1946–1994	0.527	0.97 (0.38)	0.71	0.2	0.392	0.53 (0.19)	0.566	0.231	0.466	0.44 (0.23)	0.597	0.325
63	1946–1994	0.607	3.02 (1.27)	0.759	0.201	0.481	1.59 (0.64)	0.572	0.269	0.448	1.43 (0.76)	0.666	0.292
25	1946–1994	0.618	4.01 (1.25)	0.757	0.163	0.472	2.62 (0.9)	0.675	0.21	0.449	1.40 (0.56)	0.544	0.277
11	1946–1994	0.625	2.34 (0.88)	0.736	0.194	0.464	1.31 (0.60)	0.751	0.225	0.503	1.04 (0.43)	0.502	0.304
68	1946–1994	0.74	2.01 (0.85)	0.638	0.272	0.652	1.25 (0.64)	0.566	0.331	0.548	2.83 (0.48)	0.482	0.34
39	1949–1994	0.69	4.55 (1.38)	0.614	0.201	0.521	2.98 (0.98)	0.567	0.23	0.565	1.57 (0.69)	0.426	0.342
57	1946–1994	0.607	3.44 (1.27)	0.732	0.204	0.468	2.23 (1.13)	0.715	0.272	0.35	1.21 (0.5)	0.391	0.325
	Mean:	0.651		0.705	0.202	0.514		0.632	0.248	0.503		0.537	0.302
<i>Scots pine</i>													
61	1949–1994	0.566	3.56 (1.22)	0.715	0.189	0.495	2.15 (1.03)	0.709	0.205	0.442	1.41 (0.47)	0.449	0.266
76	1946–1994	0.636	3.64 (1.21)	0.612	0.209	0.517	2.28 (1.09)	0.666	0.263	0.491	1.37 (0.53)	0.518	0.289
35	1946–1994	0.519	3.11 (1.02)	0.648	0.21	0.418	2.15 (0.82)	0.637	0.242	0.492	0.96 (0.41)	0.359	0.364
78	1950–1994	0.684	3.62 (1.29)	0.634	0.219	0.515	2.22 (1.11)	0.64	0.279	0.571	1.39 (0.60)	0.459	0.34
44	1946–1994	0.526	2.41 (1.05)	0.785	0.205	0.388	1.42 (0.86)	0.794	0.249	0.565	1.02 (0.40)	0.523	0.287
41	1955–1994	0.797	3.02 (1.75)	0.727	0.27	0.686	2.04 (1.62)	0.797	0.278	0.734	0.97 (0.46)	0.305	0.425
45	1946–1994	0.776	2.56 (1.34)	0.727	0.327	0.677	1.69 (1.02)	0.775	0.327	0.724	0.87 (0.52)	0.384	0.505
89	1946–1994	0.56	2.77 (1.06)	0.7	0.228	0.526	1.58 (0.73)	0.647	0.278	0.562	1.19 (0.52)	0.517	0.339
15	1946–1994	0.621	2.03 (0.66)	0.604	0.221	0.506	1.17 (0.46)	0.563	0.266	0.559	0.86 (0.32)	0.456	0.308
63	1946–1994	0.457	1.33 (0.41)	0.632	0.211	0.349	0.86 (0.27)	0.548	0.23	0.544	0.47 (0.19)	0.493	0.334
4	1946–1994	0.449	2.04 (0.79)	0.819	0.173	0.423	1.54 (0.66)	0.792	0.201	0.437	0.50 (0.20)	0.508	0.296
67a	1946–1994	0.629	1.99 (0.85)	0.573	0.274	0.474	1.16 (0.56)	0.559	0.278	0.68	0.83 (0.41)	0.385	0.406
67b	1946–1994	0.606	2.14 (0.75)	0.54	0.249	0.483	1.21 (0.53)	0.537	0.295	0.627	0.93 (0.34)	0.262	0.345
88	1946–1994	0.581	2.85 (1.02)	0.658	0.216	0.465	1.74 (0.70)	0.646	0.233	0.63	1.11 (0.47)	0.463	0.329
	Mean:	0.601		0.67	0.229	0.494		0.665	0.259	0.576		0.434	0.345

ologies were principally associated with a response to moisture conditions. The response pattern separated low-altitude sites with a dry and warm climate (sampled under oceanic context in western France) from higher-altitude sites with a humid climate but low SWC. The response to drought is more frequent in the lowland (1959, 1969, in addition to the already mentioned years). Nevertheless, growth variations were more pronounced at dry high-altitude sites for the droughts of 1976 and 1991.

