



Social status-mediated tree-ring responses to climate of *Abies alba* and *Fagus sylvatica* shift in importance with increasing stand basal area



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ABSTRACT

The aim of the study was to assess the effects of competition at both stand and tree levels on climate tree-growth relationships of 414 *Abies alba* and 243 *Fagus sylvatica* trees growing in 2 contrasting ecological conditions (north- and south-facing) under mountainous continental climate (mean altitude: 886 m). Stand level competition was considered through three stand basal area (SBA) modalities (Low: 32 m²/ha, Medium: 41 and High: 49) while tree level competition was assessed through three social statuses (SST, Dominant, Codominant and Suppressed trees). A strong specific response to climate was pointed out with different key periods; growth of *Abies* being mainly driven by previous and current late summer temperatures, while that of *Fagus* was controlled by April and June ones. No obvious difference between facing sides was evidenced. Competition at stand level prevailed on competition at tree level. In Low and Medium SBA, trees exhibited similar responses to climate whatever their social statuses. On the opposite, sensitivity to summer drought increased with dominance in high SBA. Inter-specific differences and consequences for forest management are discussed.

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1. Introduction

Competition is an important subject of research in ecological studies for a long time, but its definition varies according to the relative degree of emphasis on the underlying physiological mechanisms of the interaction and the natural communities considered (Larocque et al., 2013). Begon et al. (1996) defined competition as an interaction between individuals, brought about by a shared requirement for a resource in limited supply, leading to a reduction in the survivorship, growth and (or) reproduction of at least some of the competing individuals concerned. In forest stands, competition can be considered at the stand level through an indicator such as stand basal area (hereafter SBA expressed in m²/ha) or at the individual tree level through an indicator such as tree diameter or social status (SST based on tree architecture, i.e. height, diameter and crown development) (Thorpe et al., 2010; Fichtner et al., 2013; Larocque et al., 2013).

Stand-level properties affect tree response to climate. Because high SBA has been often associated with drought-induced mortality or growth reductions (Das et al., 2007; Klos et al., 2009; Galiano et al., 2010; Linares et al., 2010; Martinez-Vilalta et al., 2012a), decreasing SBA through silvicultural activities is considered as a primary tool for foresters to reduce competition for water, nutrient and light resources (Pretzsch, 2005; Moreno and Cubera, 2008; Gyenge et al., 2011; Aranda et al., 2012; Ungar et al., 2013). Most of these studies are recent and mainly focused short-term analyses from thinning experiments (Le Goff and Ottorini, 1993; Misson et al., 2003; Sohn et al., 2012; Giuggiola et al., 2013; Magruder et al., 2013; Primicia et al., 2013; Van Der Maaten, 2013) or Mediterranean contexts (Gea-Izquierdo et al., 2009; Martin-Benito et al., 2011; Martinez-Vilalta et al., 2012b). In most cases, decreasing stand density allows maintaining growth under exceptional climate and/or to enhance recovery after particular events such as summer droughts, as a consequence of a reduction of canopy rainfall interception (Aussenac and Granier, 1988; Bréda et al., 1995; Aussenac, 2000; Granier et al., 2000; Paluch and Gruba, 2012). Thus, within a stand, increasing space and canopy structure heterogeneity creates various environmental conditions (Aussenac, 2000) which, in turn, may cause significant differences in resource requirements (Paluch and Gruba, 2012) and growth-limiting

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factors inducing contrasted climatic responses among individual trees.

During the last decade, numerous studies aimed to highlight the size- or social-status-dependency of response to climate for both temperate coniferous and broadleaved species. Dominant trees were found to be either more sensitive to climate, especially spring and summer droughts than smaller trees (Mérian and Lebourgeois, 2011b; Castagneri et al., 2012; Martinez-Vilalta et al., 2012b; Zang et al., 2012) or less sensitive (Van Den Brakel and Visser, 1996; Piutti and Cescatti, 1997; Pichler and Oberhuber, 2007; Carnwath et al., 2012; Zang et al., 2012). Size-dependent response to climate also varied according to site quality and resource availability but results appeared not consensual once again. Differences in sensitivity to climate between small and tall trees were found to either increase with resource availability (Pichler and Oberhuber, 2007; Zang et al., 2012) or decrease (Mérian and Lebourgeois, 2011b; Fichtner et al., 2013). These results tend to prove that size-dependent sensitivity to climate is complex and modulated by both species-identity and environmental conditions.

Underlying ecophysiological and functional mechanisms of tree responses to competition remain difficult to identify (Aranda et al., 2012). For instance, taller trees with larger crowns (i.e. dominant trees) are assumed to be those with higher growth rates because

of longer growing seasons (Linares et al., 2009; Rathgeber et al., 2011) and the close relation between physiological processes (i.e. transpiration, photosynthesis) and crown architecture (Bréda et al., 1995; Drobyshev et al., 2007; Martinez-Vilalta et al., 2007; Rathgeber et al., 2011; Fichtner et al., 2013). The photosynthetic performance generally increases because of increasing light capture efficiency and decreasing path length for water transport (Niinemets, 2010). Crown architecture also directly affects stomatal conductance and sap flow density and thus water-use efficiency (Bréda et al., 1995; Bert et al., 1997; Lagergren and Lindroth, 2004; McDowell et al., 2006; Ringgaard et al., 2012). Frequently, dominant trees maintain higher sap flow densities in the sapwood, together with a higher spending of total water as consequence of higher inputs of radiation into tree crowns (Aranda et al., 2012). For instance, mean daily sap-flux density of sessile oak doubled from suppressed trees with low leaf area to dominant ones with large crowns (Bréda et al., 1995).

Despite abundant literature on either stand- or tree-level competition on sensitivity to climate, their relative importance remains poorly documented (Bréda et al., 1995; Cescatti and Piutti, 1998; van der Maaten, 2013). However, codominant and suppressed trees represent a large proportion of stems within stands and significantly contribute to stand wood production (Binkley, 2004).

