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# Mixed stands reduce *Abies alba* tree-ring sensitivity to summer drought in the Vosges mountains, western Europe

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ABSTRACT

In most dendroecological studies, climate–tree growth relationships are established for trees growing on pure stands. However, response to climate may be affected by inter-species interactions and local constraints, which beg the question of the effect of mixture on tree growth response under various ecological conditions. To assess these effects, climate–tree growth relationships of pure *Abies alba* stands were compared to those of three different mixtures: *A. alba* with *Fagus sylvatica*, with *Picea abies* and with both species. 151 stands (456 *A. alba* trees) were sampled in the Vosges mountains in north-eastern France under three contrasted climates, from low altitude and dry conditions (mean precipitation in July <85 mm and altitude <600 m) to high altitude and humid conditions (*P* July >115 mm and alt. >900 m). We sampled adult trees and homogeneous stand conditions to clearly assess differences in sensitivity to climate. Climate–tree growth relationships were evaluated from 12 *A. alba* chronologies (four mixtures × three climatic conditions) through pointer years and response function analyses. Late previous summer conditions and current summer soil water deficit and temperature played a major role on *A. alba* growth. Results showed greater sensitivity to temperature at high elevation, and to summer drought at low altitude and under dry conditions. Mixture allowed maintaining a higher level of *A. alba* growth during extreme climatic events and reduced *A. alba* response to summer drought especially under the driest contexts. Different facilitation processes may explain mixture effects such as changes in rooting depth, water input by stemflow and rainfall interception. This differentiated functioning of mixed forests highlights their importance for adapting forest management to climate change.

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## 1. Introduction

Ongoing climate change and extreme climatic events have already altered species distribution and tree growth in many regions throughout Europe (Lenoir et al., 2008; Way and Oren, 2010). Tree responses highly depend on both functional traits of the species (e.g. including genetic diversity and physiological characteristics) and local site conditions (e.g. elevation and soil depth). Trees can adapt to global changes, but their natural adaptive ability may be endangered by the sharp changes projected in the close future. To cope with significant adverse impacts of such events on tree vitality, recent studies suggest that forest management must be also adapted to reduce competition for resources within stands (Hemery, 2008; Doley, 2010; Lindner et al., 2010). Indeed, stand density and thinning change tree responses to climate (Bréda et al., 1995; Misson et al., 2003; Cotillas et al., 2009; Martin-Benito et al., 2010). At the tree level, tree-size and social status also modulate climate sensitivity (Cescatti and Piutti, 1998; Chhin et al., 2008; Linares et al., 2010; Mérian and Lebourgeois, 2011b).

Another way to face with environmental changes is to select more drought-resistant tree species (Bréda et al., 2006) and/or to increase tree species diversity within stands (Hooper et al., 2005). According to the principle of niche complementarity (Tilman, 1999; Hooper et al., 2005) and to the balance between competition (i.e. negative effect on the performance of individual plants) and facilitation (i.e. positive effect) (Callaway, 1995), a mixture of several species with different functional traits and strategies for resource uptake and use may have different responses to environmental constraints compared to the same species in pure stands (Kelty, 2006; Ishii and Asano, 2010; Richards et al., 2010). The complementary in resource use can be considered in two dimensions: in space, through complementarity of crown form and rooting pattern and over time by using various time windows for vital processes (e.g. leaf unfolding and blooming). Many recent studies suggest that facilitative processes and niche

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complementarity in mixed-species often lead to higher rates of biomass production, tree growth and carbon sequestration stands compared to pure stands (Pinto et al., 2008; Piotto, 2008; del Rio and Sterba, 2009; Pretzsch et al., 2010; Cavard et al., 2011; Vallet and Pérot, 2011). Other studies on herbaceous communities and on small regenerating trees also demonstrated that the relative importance of competitive and facilitative processes highly vary along gradients of abiotic stress (Choler et al., 2001; Callaway et al., 2002; Maestre et al., 2009). Thus, according to the stress gradient hypothesis, the weight of facilitation as an organising mechanism in plant communities increases with increasing abiotic ecological constraints whereas the importance of competition decreases. However, the manner in which competition and facilitation vary along abiotic stress gradients is not well-documented for mature natural forests (Callaway, 1998; Cavard et al., 2011; Kunstler et al., 2011).

In recent decades, the focus of European forests management has changed from mono-specific and production oriented forests towards mixed forests. Although mixed forests are being more and more promoted, studies on response to climate of tree species in such stands remain quite scarce. In Europe, *Abies alba*-based forests represent one of the main mixed ecosystems. For these ecosystems, recent studies clearly showed that the presence of *Picea abies* within the stand positively affected both *A. alba* site index (Pinto et al., 2008) and basal area increment (Vallet and Pérot, 2011). In spite of the importance of mixed *A. alba* forests, *A. alba* tree-ring response to climate has only been examined in pure stands (Becker, 1989; Bert and Becker, 1990; Bouriaud and Popa, 2009; Carrer et al., 2010; Lebourgeois et al., 2010b).

In this study, we seek to assess the respective effects of climate and stand composition on *A. alba* climate-tree growth relationships under a wide range of climatic conditions. The objectives were to determine (i) the main climatic factors driving *A. alba* radial growth, (ii) whether *A. alba* response to climate differs between pure and mixed stands on equivalent sites, and (iii) whether the effect of mixture on *A. alba* climate sensitivity is constant along climatic gradients (dry, mesic and humid sites). We compared the response to climate of pure *A. alba* stands to three different mixtures with *Fagus sylvatica*, *P. abies* and both of them. *A. alba* and *F. sylvatica* are shade-tolerant species, with a high need of precipitation or atmospheric humidity, and rather sensitive to summer drought and winter temperature. *P. abies* presents an intermediate shade-tolerance (Grassi and Bagnaresi, 2001) and response to summer drought, and a low sensitivity to frost (Pinto and Gégout, 2005; Lebourgeois et al., 2010b). According to the stress gradient hypothesis and the niche complementarity concept, we hypothesize that the sensitivity of *A. alba* decreases in mixed stands and that higher stress is attenuated by facilitation between species in mixed stands particularly at dry sites. Climatic factors influencing tree growth were identified with two complementary methods: the identification of -tree growth response to extreme climatic events using the analysis of pointer years and the establishment of mean relationships between tree ring and climate using response function analysis (Guiot, 1991).