Response to climate variability

For each species and each ring component, correlations were more frequent with temperature (T) than with precipitation (P) (Fig. 3). Temperature effects were mainly linked to maximal values for Norway spruce and Scots pine and minimal values

for silver fir, and corresponded generally to positive correlations during winter and early spring (high values leading to wide rings) and negative correlations for summer or autumn. For precipitation, high values during summer generally influenced ring widths positively.

Apart from these overall observations, analyses also highlighted distinct seasonal response patterns between species and ring components (Fig. 3). For Norway spruce, both ring components were negatively influenced by maximal temperature in the previous September. During the current year, 63% of the earlywood chronologies were positively influenced by late winter or early spring temperature (February, March or April). Later in the season, 65% of stands were still influenced by June conditions (T and/or P) for earlywood formation, and high summer maximal temperatures (July or Au-

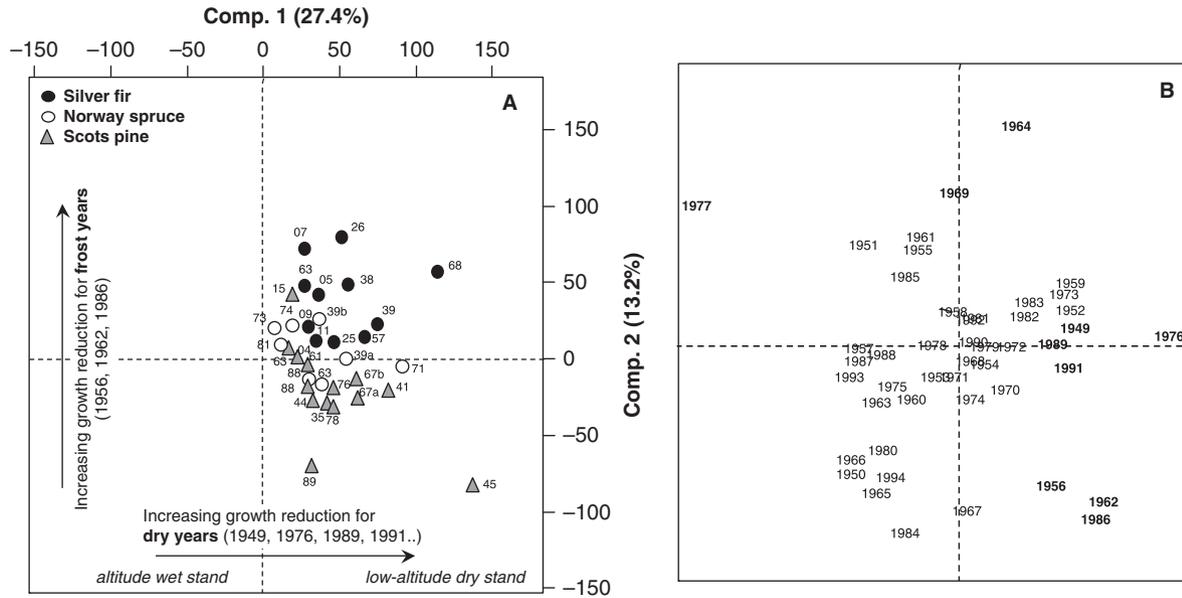


Fig. 2. PCA with pointer years calculated from the period 1949–1994 [first and second component axes; sites (a) and years (b)]. Black circle: Silver fir; open circle: Norway spruce; grey triangle: Scots pine. The number indicates the sampling area (see Fig. 1). See also Table 1 for details.

gust) led to narrow latewood widths for 75% of the sites. Silver fir had two peaks in its response to temperature. The first concerned the previous autumn conditions. Thus, maximal temperatures in September and minimal in November of the previous year influenced both ring components, with negative and positive effects, respectively. The second peak concerned the beginning of the current year, through February and April. For earlywood, 90% of silver fir chronologies reacted positively to temperature in February and 45% of them to April temperatures. As earlywood growth also correlated with the previous September precipitation for 55% of the chronologies, it could be suggested that water balance during this period was a key factor for earlywood formation. Thereafter, current summer conditions governed latewood formation, with a key period focussed around June. The pattern of response was quite different for Scots pine, which had a high response to drought in late spring and summer. In comparison to Norway spruce and silver fir, the effects of the previous autumn conditions were much less marked, even if 35% of earlywood chronologies reacted to temperature in the previous November. During the current year, as observed for silver fir stands, Scots pine presented a high response peak in February through temperature, which enhanced ring formation in about 50% of the stands. Later in the season, earlywood formation strongly responded to weather conditions during late spring

(May–June) and latewood growth responded to summer drought (July–August) (Fig. 3).