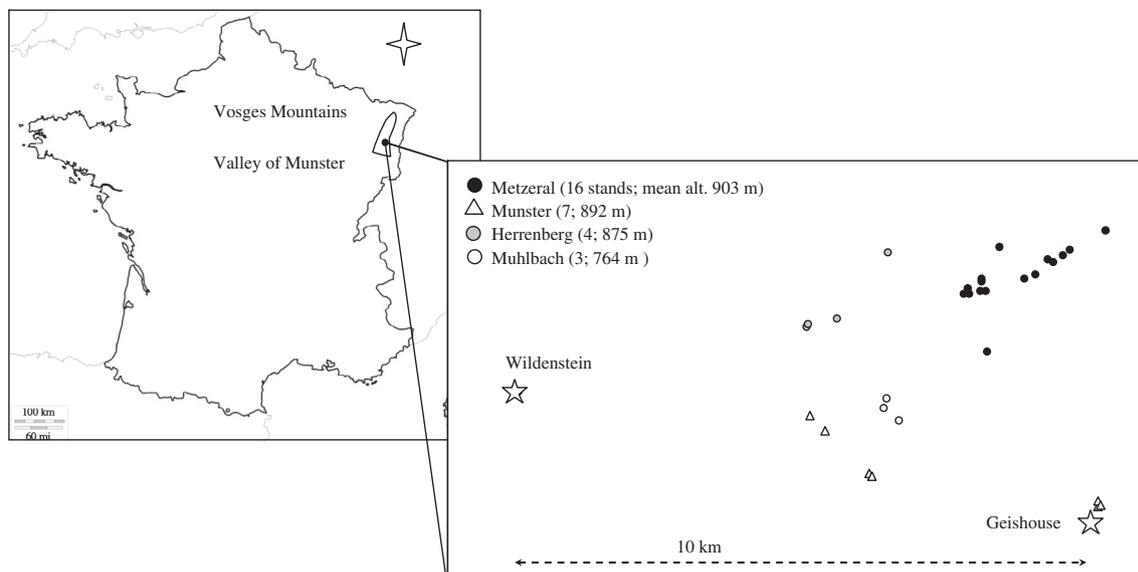


Fig. 1. Location of the 30 sampled stands (four different forests) in the Vosges Mountains in the Valley of Munster. Stars indicate the location of the meteorological stations (see text for details).

Table 1
Stand characteristics (mean and standard deviation) according to facing (South: 100 to 300 grades; North: 0–100 and 300–400 grades) and stand basal area (SBA in m²/ha). Low = [25–35]; Medium = [35–45]; High = [45–55]. N/ha = number of trees per hectare. % Aa (N) and (SBA) = proportion of *Abies alba* in the mixture expressed in number of trees (N) or stand basal area (SBA). Aa and Fs (DO/CO/SUP) = number of *Abies alba* and *Fagus sylvatica* for each social status (Dominant, Codominant, Suppressed). nd = no data.

SBA class	South facing				North facing			
	Low	Medium	High	All	Low	Medium	High	All
SBA (m ² /ha)	32.7 (4.5)	42.7 (2.8)	49.6 (2.5)	41.8 (7.4)	31.6 (3.8)	39.9 (2.4)	47.8 (6.1)	37.9 (7.7)
Age (Aa and Fs)	58 (2.1)	65 (2.9)	67 (14.2)	64 (8.2)	65 (7.4)	56 (3.3)	71 (14.5)	63 (9.9)
Slope (°)	22.4 (3.3)	23.4 (4.1)	29.8 (8.4)	25 (6.1)	25.5 (4.1)	22.8 (7.7)	27.7 (6.8)	25.2 (5.8)
Altitude (m)	950 (62)	884 (48)	836 (90)	889 (77)	893 (32)	870 (24)	900 (62)	887 (37)
Density (N/ha)	975 (88)	803 (161)	883 (261)	877 (185)	624 (199)	868 (108)	866 (225)	755 (209)
% Aa (N)	34 (21)	41 (12)	49 (16)	41 (16)	27 (7)	42 (14)	30 (10)	32 (12)
% Aa (SBA)	47 (16)	57 (18)	66 (25)	57 (20)	47 (11)	58 (16)	56 (12)	53 (13)
n plots	5	7	5	17	6	4	3	13
Aa (DO/CO/SUP)	15/13/21	45/27/41	32/15/33	62/55/95	34/17/15	26/18/17	21/11/13	81/46/45
Fs (DO/CO/SUP)	nd/17/18	16/29/27	nd/nd/10	16/46/55	22/18/39	nd/12/nd	nd/15/20	22/45/59

Studying both the effect of environmental factors at the stand level and their variations among trees through, for instance, social statuses will allow (1) a better comprehension of the distribution of the competition between trees within stands and (2) accurately supporting management decisions particularly in the context of global changes (Lindner et al., 2010).

In this study, climate tree-growth relationships of 414 *Abies alba* and 243 *Fagus sylvatica* trees from mountainous mixed stands were investigated, while considering indicators of competition at both stand (SBA) and tree (SST) levels. The main objective was to assess how contrasted levels of competition at the stand level (Low, Medium and High SBA) affect the climate sensitivity of trees of different SST (Dominant, Codominant and Suppressed trees). As local ecological conditions could highly modulate this sensitivity, we also considered two important and contrasted conditions in mountainous contexts (north- and south-facing sides). SST was expected to highly modulate tree-ring response to climate, with decreasing sensitivity from dominant to suppressed trees. Competition at the tree level was hypothesized to be lower on south-facing side under higher level of abiotic stress and to increase with stand level competition.

2. Materials and methods

2.1. Sampling design

Thirty stands were sampled in the crystalline Vosges Mountains (north-eastern France) in the Alsatian Valley of Munster between 48°00' to 47°96' latitude North and 7°00' to 7°05' longitude East (around 35 km²). The altitude ranged between 610 and 1100 m a.s.l. (mean: 886 m; 86% of the stands had an altitude up to 800 m), which corresponds to the optimal ecological conditions for both *A. alba* and *F. sylvatica* (Seynave, 1999) (Fig. 1). Sampling has been done in even-aged mixed *A. alba* and *F. sylvatica* stands to ensure homogeneity of local ecological conditions – such as soil fertility, soil water availability and altitude – when comparing