## 2. Material and methods

### 2.1. Study area and sampling design

The study area is limited to the crystalline Vosges Mountains, in north-eastern France, located between 47°33′ to 48°47′ latitude North and 5°50′ to 7°28′ longitude East (Fig. 1). This region was chosen because it represents an important part of the national *A. alba* forest resource, with both pure and mixed stands (Pinto and Gégout, 2005; Pinto et al., 2007, 2008). In this natural area of 6800 km$^2$, altitude ranges from 350 to 1400 m a.s.l. Annual precipitation average 2000 mm at the highest elevation in the southern zone and fall to 600 mm on the eastern side of the zone. Mean annual temperature ranges from 9 °C at 350 m to 4 °C at the highest elevation (Pinto and Gégout, 2005). Pure stands of *A. alba* (Aa) and the three most frequent types of mixed stands containing *A. alba* were sampled: *A. alba* with *F. sylvatica* (Aa–Fs), with *P. abies* (Aa–Pa) and with *F. sylvatica* and *P. abies* (Aa–Fs–Pa) (Table 1). Only mature stands without visible recent storm damage and owned by the government were considered to limit the effect of local perturbations and ensure homogeneity in management. Two additional conditions had to be fulfilled: (i) stand basal area (*G*) had to be larger than or equal to 20 m$^2$/ha and dominant tree diameter over 40 cm; (ii) the proportion of the *G* of *A. alba* had to be between 40% and 60% and below 5% for species other than those defined in the corresponding mixture. In the case of three species, the proportion of *G* of the less represented species had to be above 15%. Shrub composition had to be also comparable between stands.

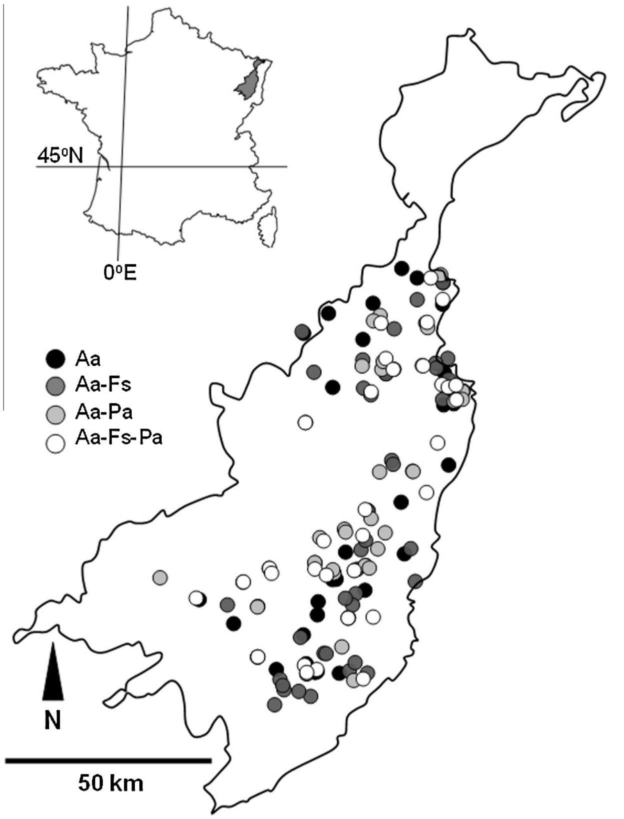

**Fig. 1.** Geographical location of the 151 sampled stands in the cristalline Vosges Mountains (northeastern France). Aa: pure *Abies alba* stands; Aa–Fs: mixed *Abies alba* and *Fagus sylvatica* stands; Aa–Pa: mixed *Abies alba* and *Picea abies* stands; Aa–Fs–Pa: mixed *Abies alba, Fagus sylvatica* and *Picea abies* stands.

To test if facilitation increased with increasing local constraints, three climatic conditions were taken into account. The first one corresponded to the low elevation and dry-warm conditions with mean July precipitation (*P* July) below 85 mm and annual temperature of about 8.5 °C (mean altitude: 550 m) (mean 1961–1990). The second one was the mesic conditions with *P* July between 85 and 115 mm and annual temperature of 8 °C (mean alt.: 710 m). The last one defined high-elevation and fresh-humid climate with *P* July over 115 mm and annual temperature below 8 °C (mean alt.: 944 m) (Table 1). To avoid interactions with other local ecological conditions, the 12 sampling strata (stratum = climatic condition x stand composition) were carefully controlled according to soil properties and soil water holding capacity (SWHC in mm). Soil

**Table 1**
Mean ecological characteristics of the 12 strata and descriptive statistics of stands and *Abies alba* trees. Values are expressed as mean (standard deviation). Climatic means are from 1961 to 1990. *P* July: precipitation of July (mm); $T_{mean}$: mean annual temperature (°C). Alt.: Altitude in m. pH and *S*/*T* (saturation rate, in%) correspond to the organo-mineral horizon; SWHC: Soil Water Holding Capacity (mm); *G*: total basal area of the stand ($m^2$/ha); n: number of *Abies alba* in the mixture; Dia.: diameter (cm) at 1.30 m; Ht.: total height (m); Nr: number of available rings; RW: ring widths calculated for the common period 1901–2000. Aa: *Abies alba*; Fs: *Fagus sylvatica*; Pa: *Picea abies*. The last line with bold values corresponds to the sum or the mean (standard deviation) of the parameter. No significant differences have been observed within each climatic condition for *P* July, $T_{mean}$ and Alt. For pH, *S*/*T* and SWHC, all values were also comparable whatever the stratum considered (no difference at the 0.05 level). For *G*, Age, Dia, and Ht of *Abies alba* trees, different letters indicate significant differences at the 0.05 level (Bonferroni test) (no difference if no letter).