PCA axes 1 and 2 explained 52.4% of the total variance of the response functions calculated for earlywood indices. The ordination of the first two axes split the chronologies into five groups (Fig. 4). Group 1 linked high-altitude stands (> 1000 m) with a rather high soil water capacity (> 100 mm) and a fresh and wet climate. The second highest elevation Norway spruce and Scots pine stands and 65% of the silver fir stands appeared in this group. Previous late summer water balance (September) and temperatures in winter (November and February) and early spring (April) controlled both earlywood and latewood formation. Within this group, latewood formation also depended on precipitation during the previous October and early summer, but responses were more heterogeneous than for the earlywood component. Low-altitude silver fir and Norway spruce stands with lower soil water capacity and warmer climate formed group 2, in which earlywood growth also depended on early summer precipitation. At these stands, latewood formation highly depended on summer water balance (May to July).

The three other groups split the response of Norway spruce and Scots pine chronologies. Low-altitude Scots pine stands (< 200 m) growing under an oceanic, dry and warm climate (< 750 mm) formed a group of similarly responding chronologies (group 5). High minimal temperature in

Table 3. Relative growth variations (%) of the pointer years observed for total ring width. For each stand, pointer years were defined as those years when at least 75% of the cross-dated trees presented the same sign of change (at least 10% of relative growth variation between two consecutive years). For each species, only the pointer years for which at least 50% of stands showed a particular growth are presented in the table. The values in bold indicate dry years and in italics frost years. Mean altitude, soil water capacity and weather conditions (mean 1961–1990) are presented.

Species	Norway spruce	Silver fir	Scots pine		
Alt. (m)	1014	1105	802	128	731
SWC (mm)	108	113	99	119	68
P Year (mm)	1320	1078	1219	691	1018
T Jan (°C)	1.2	0.7	2.1	3.7	1.9
T July (°C)	16.8	17.7	17.8	18.3	18.2
Nb of stands	8	6	5	8	6
1949	-14.1				-32.6
1950		-19.5			25.5
1951			43.4		42.5
1952			-20.5		-29.2
1955	31.0	34.5			
<i>1956</i>		-32.9			
1957					30.2
1959				-40.0	
1960				29.8	
1961			38.8		
<i>1962</i>	-26.8	-28.0	-27.1		-31.4
1963	40.4			33.5	
1964		41.8		-35.4	
1965		-21.0		39.4	
1966			29.2	55.9	
1969		33.9		-17.9	
1970		-22.2			
1971				25.9	
1973	-24.7			-17.3	
1976	-27.7	-17.5	-36.5	-26.5	-31.8
1977		37.0	77.9		
1980	5.3				46.4
1982					8.9
1983					-10.6
1984		-25.9			17.2
1985		33.7			
<i>1986</i>	-25.9	-33.2	-31.5		
1987		30.5	26.1		
1988			30.7		
1989			-20.3	-23.2	
1991				-19.1	-27.3
1992					32.9
1993	48.3	33.2			
1994				39.3	

November and spring drought (May–June) led to narrow earlywood widths, and summer drought (June to August) reduced latewood formation. Thus, water balance played a major role at these stands. Group 4 mainly grouped Scots pine stands in the northeast of France under a more humid climate (about 1000 mm per year), in which winter temperatures played a major role in earlywood formation and summer drought in latewood growth. The two warmest and driest sites of Norway spruce appeared in this group. Group 3 corresponds to the

least responding chronologies of mid-altitude Norway spruce and Scots pine stands, for which early spring water balance (June) and summer maximal temperatures (July–August) modulated earlywood and latewood formation, respectively.