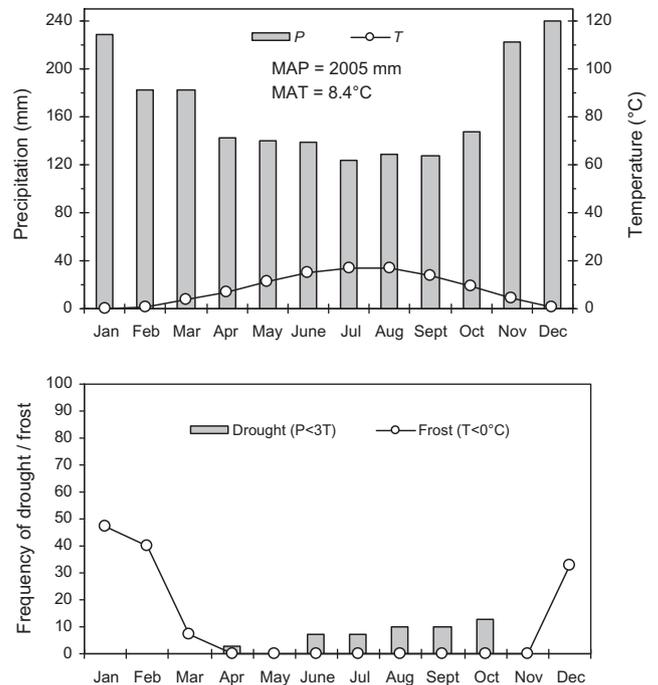


Fig. 2. Mean climatic conditions and extreme events in the Valley of Munster. Geographical location of the meteorological stations in Fig. 1. Climatic diagram: mean monthly temperatures (°C; black line) and precipitation (mm; grey bars). Extreme events: frequencies of frost (T < 0°C; black line) and drought (P < 3T; grey bars). Climatic values were calculated for the period 1961–1990. MAP and MAT = mean annual precipitation and temperature (see text for details).

responses to climate between species. The proportion of *A. alba* in the mixture was expressed as a percentage of stand basal area (SBA) and averaged 55%.

Edaphic conditions were homogenous with soils developed on Schist and Greywackes leading to rich, faintly acidic and deep soils

Table 2

Tree characteristics according to facing, stand basal area (SBA in m²/ha), species and social status (SST). DO, CO, SUP = Dominant, Codominant and Suppressed trees. RW = ring width (in mm). MS = mean sensitivity; AC = first order correlation; GINI = GINI coefficient; rbt = coefficient correlation between trees; EPS = expressed population signal. Values have been calculated on standardized values for the common period 1940–1996 (see text for details).

SBA	Low						Medium						High						
	<i>Abies alba</i>			<i>Fagus sylvatica</i>			<i>Abies alba</i>			<i>Fagus sylvatica</i>			<i>Abies alba</i>			<i>Fagus sylvatica</i>			
SST	DO	CO	SUP	DO	CO	SUP	DO	CO	SUP	DO	CO	SUP	DO	CO	SUP	DO	CO	SUP	
Facing South																			
Dia (cm)	36.7	28.4	18.7	20.5	17.5	39.5	30.3	20.9	34.4	25.2	15	44.8	32.8	19.1				17.4	
Ht (m)	21.6	20.2	16.2	20.5	16.2	23.6	21.7	18.5	24	22.7	17.1	24.9	22.6	16.3				17.7	
Ht/Dia	0.60	0.73	0.89	1.04	1.02	0.62	0.75	0.93	0.73	0.93	1.19	0.57	0.72	0.87				1.04	
Age (years)	57	53	53	58	56	62	61	59	64	62	59	73	69	56				63	
RW (mm)	2.7	2.2	1.5	1.6	1.6	2.8	2.1	1.6	2.4	1.9	1.1	2.8	2.3	1.5				1.2	
MS	0.116	0.125	0.126	0.182	0.155	0.132	0.123	0.092	0.146	0.168	0.164	0.156	0.142	0.138				0.101	
AC	0.711	0.696	0.807	0.382	0.232	0.726	0.744	0.556	0.594	0.499	0.562	0.598	0.519	0.524				0.350	
GINI	0.111	0.117	0.143	0.109	0.085	0.122	0.114	0.069	0.103	0.117	0.132	0.115	0.116	0.112				0.064	
rbt	0.312	0.270	0.290	0.345	0.095	0.285	0.242	0.063	0.369	0.284	0.114	0.232	0.083	0.165				0.048	
EPS	0.937	0.858	0.852	0.904	0.799	0.908	0.842	0.500	0.735	0.815	0.444	0.863	0.499	0.705				0.481	
N	15	13	21	17	18	45	27	41	16	29	27	32	15	33				10	
Facing North																			
Dia (cm)	42.1	33.4	22.7	31.4	27.9	16.5	35.7	28.3	18.7		22.1		45.8	36.4	22.5			26.3	15.1
Ht (m)	26.1	24.6	20	25.8	25.4	20	23.6	22.1	16.8		21.4		24.2	22.3	16.8			21.7	16.3
Ht/Dia	0.65	0.76	0.89	0.84	0.92	1.23	0.69	0.81	0.92		1.02		0.54	0.63	0.79			0.88	1.17
Age (years)	59	61	56	64	66	62	56	54	51		55		69	69	59			67	55
RW (mm)	3.2	2.4	1.8	2.4	2	1.3	2.9	2.3	1.7		1.8		3	2.3	1.6			1.8	1.3
MS	0.116	0.126	0.133	0.189	0.215	0.138	0.133	0.134	0.104		0.17		0.146	0.153	0.100			0.189	0.134
AC	0.742	0.757	0.776	0.598	0.517	0.585	0.602	0.649	0.654		0.53		0.365	0.545	0.425			0.344	0.51
GINI	0.106	0.134	0.141	0.14	0.143	0.108	0.106	0.113	0.096		0.116		0.088	0.112	0.067			0.11	0.095
rbt	0.271	0.450	0.281	0.236	0.426	0.149	0.255	0.248	0.176		0.41		0.156	0.179	0.061			0.202	0.105
EPS	0.842	0.906	0.882	0.642	0.924	0.749	0.938	0.898	0.894		0.952		0.855	0.760	0.665			0.559	0.529
N	34	17	15	22	18	39	26	18	17		12		21	11	13			15	20

with high soil water holding capacity (> to 150 mm) (Seynave, 1999). Slopes were also comparable between stands and averaged 25° (11–40°). On the contrary, stands were sampled on two contrasted mountainsides, allowing investigating properly the effect of aspect on climate sensitivity: south-facing side (SF) with an orientation from 150 to 350 grades and north-facing side (NF) between 350 and 150 grades (Table 1).

For each facing side, three stand basal area (SBA) classes (in m²/ha) were considered: Low ([25–35]), Medium ([35–45]) and High ([45–55]) (Table 1). Within each stand, trees were characterized by their social status: dominant (Do), codominant (Co) and suppressed (Sup). This classification procedure was made in the field and corresponded with stratification based on tree architecture (i.e. height and diameter) and on crown layer competition. Suppressed trees were the smallest trees in height (and consequently in diameter) with a lesser accessibility to light (Tables 1 and 2).