| Stratum (climate × mixture) | Nb. plots | *P* July (mm) | $T_{mean}$ (mm) | Alt. (m) | pH | *S*/*T* (%) | SWHC (mm) | *G* ($m^2$/ha) | *Abies alba* trees | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | | | *n* | Age | Dia. (cm) | Ht. (m) | Nr | RW (mm) |
| *Dry (<85)* | | | | | | | | | | | | | | |
| Aa | 8 | 75(3) | 8.5(0.6) | 526(179) | 4.2(0.4) | 33(28) | 96(65) | 45(4) ac | 26 | 115(46) | 55(11) | 31.1(5.3) a | 2403 | 2.2(1.5) |
| Aa–Fs | 8 | 78(5) | 8.3(0.6) | 566(131) | 4.0(0.3) | 18(11) | 95(51) | 44(5)c | 24 | 102(15) | 60(11) | 33.7(5.3) ab | 2202 | 2.5(1.6) |
| Aa–Pa | 7 | 74(3) | 8.5(0.7) | 510(143) | 4.2(0.4) | 25(9) | 87(57) | 52(13)b | 22 | 109(18) | 61(9) | 35(3.1) b | 2105 | 2.5(1.6) |
| Aa–Fs–Pa | 7 | 78(5) | 8.2(0.6) | 565(117) | 4.2(0.6) | 27(28) | 86(36) | 51(4) ab | 18 | 109(11) | 60(10) | 34.4(3.3) ab | 1759 | 2.3(1.4) |
| *Mesic [85–115]* | | | | | | | | | | | | | | |
| Aa | 20 | 99(9) | 8(0.9) | 687(147) | 4.4(0.4) | 41(28) | 86(31) | 51(8) ac | 65 | 106(24) | 61(10) a | 31.9(3.7) ad | 5980 | 2.6(1.4) |
| Aa–Fs | 22 | 98(8) | 7.7(0.8) | 749(147) | 4.2(0.4) | 24(21) | 87(30) | 45(7) b | 64 | 110(21) | 58(10) ab | 32.7(4.2) ac | 5964 | 2.4(1.5) |
| Aa–Pa | 16 | 99(8) | 7.9(0.7) | 665(137) | 4.2(0.5) | 29(25) | 86(31) | 54(ll)c | 49 | 110(28) | 60(9) ab | 34.1(3.3) be | 4578 | 2.5(1.4) |
| Aa–Fs–Pa | 14 | 98(8) | 7.9(0.9) | 740(174) | 4.1(0.4) | 24(22) | 87(21) | 46(9) ab | 42 | 100(15) | 55(10) b | 30.4(4.1) d | 3841 | 2.4(1.4) |
| *Humid (>115)* | | | | | | | | | | | | | | |
| Aa | 14 | 125(5) | 7.7(0.6) | 951(84) | 4.1(0.4) | 21(23) | 82(30) | 49(7) a | 46 | 112(16) a | 62(10) | 31.2(3.3) | 4474 | 2.6(1.4) |
| Aa–Fs | 16 | 127(6) | 7.5(0.7) | 944(99) | 4.2(0.4) | 24(21) | 77(30) | 45(8) b | 43 | 137(30) b | 65(13) | 30.9(5.7) | 4193 | 2.0(1.3) |
| Aa–Pa | 8 | 121(6) | 7.1(0.5) | 969(77) | 4.2(0.4) | 30(20) | 99(32) | 55(7) c | 25 | 117(36) a | 58(11) | 30.8(3.2) | 2361 | 2.2(1.1) |
| Aa–Fs–Pa | 11 | 124(4) | 7.5(0.7) | 916(86) | 4.4(0.3) | 31(19) | 93(35) | 50(8) ac | 32 | 142(39) b | 65(11) | 32.5(5.3) | 3176 | 2.1(1.3) |
| | **151** | **103(19)** | **7.9(0.8)** | **752(199)** | **4.2(0.4)** | **28(23)** | **87(36)** | **49(9)** | **456** | **113(26)** | **60(11)** | **32.2(4.3)** | **24,991** | **2.4(1.5)** |

fertility was assessed from floristic relevés, humus forms and chemical analyses from soil trenches for each sampled plot of 0.1 ha (Pinto et al., 2007, 2008). Based on textural properties, depth and percentages of coarse element of each soil horizon, SWHC was calculated in each plot (soil depth of 1 m). Soils are acidic (pH ranging from 4.0 to 4.4) with a low mineral availability (*S*/*T*% between 18 and 41) and a mean SWHC (from 77 to 98 mm). No significant differences (at the $p = 0.05$ level) has been observed between strata (Table 1).

For each plot, height and diameter were inventoried for all trees of diameter greater than 17.5 cm at 1.3 m (d.b.h) and stand basal area (*G* in $m^2$/ha) calculated. The nine largest trees were identified regardless of their species and ordered according to decreasing d.b.h. For each species, the three trees closest to the first, fifth and ninth trees were cored at breast height (one core per tree). Depending on stand composition (pure or mixed with one or two species), three, six or nine cores were taken per plot. The 151 sampled plots (456 cored *A. alba*) were finally assigned to the 12 strata to reach 7–22 plots per stratum (Table 1). Thus, in each stratum, the number of cored *A. alba* ranged from 18 to 65. As observed by Pinto et al., 2008, mixture with *P. abies* tended to increase the height of *A. alba* (significant differences under dry and mesic conditions) (Table 1). For diameters, no significant difference was observed between the three climatic conditions (mean: 60 cm). Concerning ages, the two mixed stands with *F. sylvatica* under humid conditions were older than other stands (139 years against 110 years). Stand basal area (*G*) were comparable between climatic conditions and averaged 49 $m^2$/ha. However, comparatively with pure stands, *G* tended to be slightly higher in mixed Aa–Pa stands ($\Delta = +5.3$ $m^2$/ha) and lower in mixed Aa–Fs ($\Delta = -3.7$ $m^2$/ha) within each climatic condition (Table 1).

### 2.2. Ring-width measurements and chronologies statistics

The 43,036 ring widths were measured with the image analysis system WinDendro 6.3a (Regent Instruments, 1996). For each stratum, the individual ring widths series were carefully measured and cross-dated afterwards by progressively detecting regional pointer years. Methods and thresholds to define pointer years are still a subject of debate and literature gives various approaches (Cropper, 1979; Becker, 1989; Rolland et al., 2000; Schweingruber and Nogler, 2003; Neuwirth et al., 2007; Bijak, 2008). Bijak (2008) showed that an application of more strict conditions in pointer year determination (i.e. higher threshold values) results in smaller numbers of pointer years. This author also underlines that in most studies the choice of a particular threshold is rather subjective and highly depends on the target of the study. Here, we used the method developed by Becker (1989) and largely used since (Lebourgeois et al., 2010b; Mérian and Lebourgeois, 2011a,b). Three conditions must be fulfilled to define pointer years: (i) the absolute radial growth variation between two consecutive years must be at least 15%, (ii) calculation must be performed on at least ten trees and (iii) at least 70% of the cross-dated trees must have the same behaviour. The radial growth variation (RGV%) expresses to which extend the ring of the current year is narrower (negative value) or wider (positive value) than the previous one. RGV% was calculated using the following equation:

$$\mathrm{RGV\%} = 100 \times \left(\frac{\mathrm{RW}_n - \mathrm{RW}_{n-1}}{\mathrm{RW}_{n-1}}\right)$$

where $\mathrm{RW}_n$ is the ring width of the year *n*, and $\mathrm{RW}_{n-1}$ the ring width of the previous year. Thus, a pointer year is a year for which at least 70% of the cross-dated trees present a RGV% of at least 15%. Absolute dating was checked by the application INTERDAT (Becker, 1989) which identifies locations within each ring series that may have erroneous cross-dating. The three restrictive conditions applied in this method strongly limit the appearance of “false” pointer years. Moreover, pointer years defined with the Becker’s method are highly comparable with pointer years calculated by other authors and methods (Rolland et al., 2000; Schweingruber and Nogler, 2003).

Using the R software (R Development Core Team, 2010) and the “dplR” package (Bunn, 2010), the tree ring series were computed on the maximum period common to all strata (1901–2000) 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, we calculated the expressed population signal (EPS) to quantify the degree to which the chronology expressed the population chronology (Wigley et al., 1984). The EPS was defined as:

$$\mathrm{EPS} = \frac{rbt}{rbt + \frac{1-rbt}{N}}$$

where $N$ is the number of cored trees per plot and $rbt$ the mean inter-tree correlation (Briffa and Jones, 1990). EPS estimates the proximity between the theoretical population chronology and the chronology obtained by averaging the $N$ sampled individual chronologies by reducing the uncommon variability of the $N$ chronologies from $1 - rbt$ sampled $(1 - rbt)/N$. Thus, EPS highly depends on $N$ and yields 1 when the growth chronology mirrors the population signal. The mean sensitivity and the first-order auto-correlation coefficient were also calculated for each tree and averaged per stratum to measure the year-to-year variability and the influence of growth of the previous year on the current year growth, respectively (Table 2).