Discussion

Most of the pointer years (especially 1956, 1962, 1976, 1986, 1991) defined in our study have already been observed throughout Europe in high-altitude coniferous (Becker 1989; Bert & Becker 1990; Desplanque et al. 1999) and broadleaf stands (Schweingruber & Nogler 2003; Lebourgeois et al. 2005). In our study, growth variations linked to extreme frosts correspond to a deviation of February temperature by about -8°C from the average conditions. A decrease in May to July rainfall of about 40–50% also leads to extreme growth reductions (between 20% and 40%) in most of the coniferous forests. As expected, local ecological conditions highly modulate climate response patterns. Thus, the growth decrease linked to frost mainly concerns high-altitude forests and increases with altitude, whereas the growth reduction linked to early drought increases with altitude or an SWC decrease. Concerning the mean response to climate variability, the distinguishing factors between the three species are linked to the previous late summer water balance, current February temperature and summer drought (mainly June–July). Thus, both pointer years and response function analyses underline the key roles of winter temperature and early summer drought in wood formation. Response functions also underline that local ecological conditions affect latewood more strongly than earlywood. Because of the different sensitivity of the two ring compartments to annual weather variations and site conditions, expected climate changes could modify the anatomical traits and thus wood properties of each species.

For silver fir, the general pattern observed in our study is consistent with previous studies made on total ring widths in the Vosges and Jura Mountains (Becker 1989; Bert 1993), in the Spanish Pyrenees (Macias et al. 2006) and in the internal Alps (Desplanque et al. 1998). Thus, previous late summer or autumn conditions and February temperature appear to be the main driving climatic factors for this species. The general pattern is rather similar for Norway spruce, although the key periods appear more varied between stands. Mild conditions in the previous September and during late winter

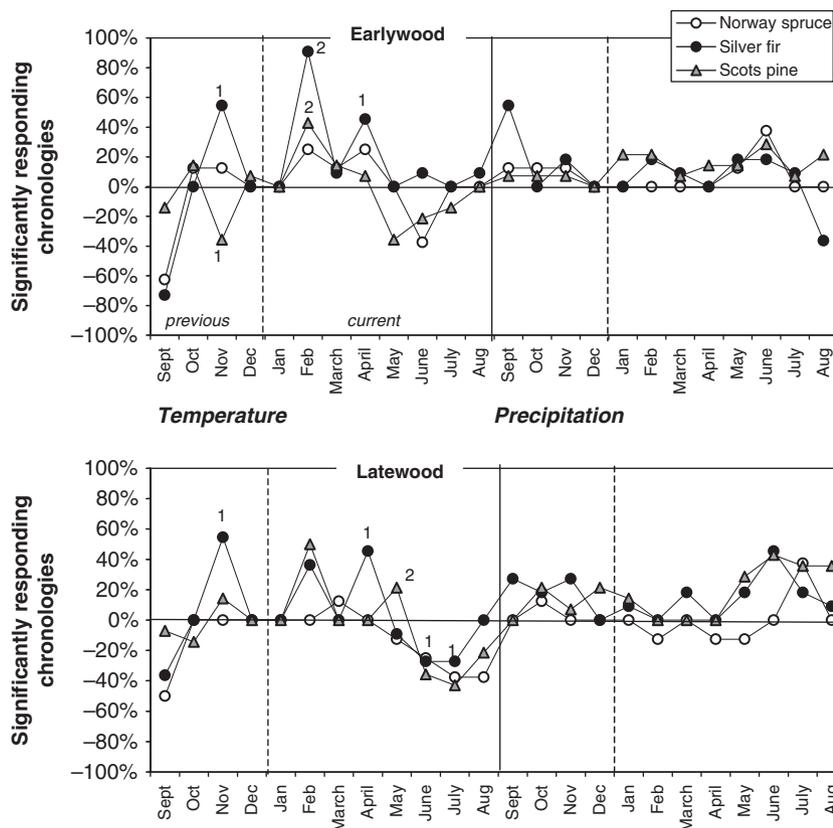


Fig. 3. Summarized growth responses for earlywood and latewood to monthly temperature and precipitation. Percentage chronologies with a significant ($P < 0.05$) negative or positive response for each species from September ($n - 1$) to August (n) are shown. 100% = 8, 11 and 14 chronologies for Norway spruce, silver fir and Scots pine, respectively. Temperature = Tmax except 1 = significant response for Tmin, and 2 = significant response for Tmin or Tmax depending on the stand.