Dominant trees were the tallest trees with a fully access to light. Codominant trees had an intermediate position (Seynave, 1999).

Finally, 36 theoretical strata were defined combining two species (*A. alba*/*F. sylvatica*), two facing sides (NF/SF), three stand basal areas (Low/Medium/High) and three social statuses (Do, Co, Sup). The absence of *F. sylvatica* in few strata led to an unbalanced sampling, especially for dominant beeches which were available in two cases (SF43 and NF32) (Tables 1 and 2). Consequently, only 30 strata over 36 were effective. For each stratum, 10–45 trees were available for a total of 657 sampled trees. For each tree, diameter (cm) and total height (m) were carefully measured (Table 2).

2.2. Ring-width measurements and chronologies statistics

Each sampled tree was cored to the pith at breast height with an incremental borer in winter 1997 (one core per tree). Ring widths

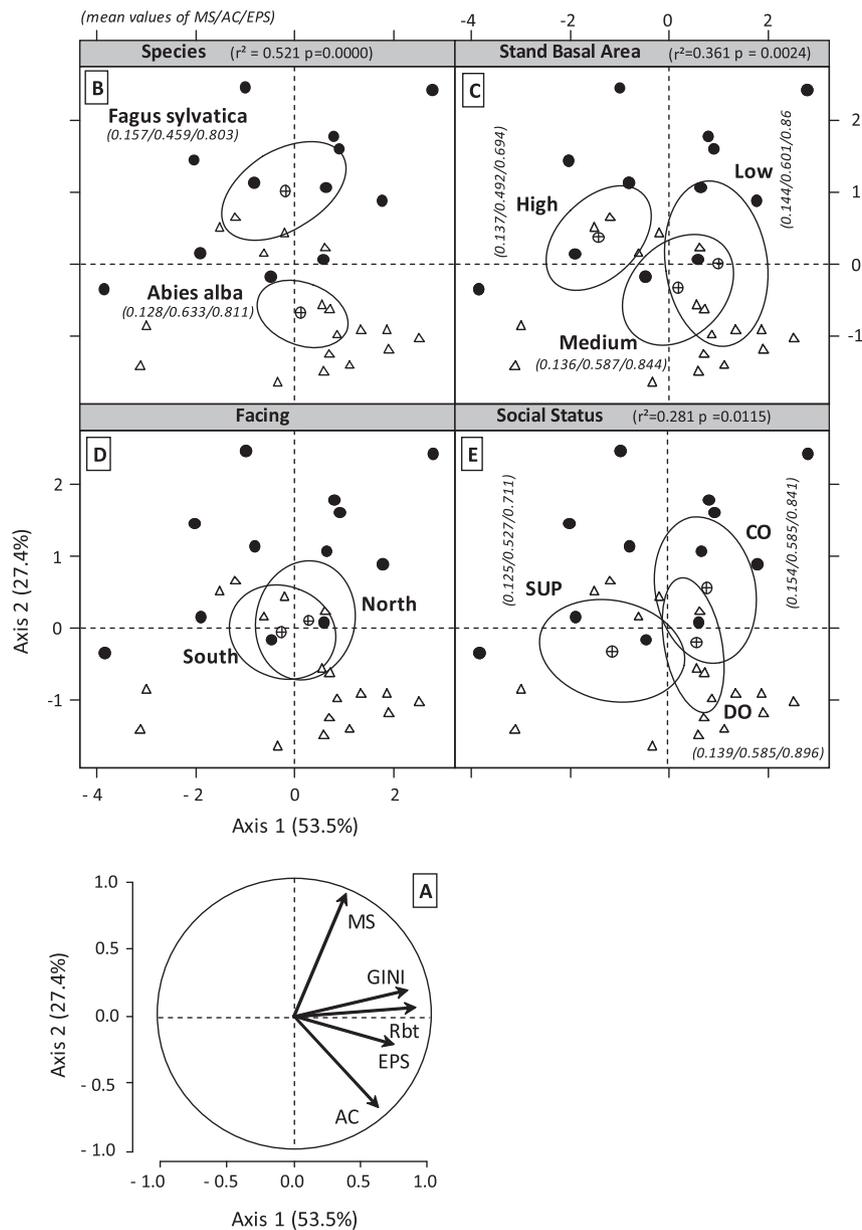


Fig. 3. Scatter plots of principal component analysis (PCA, axes 1 and 2) performed on the ring characteristics for the 30 combinations. MS = mean sensitivity; EPS = expressed population signal; rbt = coefficient correlation between trees; AC = first order correlation; GINI coefficient. All the values have been calculated on the standardized values from the common period 1940–1996. *Fagus sylvatica*: black circles; *Abies alba*: white triangles. The figures show the 95%-ellipse confidence regions for each qualitative variables: species (*Fagus sylvatica* versus *Abies alba*); stand basal area (High, Medium, Low); facing (North versus South); social status (SUP, CO, DO). For SBA and SST, the coefficient correlation with the first component is given and with the second component for species.

were measured with the image analysis system WinDendro 6.3a (Regent Instruments, 1996). Tree ages were comparable between strata and averaged 60 years (Table 2). Afterwards, the 657 individual tree-ring widths series were carefully cross-dated by progressively detecting regional pointer years, using the method developed by Becker (1989) and largely applied since (Mérian and Lebourgeois, 2011b; Lebourgeois et al., 2012). Here, a pointer year was a year for which at least 70% of the cross-dated trees presented a radial growth variation (RGV) of at least 10%. The RGV (%) expressed the extent to which the ring of the current year was narrower (negative value) or wider (positive value) than the previous one. Absolute dating was checked by the application INTERDAT (Becker, 1989) which identifies locations within each ring series that may have erroneous cross-dating. Pointer years are detailed in Supplementary S1.

Using the R software (R Development Core Team 2010) and the “dplr” package (Bunn, 2008; Mérian, 2012), the tree ring series were computed on the maximum period common to all strata (1940–1996, 57 years) and standardized individually to emphasize the inter-annual climatic signal. A double-detrending process was thus applied, based on an initial negative exponential or linear regression followed by a fitting of a cubic smoothing spline with 50% frequency response cut-off and with a rigidity of 33% of series length (Cook and Peters, 1981). Dimensionless indices were obtained by dividing the observed ring width value by the predicted one. This process creates stationary time series for each tree with a mean of 1 and a homogeneous variance.