Dendroclimatological studies aim to estimate the climate sensitivity of a target population from a sample, i.e. a finite number of cored trees accurately selected to be as representative as possible of the population. The accuracy of both regional chronology and climate–tree growth relationships increases with sampling effort (Mérian and Lebourgeois, 2011a). Indeed, growth chronology built with a reduced number of trees leads to a systematic increase of the growth chronology variance (Mérian et al., 2013), which induces an underestimation of the climate sensitivity and a risk of estimating “false” non-significant correlations (Mérian et al., 2012). Thus, to avoid misestimating climate-tree growth relationships owed to an unbalanced sampling among strata (18–65 cored trees), chronology variance and bootstrapped correlation coefficients were corrected by EPS values with the method proposed by Mérian et al., 2013.

### 2.3. Climatic data and soil water balance modelling

Over the period 1901–2000, mean monthly temperature ($T_{\mathrm{mean}}$) and precipitation ($P$) data were computed per stratum from local and homogenized series gathered in the meteorological stations of the French National Climatic Network Météo-France (45 stations; $T_{\mathrm{min}}$ and $T_{\mathrm{max}}$ not available for the whole period) (Moisselin et al., 2002). Soil water balance was calculated using SWHC values and climatic data. The Thornthwaite formula was chosen to compute soil water balance (Thornthwaite and Mather, 1955) because this method gives accurate estimations of monthly water content fluctuations with a limited number of parameters (Piedallu et al., 2012). This method allows estimating monthly water content fluctuations driven by precipitation ($P$) and potential evapotranspiration (PET). When evapotranspirated water exceeds $P$, part of the water demand is supplied by soil moisture, which decreases soil water content (SWC) in a manner that follows an exponential negative curve. The actual evapotranspiration (AET) is the amount of water that can be evaporated and transpired given the level of soil water availability. AET becomes lower than PET when the amount of water remaining in the soil decreases. A soil water surplus (SWS) appears when precipitation offset PET and SWC variations. A soil water deficit (SWD) appears when the evaporative demand is not met by the available water (Piedallu et al., 2012). SWC calculation is based on the difference between $P$ and PET for a given month $t$:

- If $P_t \geqslant \mathrm{PET}_t$, then:
  - $\mathrm{SWC}_t = \mathrm{MINIMUM}(\mathrm{SWC}_{t-1} + P_t - \mathrm{PET}_t; \mathrm{SWHC})$
  - $\mathrm{AET}_t = \mathrm{PET}_t$
  - $\mathrm{SWD}_t = \mathrm{PET}_t - \mathrm{AET}_t = 0$
  - $\mathrm{SWS}_t = P_t - \mathrm{PET}_t - (\mathrm{SWC}_t - \mathrm{SWC}_{t-1})$
- If $P_t < \mathrm{PET}_t$, then
  - $\mathrm{SWC}_t = \mathrm{SWC}_{t-1} \times \exp\left(\frac{P_t - \mathrm{PET}_t}{SWHC}\right)$
  - $\mathrm{AET}_t = P_t - (\mathrm{SWC}_t - \mathrm{SWC}_{t-1})$
  - $\mathrm{SWD}_t = \mathrm{PET}_t - \mathrm{AET}_t$
  - $\mathrm{SWS}_t = 0$

In the studied climatic contexts, SWD mainly occurred during late spring and summer months (June–September) (Fig. 2). For the other months, the evaporative demand was usually largely counterbalanced by precipitation leading to SWS.

**Table 2**

Summarized pointer years and chronology statistics of *Abies alba* for the 12 strata on the period 1901–2000. RGV%: relative growth variation (%); Nb.: number of pointer years; MS and AC1: mean sensitivity and first order autocorrelation of master chronologies; EPS: Expressed population signal; Aa: pure *Abies alba* stands; Aa–Fs: mixed *Abies alba* and *Fagus sylvatica* stands; Aa–Pa: mixed *Abies alba* and *Picea abies* stands; Aa–Fs–Pa: mixed *Abies alba*, *Fagus sylvatica* and *Picea abies* stands.

| Stratum (mixture × climate) | Total Nb. of pointer years | Negative pointer years | | Positive pointer years | | Statistics | | |
|---|---|---|---|---|---|---|---|---|
| | | Nb. | RGV% | Nb. | RGV% | MS | AC1 | EPS |
| *Dry (<85)* | | | | | | | | |
| Aa | 24 | 12 | −29 | 12 | 66 | 0.181 | 0.404 | 0.878 |
| Aa–Fs | 15 | 5 | −28 | 10 | 46 | 0.138 | 0.446 | 0.805 |
| Aa–Pa | 15 | 7 | −28 | 8 | 83 | 0.160 | 0.375 | 0.799 |
| Aa–Fs–Pa | 17 | 10 | −29 | 7 | 43 | 0.158 | 0.393 | 0.759 |
| Mean | 18 | 8 | −29 | 9 | 59 | 0.159 | 0.405 | 0.810 |
| *Mesic [85–115]* | | | | | | | | |
| Aa | 14 | 6 | −27 | 8 | 48 | 0.124 | 0.310 | 0.902 |
| Aa–Fs | 9 | 5 | −27 | 4 | 40 | 0.120 | 0.500 | 0.918 |
| Aa–Pa | 14 | 8 | −29 | 6 | 41 | 0.139 | 0.326 | 0.909 |
| Aa–Fs–Pa | 12 | 7 | −27 | 5 | 40 | 0.125 | 0.316 | 0.858 |
| Mean | 12 | 6 | −28 | 6 | 42 | 0.127 | 0.363 | 0.897 |
| *Humid (>115)* | | | | | | | | |
| Aa | 13 | 6 | −33 | 7 | 42 | 0.133 | 0.453 | 0.925 |
| Aa–Fs | 10 | 5 | −34 | 5 | 44 | 0.133 | 0.452 | 0.912 |
| Aa–Pa | 11 | 5 | −32 | 6 | 36 | 0.137 | 0.507 | 0.910 |
| Aa–Fs–Pa | 10 | 6 | −31 | 4 | 43 | 0.128 | 0.349 | 0.864 |
| Mean | 11 | 5 | −32 | 6 | 42 | 0.133 | 0.440 | 0.903 |