followed by a good water supply in June enhance earlywood formation, whereas a warm dry summer reduces latewood width. For Norway spruce, the importance of climatic conditions during the year prior to ring formation and during the current summer was also observed in mountain forests (> 1400 m) in the French Massif Central (Rolland & Lempérière 2004) and Alps (Desplanque et al. 1998). Moreover, whereas growth was negatively correlated with high-summer temperatures in our study, warm summers enhance growth in the French Massif Central and Alps, mainly as a consequence of higher-elevation stands. For Scots pine, the major effect of summer water balance on ring formation is in agreement with patterns observed in many Mediterranean forests (Gutiérrez 1989; Tessier 1989; Andreu et al. 2007) and in Alpine valleys in Switzerland and Austria (Oberhuber & Kofler 2002; Rebetez & Dobbertin 2004; Bigler et al. 2006; Weber et al. 2007).

The role of the previous late summer weather conditions on the seasonal dynamics of carbohydrate storage, root elongation (Barbaroux & Bréda

2002) and bud formation (Weber et al. 2007) could explain the lag effects. As the photosynthetic capacity of the crown depends highly on the number and size of buds that are formed each year, unfavourable conditions during this period can impact ring formation by decreasing carbon assimilation in the following growing season. Because needles remain active for several years, such a phenomenon can influence radial growth over a long period, particularly for silver fir and Norway spruce, in which the number of needle generations on branches is higher than for Scots pine (6–8 years against 2–3 years) (Becker et al. 1995). This difference could partly explain the importance of lag effects in silver fir and Norway spruce.

The strongest and earliest response is observed in February for silver fir, which appears to be the more sensitive species to winter conditions. High-winter temperatures generally promote growth, but extreme frosts cause substantial growth reductions. Silver fir and Norway spruce reacted strongly to extreme frosts, but silver fir was more affected than Norway spruce, confirming higher sensitivity to

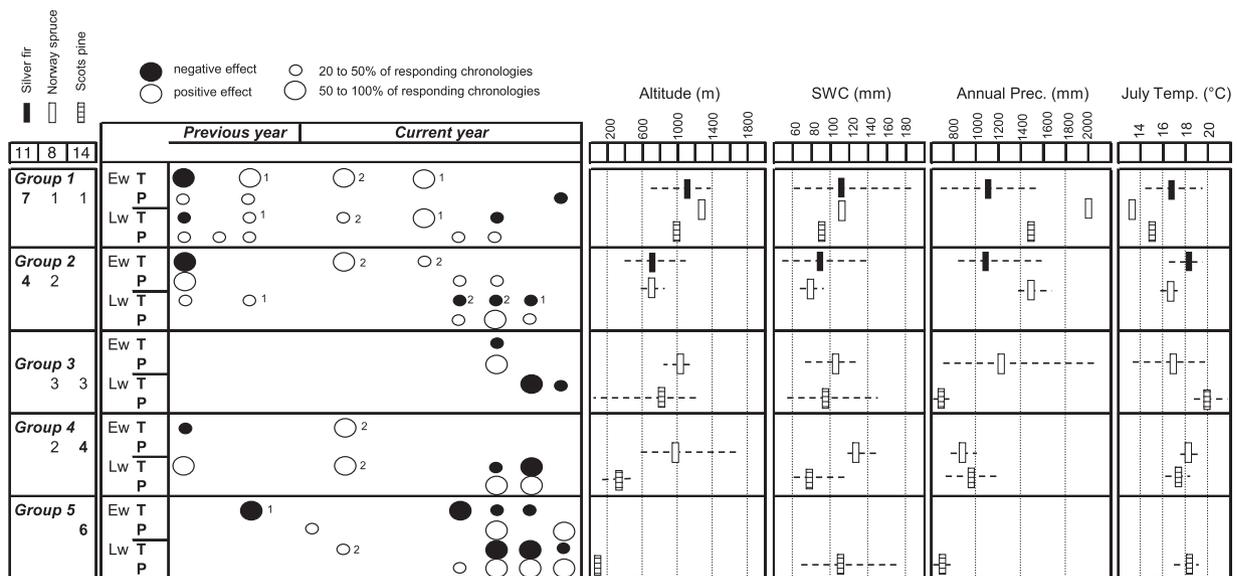


Fig. 4. Summarized growth responses for earlywood (Ew) and latewood (Lw) to monthly temperature and precipitation for each group defined by the PCA (bootstrapped response function coefficients for earlywood). For each group and each species, the range of soil water content (SWC), altitude (m), annual precipitation (mm) and July temperature ($^{\circ}\text{C}$) is presented. The dotted horizontal line represents the range of variation of the parameter in the group for each species, and the vertical bar is the average value for the parameter. T = Tmax except 1 = Tmin and 2 = Tmin or Tmax. P = precipitation.