For each stratum, the individual detrended tree-ring series were averaged by year using a bi-weighted robust mean to develop a

chronology which represented the common high frequency variation of the individual series (Cook, 1985). To avoid misestimations in dendroecological analyses due to an unbalanced sampling among plots (10–45 cores) (Mérian and Lebourgeois, 2011a; Mérian et al., 2013b), mean growth chronology variance was corrected per stratum with the method proposed by Mérian et al. (2013a). Moreover, five statistics were calculated from the detrended series (Table 2; Fritts, 1976; Biondi and Qeadan, 2008): mean sensitivity (MS) quantifying the year-to-year variability; first-order auto-correlation (AC) expressing the influence of growth of the previous year on the current year growth; gini coefficient (GINI) and mean inter-series correlation (r_{bt}) both giving a synthetic quantitative measure of inter-series heterogeneity among detrended series; and expressed population signal (EPS) quantifying the degree to which the chronology expressed the population chronology (Wigley et al., 1984). EPS is defined as:

$$EPS = \frac{r_{bt}}{r_{bt} + \frac{1-r_{bt}}{N}}$$

where *N* is the number of cored trees per stratum and *r_{bt}* the mean inter-tree correlation. EPS yields 1 when the chronology mirrors the population signal.

2.3. Climatic data

Monthly precipitation sum (*P*) and mean temperature (*T_{min}* and *T_{max}* not available) data on 1940–1996 were gathered from series available to the nearest of the sampling area (French National Climatic Network, Météo-France; Moisselin and

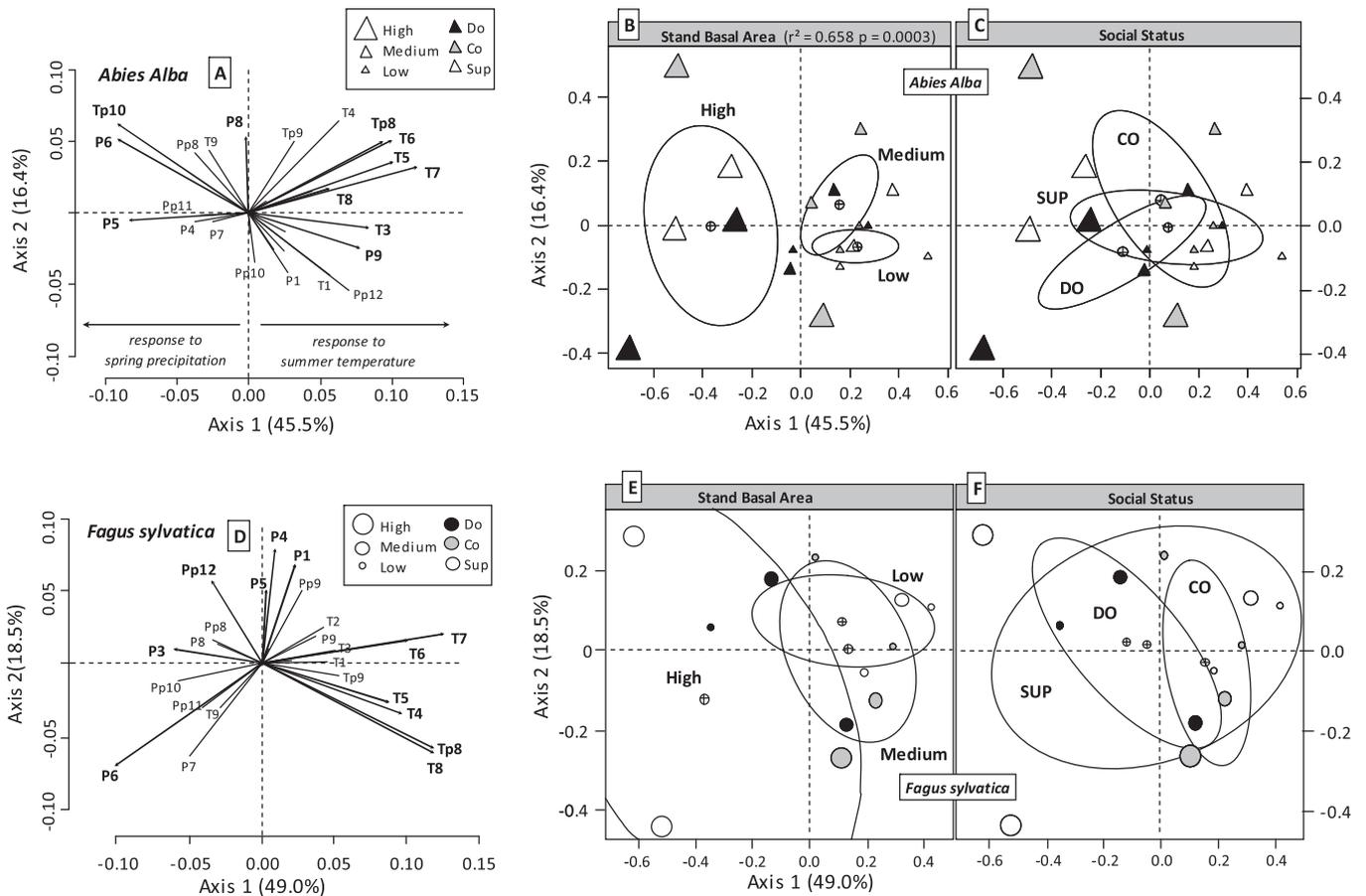


Fig. 4. Scatter plots of principal component analysis (PCA, axes 1 and 2) performed on the bootstrapped correlation coefficients (BCC) for *Abies alba* and *Fagus sylvatica* (period 1940–1996). The figures show the 95%-ellipse confidence regions for the qualitative variables stand basal area (High, Medium, Low) and social status (SUP, CO, DO). For *Abies alba* and SBA, the coefficient correlation with the first component is given. T = temperature; P = precipitation; p = previous; the number indicates the month of the year.