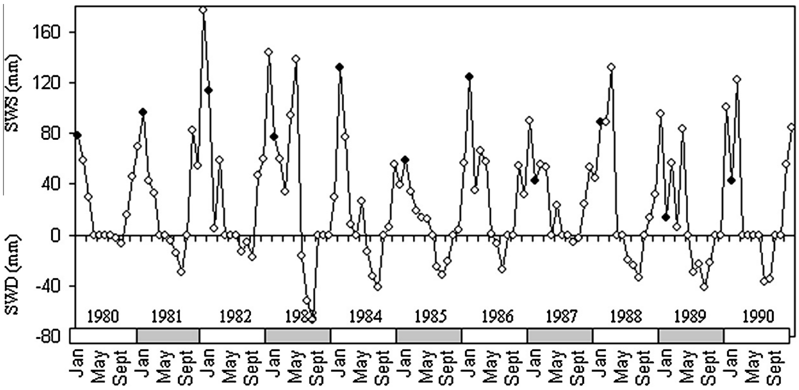

**Fig. 2.** Example of soil water dynamic for the period 1980–1990 for the pure and dry *Abies alba* stratum (SWHC: 96 mm). SWS: soil water surplus (mm); SWD: Soil Water Deficit (mm) (see text for details). Each filled circle represents January.

### 2.4. Statistical analysis

Climate–tree growth relationships over the 100-year period were investigated per stratum through the calculation of bootstrapped response functions using the growth chronology as dependent variable (Guiot, 1991) and 28 monthly climatic regressors: 14 $T_{\mathrm{mean}}$, 6 SWD (previous August and September and current June to September) and 8 SWS (other months) values, organised 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 (Zang and Biondi, 2012). To detect to which extent climate–tree growth relationships differed between mixtures and local xericity, principal component analyses (PCA) were performed on both pointer years (matrix: rows = strata; columns = pointer years) and bootstrapped response function coefficients (matrix: rows = strata; columns = bootstrapped correlation coefficients). PCA were calculated from variance–covariance matrix since descriptors were of the same kind

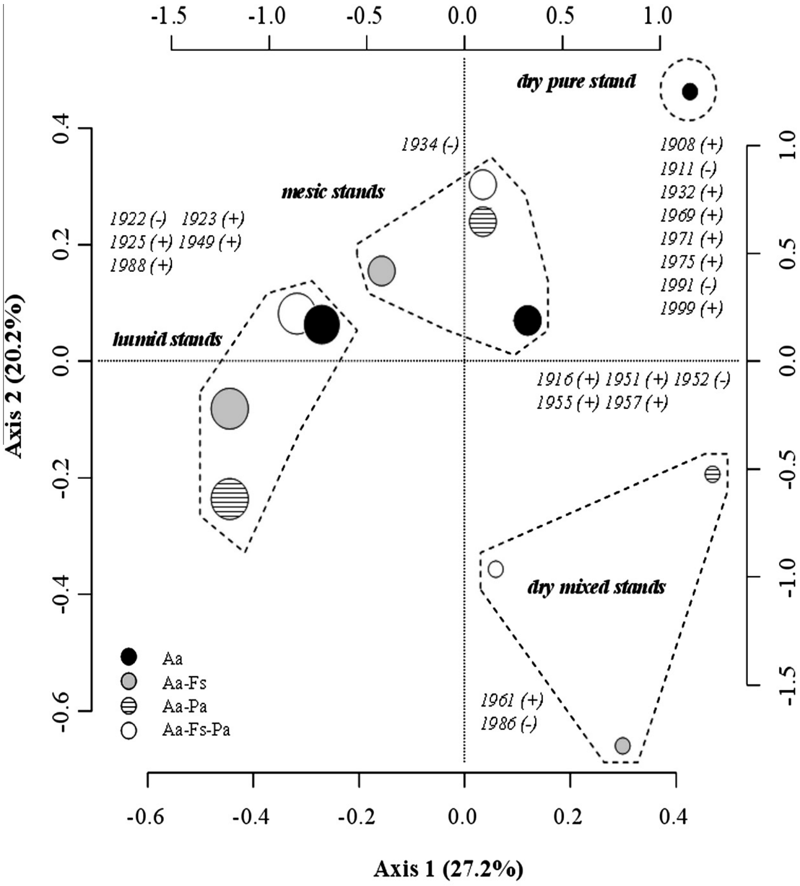

**Fig. 3.** Scatter plots of principal component analysis (PCA, axes 1 and 2) performed on the 44 pointer years (presence/absence). To improve the readability of the figure, only the most differential pointer years are written. (+): positive pointer years; (−) negative pointer years. Aa: pure *Abies alba* stands; Aa–Fs: mixed *Abies alba* and *Fagus sylvatica* stands; Aa–Pa: mixed *Abies alba* and *Picea abies* stands; Aa–Fs–Pa: mixed *Abies alba, Fagus sylvatica* and *Picea abies* stands. The size of the circle indicates the mean level of July precipitation over the period 1961–1990; small circle: dry (<85 mm); medium circle: mesic [85–115] mm; big circle: humid (>115 mm).

and shared the same order of magnitude (Legendre and Legendre, 1998). Each stratum was then characterised by its position on the components. PCA analyses were performed with the statistical software S-Plus 2000.

## 3. Results

### 3.1. Response to extreme events

From 1901 to 2000, the number of pointer years averaged 14 (from 9 to 23 between the 12 strata) which corresponded to the classical range of 1 or 2 pointer years per decade (Becker, 1989; Bert and Becker, 1990; Desplanque et al., 1998; Lebourgeois et al., 2010b) (Table 2 and Supplementary File 1). Three negative years have been observed in at least 11 strata (1948, 1956, 1976) and four in at least 8 strata [1922 (−), 1923(+), 1925 (+), 1977 (+), 1998 (+)]. Most of pointer years corresponded to dry and warm climatic conditions (e.g. 1934, 1952, 1962, 1976) and frost years (1956, 1986) (related climatic data not shown), confirming the high sensitivity of *A. alba* to drought and frost. The ordination along the first PCA axis performed on pointer years explained 27.2% of the total variance and highly discriminated dry conditions from mesic and humid ones (only negative coordinates) (Fig. 3). *A. alba* growing under the driest climate displayed higher mean sensitivity values and number of pointer years compared with other conditions confirming the importance of local xericity on tree growth response to climate (Supplementary File 1, Table 2 and Fig. 4). Under dry conditions, mixture also modulated response to climate, *A. alba* growing in mixture exhibiting lower mean sensitivity values and number of pointer years (Table 2). Among the ten drought-induced negative pointer years observed in pure *A. alba* stands, only 6, 5 and 2 were respectively observed in the mixture Aa–Fs–Pa, Aa–Pa and Aa–Fs (Fig. 4). When comparing the six common pointer years of Aa and Aa–Pa–Fs, the mean relative growth variation (mRGV) was respectively −30.3% (standard deviation: 5.2) and −23.9% (5.9) (difference: 6.4 points; *p-value* = 0.085). Similarly, for Aa and Aa–Pa, the mRGV was respectively −30.3% (5.8) and −28% (7.1) (*n* = five pointer years, no significant difference). Under