extreme cold years (Desplanque et al. 1999). Scots pine has the lowest sensitivity, with no marked growth reductions during extreme cold years and a positive effect of winter temperature only for stands sampled in the northeast of France. The observation that high winter or early spring temperatures generally promote growth is consistent with the fact that cambial reactivation of evergreen conifers is strongly triggered by a rise in temperature (Rossi et al. 2007, 2009). Because photosynthesis is possible in conifers in winter (Guehl 1985), high temperatures during the winter period could play a positive role in improving carbohydrate storage and growth in the following year. Warmer winters might also decrease embolism (Cochard et al. 2001) and accelerate snowmelt (or at least stop snow accumulation), favouring soil warming and promoting mycorrhizal root growth. Such conditions promote bud formation and needle and shoot maturation, thus increasing the growing season of the following year. Finally, these factors, in combination with sufficient water supply, promote earlywood formation during spring.

In the context of climatic change, it is critical to understand whether climatic conditions are becoming favourable or unfavourable to growth. The observed correlations allow identification of factors and periods that are at present most influential on tree growth. Moreover, changes in frequency of

extreme years for drought and winter temperature, as predicted consequences of climate change (Chauvin & Denvil 2007), may shift the dynamics of growth more or less abruptly in favour of the less-sensitive tree species (Bréda et al. 2006). In the absence of long-term climatic data for most of our studied sites, it was not possible to test the temporal stability in the climate–growth relationship. Some studies highlight a clear variation in the growth–climate association (Wilson & Elling 2004; Andreu et al. 2007) while other studies did not observe temporal instability during the 20th century growth responses to climate (Miina 2000; Helama et al. 2004; Büntgen et al. 2007). In the Iberian Peninsula, Andreu et al. (2007) showed enhancement of growth synchrony among forests, which indicates that the climate might have become more limiting for trees. The increased similarity in tree growth seems to be linked to strengthening water stress during the late summer prior to ring formation, which agrees with the increasing temperature trend observed in these months.

Because temperature appears to be a major driving factor for most stands, prolongation of the growing season caused by warming in winter or early spring would be particularly beneficial, especially for the highest altitude silver fir stands. Moreover, an increase in summer or autumn drought could compensate for this effect and lead to

a growth decrease, as observed for exceptional drought years. In general, trees may survive infrequent extreme events but finally die if the frequency and duration of such events increases. Thus, both pointer years and response function analyses suggest that many coniferous stands will be at risk if the climate becomes drier. For silver fir, our results suggest a threshold of about 100 mm for SWC and about 1000 m for altitude. These thresholds strongly agree with the ecological conditions of declining silver fir stands observed following the dry years 2003 and 2004 (Le Meignen & Micas 2008; Micaux 2008). For Scots pine, the drought-induced mortality observed in a Swiss valley (Rebetez & Dobbertin 2004; Pichler & Oberhuber 2007) and in stands of the NE Iberian Peninsula (Martinez-Vilalta & Pinol 2002) suggest that some pine populations will also be at risk if the climate becomes drier. In our study, greater sensitivity to drought was observed under oceanic conditions. Although most pines tend to be more efficient in terms of water conductivity than the other conifers, they are generally more vulnerable to embolism after severe water stress. Scots pine has higher water potential gradients and, hence, higher levels of embolism (Martinez-Vilalta et al. 2004).

Finally, our results indicate that silver fir stands may benefit from winter warming but may suffer from increasing summer droughts, particularly at lower elevations on shallow soils. Increasing summer droughts may also change Norway spruce growth at lower elevations and Scots pine dynamics, particularly for trees growing in the lowlands under an oceanic climate. In the future, one of the most probable hypotheses is an upward shift at the rear edge of species distribution.

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