Canellas, 2005). Precipitation came from the station of Wildenstein (47°58'30"N, 06°57'36"E; alt. 560 m) at 10 km away from our sampling sites, and temperatures from the station of Colmar (47°55'42"N, 7°24'24"E; alt. 207 m) at 55 km away from the stands. The altitude of Colmar being very different from that of our sampled stands (207 m against 886 m), monthly temperature series were compared to those of the station of Geishouse (47°52'48"N, 07°03'06"E; alt. 660 m) to verify the accuracy of Colmar's data. Geishouse is located at 0–6 km from our sampling sites (Fig. 1) and displays both a comparable altitude to them. However, records cover the period 1965–1996 (32 years) which is too short to precisely estimate climate-tree growth relationships. These records were used to correct Colmar's data month per month through linear regressions (Colmar ~ Geishouse) on the common period 1965–1996. The slope of the regression allows correcting the magnitude of interannual variability. The y-intercept allows correcting the mean differences between meteorological sources (Lebourgeois et al., 2012). The slopes and the y-intercepts ranged from 0.68 to 0.90 and from 1.30 to 8.16 respectively, revealing that Colmar's data overestimated both monthly temperatures and their inter-annual variability. They were thus corrected using previous linear regressions to obtain series with characteristics (mean value and inter-annual variation) as close as possible to those of Geishouse.

Finally, the corrected series of Colmar's temperatures (*T*) and raw Wildenstein series of precipitation (*P*) were used for climate-tree growth analyses over the period 1940–1996. These data showed that the weather conditions under study corresponded to a mountainous climate characterized by very high annual precipitation (>2000 mm) with a peak in winter and autumn (>200 mm per month) and a relative decrease in summer (<130 mm). Winters were cold with a high frequency of frost and summers rather fresh with scarce exceptional droughts (Fig. 2).

2.4. Statistical analyses

Climate-tree growth relationships were investigated per stratum from the period 1940–1996 through the calculation of bootstrapped correlation functions using the growth chronology as dependent variable (Guiot, 1991) and 28 monthly climatic regressors: 14 *T* and 14 *P* values, organized from August of the previous growing season to September of the year in which the ring was formed. The statistical significance of the coefficients was assessed by calculating 95% confidence level based on 1000 bootstrap resamples of the data. These analyses were achieved with the "bootRes" package (Mérian, 2012; Zang and Biondi, 2013).

To identify the structuring of chronologies statistics among strata, a first principal component analysis (PCA) was performed on tree ring characteristics (matrix: rows = 30 strata; columns = five chronologies statistics values – MS, AC, rbt, EPS, GINI). A second one was performed from the bootstrapped regression coefficients (30 strata and 28 climatic regressors) to identify the inter-strata variability of sensitivity to climate. This latter PCA was calculated from variance–covariance matrix since descriptors were of the same kind and shared the same order of magnitude. For both PCA, 95% confidence ellipses highlighting potential groupings in the factorial maps according to qualitative variables (Species, Facing, Stand Basal Area and Social status) were drawn. PCA analyses were performed with the "FactoMineR" package (Husson et al., 2013).

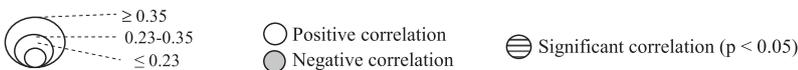
3. Results

3.1. Chronologies statistics

The two first axes of the PCA (PC1 and PC2) performed on the ring characteristics explained 53.5% and 27.4% of the total variance

Table 3
Correlation functions of the 18 *Abies alba* chronologies classified according to stand basal area (SBA in m²/ha), social status and facing. Open circles positive bootstrapped correlation coefficients (BCC); grey circles negative BCC; striped circles significant BCC (*p* < 0.05); increasing circle size with increasing correlation; Nsig number of significant BCC. Low SBA = 32 and 33 m²/ha; Medium SBA = 40 and 43 m²/ha; High SBA = 48 and 50 m²/ha. N and S = North and South facing; DO, CO and SUP = Dominant, Codominant and Suppressed trees.

		PRECIPITATION										TEMPERATURE										Nsig.																			
		previous year					current year					previous year					current year																								
		Aug	Sept	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	June	Jul	Aug	Sep	Aug	Sept	Oct	Nov	Dec	Jan		Feb	Mar	Apr	May	June	Jul	Aug	Sep											
Low SBA	N-Do	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	5											
	S-Do	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	2											
	N-Co	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	2											
	S-Co	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	6											
	N-Sup	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	4											
	S-Sup	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	3											
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Medium SBA	N-Do	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	2											
	S-Do	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	2											
	N-Co	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	5											
	S-Co	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	4											
	N-Sup	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	1											
	S-Sup	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	3											
		1					1					4					1					3					2					5									
High SBA	N-Do	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	1											
	S-Do	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	3											
	N-Co	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	3											
	S-Co	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	0											
	N-Sup	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	2											
	S-Sup	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	6											
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respectively (Fig. 3A). The main structuring statistics on PC1 were GINI (correlation with PC1 scores $r^2 = 0.839$, $p < 0.001$), rbt ($r^2 = 0.717$, $p < 0.001$), EPS ($r^2 = 0.620$, $p < 0.001$) with mainly positive coordinates for series with EPS values up to 0.85. The discriminating statistics on PC2 were MS ($r^2 = 0.829$, $p < 0.001$) and AC ($r^2 = 0.453$, $p < 0.001$) (Fig. 3A).

PC1 evidenced that statistics variability was linked to both stand basal area (SBA) and social status (SST). PC1 scores were negatively correlated with SBA ($r^2 = 0.361$, $p = 0.0024$) (Fig. 3C) and positively with SST ($r^2 = 0.281$, $p = 0.0115$) (Fig. 3E). EPS, rbt and GINI values were lower in densely stocked stands suggesting that the inter-tree common growth signal decreased with stand level competition (Table 2). Moreover, AC values decreased with SBA, implying a stronger role of the previous year on the current year growth under high stand level competition. EPS, rbt and GINI were also lower for suppressed trees while MS tended to increase suggesting that suppressed trees showed a weaker common growth signal.

PC2 revealed a nearly complete separation between the two species ($r^2 = 0.521$, $p < 0.001$) with *F. sylvatica* characterized by

positive coordinates and *A. alba* by negative ones (Fig. 3B). *F.* had higher MS and lower AC values than *Abies* suggesting a greater response to interannual climatic variability and a lesser dependency on the previous climatic conditions. At least, no significant differences appeared between facing (Fig. 3D).

3.2. Response to climate variability

As the PCA led on chronologies statistics clearly split the two species, PCA on bootstrapped correlation coefficients (BCC) have been performed on *A. alba* and *F. sylvatica* separately to better evidence intra-specific variability. Regardless of the species, no significant difference in climate tree-growth relationships was found between north- and south-facing sides (not shown).