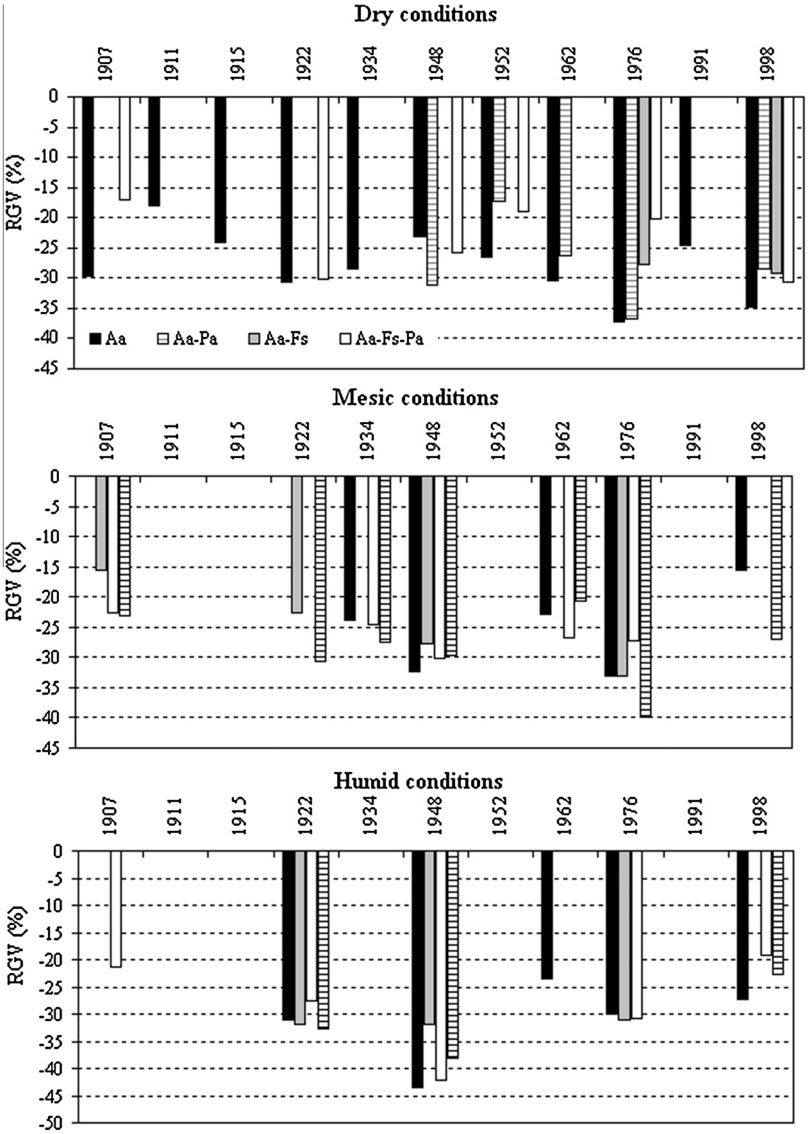

**Fig. 4.** Relative growth variation (RGV in%) of *Abies alba* for pointer years characterised by extreme drought. Stand composition abbreviations identical to Fig. 3. 1907, 1934, 1952, 1962, 1998: drought in June–July; 1911, 1915, 1976, 1991: from June to September. Dry conditions: <85 mm for July precipitation (mean 1961–1990); mesic conditions: [85–115] mm; humid conditions: >115 mm.

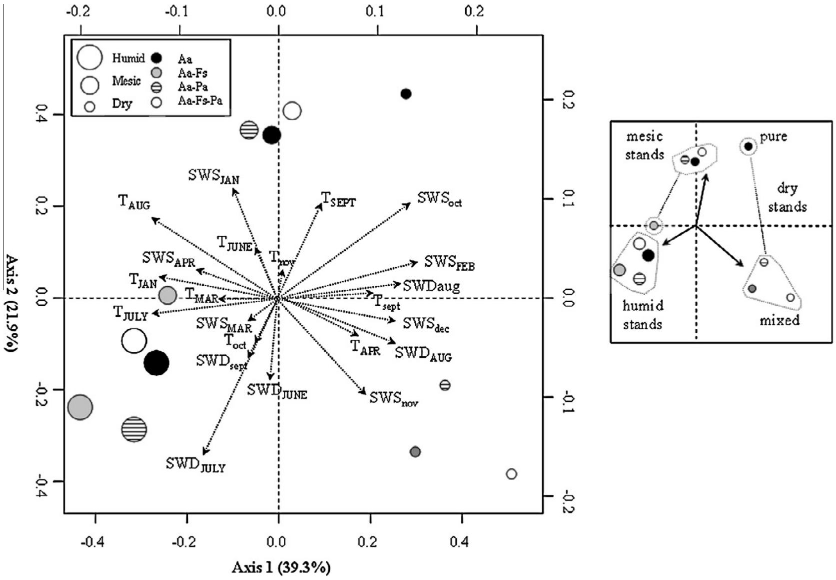

**Fig. 5.** Scatter plots of principal component analysis (PCA, axes 1 and 2) performed on the bootstrapped response function coefficients. To improve the readability of the figure, only the most influencing climatic parameters are showed. Legend and abbreviations identical to Fig. 3. For climatic parameters, the capital letters correspond to the current year (previous year otherwise). *T*: mean temperature; SWS: soil water surplus; SWD: soil water deficit (see text for details).

mesic and humid climate, *A. alba* exhibited rather similar feature with no clear strong difference according to mixture (Supplementary File 1, Table 2 and Fig. 4).

### *3.2. Sensitivity to climate and its modulation by ecological conditions and mixture*

The PCA axes 1 and 2 explained 61.2% of the total variance and the key factors appeared to be linked to previous autumn, winter and current summer conditions (Figs. 5 and 6). As already observed for pointer years, the ordination along the first axis highly discriminated stands growing under dry conditions (negative coordinates) from those growing under mesic and humid conditions (positive coordinates). Under humid climate, ring width was negatively influenced by previous temperature in September and soil water surplus in December, whereas high winter temperature (January and February) often favoured it. During current August, warm conditions strongly enhanced radial growth while great SWD reduced it (Fig. 6). Under mesic conditions, the response to winter temperature appeared rather similar but the role of temperature in previous September, soil water deficit during the whole summer (June to August) and August temperature increased. Under mesic and humid conditions, *A. alba* displayed a rather similar response whatever the mixture considered (Fig. 6).

The pattern on dry sites was found to differ amongst stand compositions (Fig. 6). Indeed, pure *A. alba* stands highly and significantly responded to summer conditions through negative correlations with SWD (previous September and current June, July) and positive ones with temperature (August). In mixed stands, response patterns highly changed with an increasing role of April temperatures and a decreasing effect of summer soil water deficit (bootstrapped response coefficients significant at the $p = 0.010$ level only in Aa–Pa stand).