A. alba growth was mainly and positively controlled by temperature in August irrespective of the stratum (11 significant BCC among 18 strata for current and 7/18 for previous) (Fig. 4A and Table 3). To a lesser extent, current May (6/18) and July (5/18) temperatures also positively influenced growth as well as precipitation in previous September (5/18) and current February (5/18). PC1 explained 45.5% of the total variance and clearly separated *A. alba* climatic responses according to SBA (Fig. 4B). Current spring precipitation (mainly June), previous December precipitation and October temperature were the most important climatic parameters under the highest SBA whereas summer temperature played a major role under the lowest SBA (mainly previous and current August temperature) (Table 3). The ellipses-based grouping according to social status (SST) was not significant, although SST effect seemed to be modulated by SBA (Fig. 4C). Indeed, dominant trees were more sensitivity to precipitation in June as SBA increased, as well as suppressed trees for previous autumn and winter conditions (Table 3 and Fig. 5).

Key periods were different for *F. sylvatica*. June (9/12) and April (7/12) temperatures influenced negatively tree growth while precipitation in February promoted it (7/12) (Fig. 4D and Table 4). To a lesser extent, temperature in January (5/12) and precipitation in August (5/12) also positively influenced growth. The difference between SBA classes was less pronounced compared with *Abies* (Fig. 4E). Nevertheless, the positive effect of June precipitation and the negative one of temperature were strengthened under high SBA (Table 4 and Fig. 5). Because of an unbalanced design, the effect of SST could not be properly investigated (Fig. 4F). Finally, for both species, the dependency to early summer precipitation increased with increasing SBA.

4. Discussion

4.1. Reliability of the experimental design

Most of tree-ring studies sample dominant trees (i.e. the tallest and largest-diameter trees) to analyse the effect of climate on growth. It is generally assumed that such trees grow faster despite few counterexamples (Cherubini et al., 1998) linked with temporal instabilities of social status. Such instabilities may seriously affect long-term analysis and lead to erroneous interpretations of the results (Cherubini et al., 1998). Focusing on our data, Seynave (1999) showed that the social status of silver firs was very stable over time after 20 years old, while that of beeches tended to stabilize at 20–40 years old. As this latter species highly responds to improvement of local light conditions, small-diameter trees more often acquire an upper position within the canopy. These observations can explain the general less significant results obtained for *F. sylvatica* concerning the effects of tree level competition on tree-ring response to climate.

Trees were sampled in mixed stands to ensure inter-specific homogeneity in silviculture and ecological conditions. The intrinsic

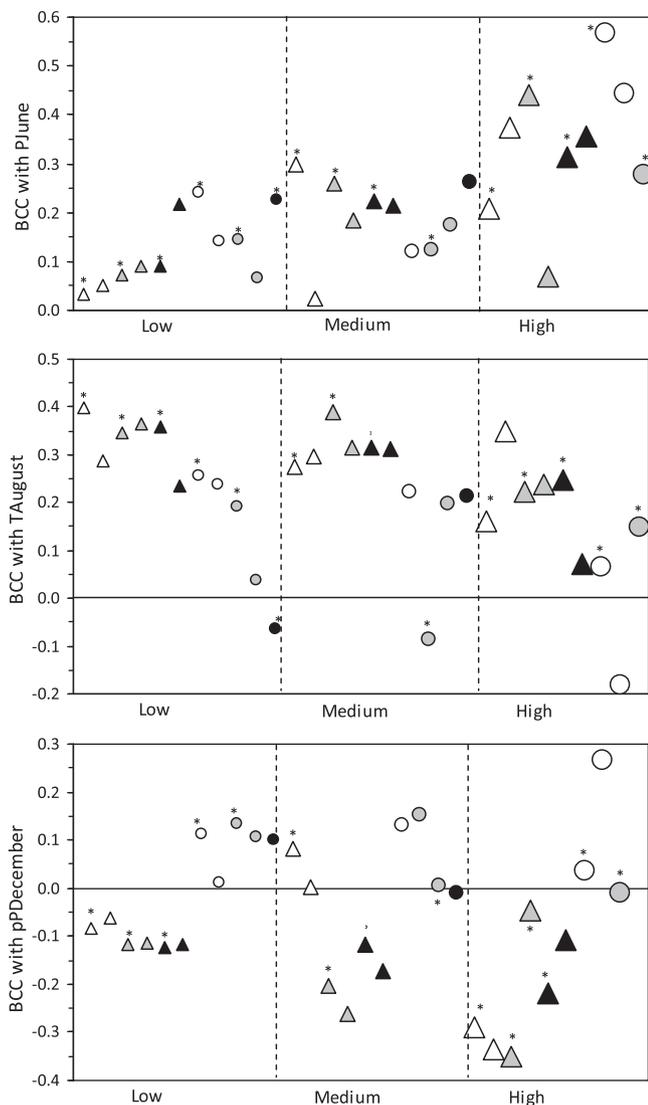


Fig. 5. Relationships between bootstrapped correlation coefficients (BCC) and precipitation in June and previous December, temperature in August according to stand basal area (size of the symbols proportional to SBA: Low, Medium, High in m^2/ha) and social status. Suppressed trees = white, codominant = grey and dominant = black. *Fagus sylvatica* = circles and *Abies alba* = triangles. * = north facing (south otherwise).

Table 4
Correlation functions of the 12 *Fagus sylvatica* chronologies classified according to stand basal area (SBA in m²/ha), social status and facing. Open circles positive bootstrapped correlation coefficients (BCC); grey circles negative BCC; striped circles significant BCC ($p < 0.05$); increasing circle size with increasing correlation; Nsig number of significant BCC. Low SBA = 32 and 33 m²/ha; Medium SBA = 40 and 43 m²/ha; High SBA = 48 and 50 m²/ha. N and S = North and South facing; DO, CO and SUP = Dominant, Codominant and Suppressed trees.