## 4. Discussion

### *4.1. Global response pattern and effects of local climatic conditions*

The global pattern showed that late previous and current summer months were the main periods for *A. alba* radial growth. Thus, *A. alba* appeared particularly sensitive to lag-effects of late summer conditions (here mainly September) and current summer soil water deficit (June, July or August) and temperature (mainly August). Our results agreed with climate responses observed throughout its distribution area. Indeed, similar feature have been already pointed out in the French mountains (Bert and Becker, 1990; Desplanque et al., 1998; Rolland et al., 2000; Lebourgeois et al., 2010b, 2012; Cailleret and Davi, 2011), in eastern Carpathian (Kern and Popa, 2007; Bouriaud and Popa, 2009), in the Swiss and Italian Alps (Battipaglia et al., 2009; Carrer et al., 2010) and in Spanish Pyrenees (Macias et al., 2006; Pasho et al., 2011). This drought sensitivity can be linked with the ecophysiological functioning of this species and particularly its low water-use efficiency and its drought-avoidance strategy (Aussenac, 2002). Soil water deficit negatively affected tree-ring formation by inhibiting cell division and enlargement (Gricar and Cufar, 2008) and by reducing carbon assimilation via stomatal control of photosynthesis and transpiration. Disruption in seasonal dynamics of carbohydrate storage (Michelot et al., 2012), root elongation or bud formation (Morin et al., 2007) could explain the negative correlation with previous late summer conditions.

Our findings also supported common knowledge, such as sensitivity to temperature at high elevations and to drought-stress at low altitude or under dry conditions. Indeed, significant response to warm winter temperature (January–February) was mainly observed under humid conditions which also corresponded to the highest altitudes in our study (>900 m). This result was also in agreement with the role of winter temperature in primary growth already seen for *A. alba* in the same ecological contexts (Pinto et al., 2008). Increasing rate of winter photosynthesis (Guehl, 1985), earlier start of cambial activity resumption (Rossi et al., 2007) or decreasing embolism (Cruiziat et al., 2002) under warmer conditions have been often listed to explain this positive correlation. Snow cover might be evoked, since warmth reduce snow accumulation or accelerate melt. This favours soil warming and water availability, which promote the onset of physiological activities and lengthen the growing season. Concerning summer drought-stress, the response to soil water deficit varied with altitude (and thus precipitation). In low elevation and dry sites (< 600 m; *P* July <85 mm), *A. alba* pure stands highly responded to early summer

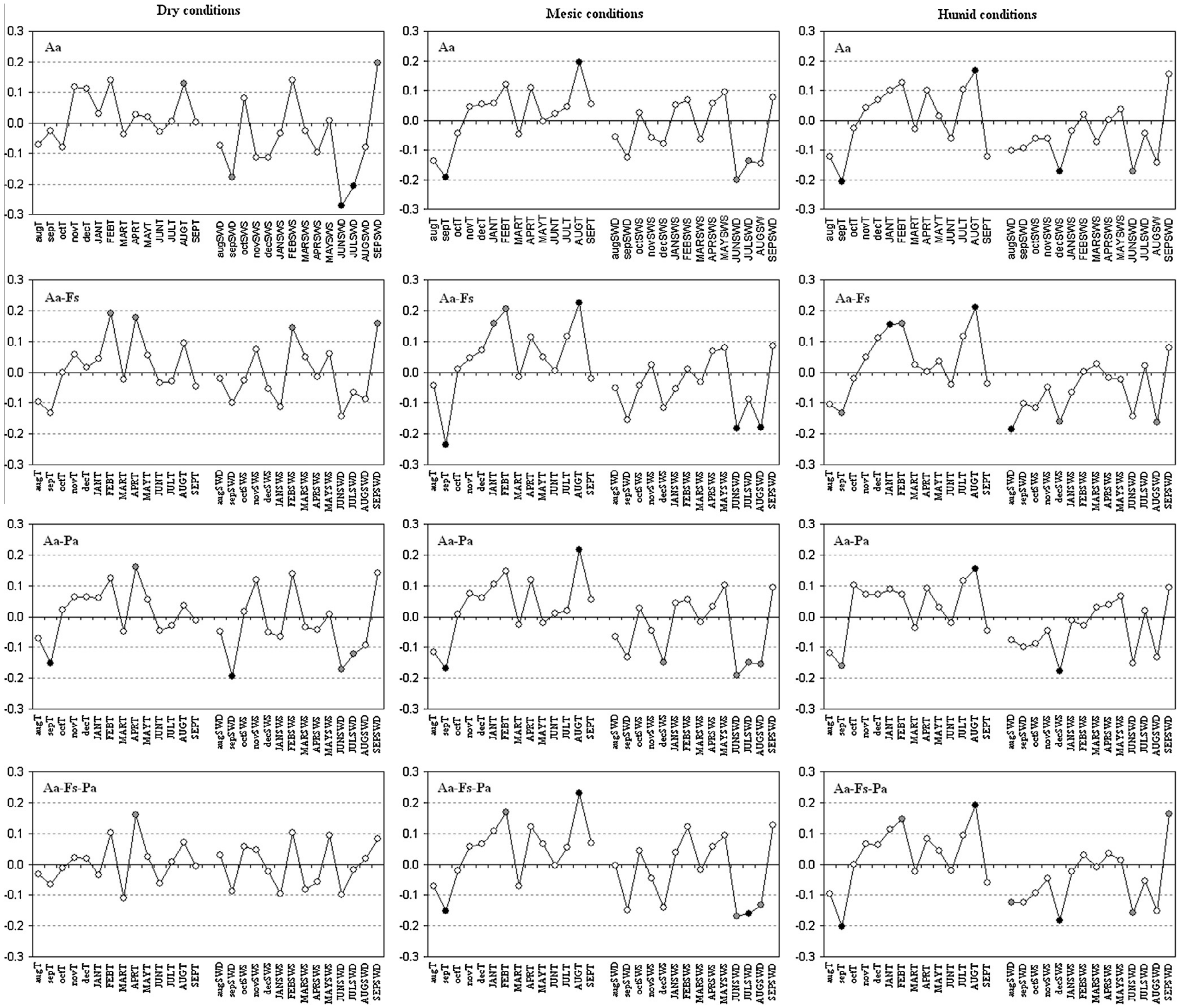

**Fig. 6.** Bootstrapped response coefficients (BRC) for the 12 strata over the period 1901–2000. Black and grey circles indicate BRC significant at the levels of 0.05 and 0.10 respectively. Abbreviations identical to Fig. 5.

drought (June–July). Increasing precipitation delayed summer drought in time, putting the response back to August.

### 4.2. Mixture effect on *A. alba* climatic responses

For trees, the balance between negative and positive interactions is particularly complex to analyse as they display long live span (Filipescu and Comeau, 2007; Cavard et al., 2011). Thus, studies based on the growth for mature tree are scarce and give rather contradictory results. Whereas facilitative interactions were reported between *Abies* and *Pinus* at timberline in highly stressful conditions in the northern Rocky Mountains (Callaway, 1998), Coomes and Allen (2007) did not unearth clear evidence to facilitation for *Nothofagus* in the New Zealand Alps along an altitudinal gradient. In their recent study led on 16 forest trees species in French eastern mountains (Jura and Vosges), Kunstler et al. (2011) showed that competitive importance increased under non-restrictive habitats (i.e. high water budget or high degree-days sums) particularly for shade-tolerant species (such as *A. alba* and *F. sylvatica*). On the other hand, none of the 16 species demonstrated a shift to facilitation.

In our study, to accurately compare the response to climate according to mixture, all other sources of variation were carefully controlled across the three climatic strata. The similar values of soil water availability, soil fertility, tree-age and size (Table 1) allowed highlighting that local climatic conditions highly influenced the importance of complementarity in mixed forest ecosystems. Indeed, mixture changed *A. alba* response to summer drought but only under the most limiting conditions. This result, in agreement with the stress gradient hypothesis, suggests that the facilitative processes between *A. alba* and other species increase when resources are limited. In our study, the loss of sensibility of *A. alba* under the driest conditions may be a result of improved soil water availability for this species. In mixed stands, the identity of the species in the mixture plays a key role and facilitative processes are expected to increase for species with different growth patterns and ecological demands (Cavard et al., 2011). This could explain why the low response of *Abies* to summer drought was particularly evident when mixed with *Fagus* and not with *Picea*. On the other hand, under low-restrictive conditions (especially mesic climate), competition for water remained high which maintained a high sensitivity of *A. alba* to summer drought.

The weak differences in stand basal area (*G*) between mixtures cannot explain our results (Table 1). Indeed, all *G* values were high (44 to 55 $m^2$/ha) and absolute mean differences in *G* between pure and mixed stands averaged only 8% (Table 1) which appeared too low to strongly influence tree growth sensitivity to climate (Bréda et al., 1995; Misson et al., 2003; Kohler et al., 2010). Even if the modulation of climate sensitivity by *G* is still debated, high *G* values have been frequently associated with greater drought-induced growth reductions (Cescatti and Piutti, 1998; Misson et al., 2003; Novak et al., 2010) and lower resilience after extreme drought (Kohler et al., 2010; Martinez-Vilalta et al., 2012). Thus, if we hypothesize that such differences in *G* modify tree-ring sensitivity to climate, we should have observed greater drought sensitivities with higher *G* values and lower responses with lower values, whatever the mixture considered and particularly under the driest conditions. As our results contradicted this hypothesize (Table 1 and Fig. 6), it can be concluded that differences in *G* values do not interfere with the mixture effect.

Differences in sensitivity to climate between pure and mixed stands can be related to different strategies of water extraction by roots, as *A. alba* has a deeper root system than those of *F. sylvatica* and *P. abies* (Konôpka, 2001; Schmid and Kazda, 2001; Nicoll et al., 2006). A deeper fine rooting favours water (and nutrients) uptake throughout the growing season, especially during dry years (Leuschner et al., 2004; Bréda et al., 2006). Despite a growing body of literature on mixed stands, studies on root production and architecture according to mixture remain scarce, particularly for *A. alba*. Recent studies suggested that European beech is more drought-tolerant than Douglas-fir (Reyer et al., 2010), Norway spruce (Schmid and Kazda, 2001; Schume et al., 2004; Bolte and Villanueva, 2006) or Sessile oak (Jonard et al., 2011) in mixed stands through changes in fine rooting characteristics (i.e., expansion of fine roots in deeper layers and superficial root concentration of the co-existing species) or rainfall portioning. In *Populus* – *Picea* – *Abies* mixed stands, Brassard et al. (2011) founded that fine root productivity was higher in mixed than pure *Populus* stands and that mixed-species stands had lower horizontal and higher vertical fine root biomass heterogeneity, respectively, indicating that soil volume is more fully explored by fine roots in mixture. In *Abies*–*Fagus* stands, *A. alba* influenced topsoil moisture more strongly than did beech; upper layers soil water content highly decreasing with increasing fir density within the stand (Paluch and Gruba, 2012). Increasing water input due to smaller interception by beech foliage (Aussenac, 2000) and higher stemflow by smooth bark and funnel-like branching architecture (Levia and Frost, 2003; Schume et al., 2004) could explain these observations. On the other hand, in *Picea*–*Abies* stands, the tendency of soil moisture to decrease as local density increased was approximately twice stronger for *Picea* compared to *Abies*, which could be linked to a higher interception efficiency of Norway spruce canopies (Paluch and Gruba, 2012).

The higher sensitivity of *A. alba* to April temperature in mixed low-altitude stands may be related to the heterogeneity of the canopy structure or to differences in leaf development. For example, when mixed with beech, it can be hypothesized that *A. alba* takes advantage of increasing temperature and radiation within its crown linked to the absence of beech foliage in early spring (Ishii and Asano, 2010; Lebourgeois et al., 2010a). This can hasten forcing temperature accumulation and thus lengthen the growing season by hastening leaf unfolding.

The lower drought sensitivity at low-altitude and in dry and mixed stands could have important consequences for forest management with regard to the predictions of climate change toward drier conditions (Planton et al., 2008). Indeed, the succession of dry years affects tree growth for several consecutive years and might induce forest decline and tree mortality (Allen et al., 2010). Decreasing soil water constraints by mixture could counteract environmental changes and partly prevent forest ecosystems from decline in the future. Although climate change has already influenced species distribution (Lenoir et al., 2008; Bertrand et al., 2011) and enhanced tree growth (Way and Oren, 2010) at high altitudes, forests in such conditions may also suffer from drought in the future which could reduce their growth and alter their vitality. Hence, foresters could already favour mixture to better cope with future climatic conditions. In our study, the mixture with *F. sylvatica* appeared more “interesting” than that with *P. abies*, the presence of *Fagus* deceasing *Abies* sensitivity to exceptional drought. This confirms that the benefits of the mixture are all the more effective that the species display differentiated ecophysiological traits and complementary ecological niches (Hooper et al., 2005).

## 5. Conclusion

Our analysis evidences that stand composition can modify tree response to climate in western European mountains. In agreement with the stress gradient hypothesis and the principle of niche complementarity, mixture reduces *A. alba* sensitivity to late spring and summer drought by decreasing competition for water resource under the most limiting conditions. Different facilitation processes can be evoked to explain mixture effects, such as changes in root biomass, in architecture, in water input by stemflow or in rainfall interception and portioning. Such composition-related forest functioning is of interest to reduce the impact of climatic change on tree growth and vitality by adapting forest management. Mixture may help forest tree species to survive in areas where their distribution in pure stands is questioned under future climatic conditions.

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## 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.2013.04.003.

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