		PRECIPITATION										TEMPERATURE										Nb sig.																			
		previous year					current year					previous year					current year																								
		Aug	Sept	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	June	Jul	Aug	Sep	Aug	Sept	Oct	Nov	Dec	Jan		Feb	Mar	Apr	May	June	Jul	Aug	Sep											
Low SBA	N-Do	○	○	○	○	○	○	⊖	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	⊖	○	⊖	⊖	○	○	4											
	S-Do																																								
	N-Co	○	○	○	○	○	⊖	⊖	○	○	○	○	○	○	○	○	○	○	○	○	⊖	○	○	○	○	○	○	○	○	3											
	S-Co	○	○	○	○	○	○	⊖	○	○	○	○	○	○	○	⊖	○	○	○	○	⊖	○	○	⊖	○	⊖	○	○	○	5											
	N-Sup	○	○	○	○	○	○	⊖	○	○	○	○	○	○	○	○	○	○	○	○	⊖	○	○	○	○	○	○	○	○	5											
	S-Sup	○	○	○	○	○	○	⊖	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	⊖	○	○	○	○	○	3											
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Medium SBA	N-Do																																								
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	N-Co	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	3											
	S-Co	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	4											
	N-Sup																																								
	S-Sup	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	6											
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High SBA	N-Do																																								
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	N-Co	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	2											
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	N-Sup	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	6											
	S-Sup	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	5											
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effect of mixture on sensitivity to climate was not investigated in the present study. Nevertheless, a previous analysis led in the Vosges Mountains in pure and mixed *A. alba* forests (with *F. sylvatica* and/or *Picea abies*) showed that mixture reduced drought sensitivity of firs but only under the more xeric conditions (mean July precipitation below 85 mm and altitude <600 m) (Lebourgeois et al., 2013). As such conditions were not sampled in the present study (more humid at higher altitude, Table 1 and Fig. 2), it has been assumed that the effect of mixture is negligible compared with those of stand and tree levels competition.

4.2. Response to climate and its modulation by competition

Our findings confirm the common knowledge that temperature plays a key role in the radial growth for tree growing at high elevation. The difference in the key periods from early summer for *F. sylvatica* to late summer for *A. alba* is also highly consistent with the general feature observed under mountainous continental climate (Becker, 1989; Bert et al., 1997; Desplanque et al., 1998; Dittmar et al., 2003; Lebourgeois et al., 2005; Bouriaud and Popa, 2009; Friedrichs et al., 2009; Lebourgeois et al., 2010; van der Maaten-Theunissen et al., 2012; Lebourgeois et al., 2013). Specific features in seasonal dynamics of carbohydrate storage, root elongation, cambial reactivation or leaf unfolding are classically evoked as functional explanation of these differences.

Stand-level competition (SBA) prevails on tree-level competition (SST) with no obvious difference between local ecological conditions (north- and south-facings). In the less densely stocked stands (SBA < 45 m²/ha), all *A. alba* trees exhibit a strong common signal and a similar response to late summer temperature whatever their social status. The absence of significant correlations with precipitation suggests that water availability is not a limited supply in these stands. These results agree with ecophysiological

studies which have already showed that decreasing canopy cover improves the soil water recharge by the rainfall (Aussenac, 2000) and maintains a higher level of soil moisture (Gyenge et al., 2011; Paluch and Gruba, 2012) and tree water status (Moreno and Cubera, 2008). The decrease of competition for water at the stand-level leads to a higher and more common positive response to temperature among trees that xylogenesis highly depends in mountainous contexts (Rossi et al., 2008).

On the opposite, under higher SBA (>45 m²/ha), dominant trees are more sensitive to early summer drought whereas growth of suppressed trees mainly relies on conditions of previous year. Because of an unbalanced experimental design, such SBA-SST interaction could not be accurately investigated for *F. sylvatica*. Nevertheless, as observed on firs, sensitivity to early summer drought tends to increase with SBA. Increasing SBA enhances differences in response to climate among social statuses, dominant trees being more sensitive to summer drought and suppressed trees more sensitive to previous autumn and winter periods. The low sensitivity of suppressed trees under high SBA could be partly explained by physiological adjustment. They could take advantage of the climate conditions buffering relative to the closed and densely foliated canopy, which could reduce thermal stress and transpiration during summer, and thus sensitivity to drought (Aussenac, 2000; Bréda et al., 2006; Niinemets, 2010). On the other hand, for the suppressed trees, we can hypothesize a greater dependence on previous year reserves and translocation as the role of prior conditions to ring formation increases.

Our findings do not support the hypothesis of a strong interaction between the competition and the level of abiotic stress. We can hypothesize that the optimal growth conditions observed for the sampled stands concerning soil fertility, soil water reserve and altitude (Seynave, 1999) thwart the effects of the two contrasted facing sides considered.

4.3. Consequences for forest management

Our study highlights the importance of assessing tree growth response among various competition characteristics, especially various stand densities and tree social statuses, rather than focusing on dominant trees in closed canopy. Even if the sampled area corresponds to optimal growth conditions for the two species, ranges stand and tree level competitions led to heterogeneous sensitivities to climate, particularly to spring and summer droughts. Such variability in climate sensitivity shows that silvicultural practices, through thinnings, are a powerful tool to manage the effects of climate-related limiting factors of growth.

Sampled trees are relatively young trees (60 years) and in “active” growth (diameter between 35 and 45 cm). The silvicultural guide for silver fir stands in the Vosges Mountains recommends SBA around 30 m²/ha (25–35 m²/ha) for an optimal management of both pure and mixed *A. alba* based forests. Since high SBA are still very frequent in managed forests, current forest management does not appear “optimised” to prevent stands from increasing drought constraints. The decreasing drought sensitivity with decreasing stocked stand could have important consequences for forest management with regard to the predictions of climate change toward drier conditions. Different studies showed that the accumulation of particular dry years affect the growth and competitive strength of tree species for several consecutive years and induce forest decline and tree mortality (Allen et al., 2010). Thus, from the practical point of view, the “simple” application of the recommendation could counteract environmental changes and partly prevent forest ecosystems from decline in the future. Even if recent results showed that climate changes have already influenced species distribution (Lenoir et al., 2008) and tree growth (Charru et al., 2010) particularly at high altitudes by reducing thermal constraints, it is reasonable to expect that trees at upper elevation sites may also suffer from drought in the future which could alter their growth and vitality. Therefore, even if climate does not shift yet toward extremes that *A. alba* or *F. sylvatica* could not withstand, forester could already decrease or maintain low SBA at upper elevation sites to better cope with future climate change.

5. Conclusion

Our analysis evidenced that temperature played a more important role than precipitation in the radial growth of *A. alba* and *F. sylvatica* growing in western European mountains. The two species responded contrastingly to climate variability with quite different key periods: temperature in previous and current late summer (August) for the conifer, and in spring (April) and early summer (June) for the broad-leaf. Stand level competition prevailed on tree level competition as factor modulating tree-ring sensitivity to climate. Under Low and Medium SBA (<45 m²/ha), trees of a given species exhibited similar responses to climate whatever their social status, while the sensitivity to drought increased with tree dominance under high SBA (>45 m²/ha). No obvious differences were found between local ecological conditions (north- and south-facing sides).

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.foreco.2014.05.038>.

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