



Differing growth responses to climatic variations and soil water deficits of *Fagus sylvatica*, *Quercus petraea* and *Pinus sylvestris* in a temperate forest

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ABSTRACT

In addition to global warming, the frequency and the intensity of droughts will probably increase in central and southern Europe. Resulting climate changes and soil water deficits could alter tree growth, according to sensitivity of each species. The aim of this study was to compare the growth response of three European species (*Fagus sylvatica*, *Quercus petraea* and *Pinus sylvestris*) to climatic variations and soil water deficits in the same temperate forest. Three mature stands per species were sampled to obtain earlywood, latewood and total ring chronologies from 1960 to 2007. Climate–growth relationships were established by bootstrapped correlations and response function analysis. Monthly bioclimatic regressors were simulated by a physiological water balance model that used daily climatic data and stand parameters to estimate soil water deficits.

Our results highlighted a common sensitivity to precipitation from May to July for the dominant tree growth of the three species but also differences in the species vulnerability to climate and soil water deficits. Beech was the most sensitive species to the climatic conditions of the current growing season. Beech growth was positively correlated with precipitation from May to July and negatively with maximal temperatures in June and July. Oak growth was negatively correlated with minimal temperatures in the previous August and September and positively with precipitation in the previous October and December during pointer years. This led to long-term consequences for growth, probably due to carbon reserve depletion. Pine growth was positively influenced by warm December but was also vulnerable to maximal temperatures and soil water deficits from June to August. The climate in August only influenced the pine growth probably because the growing season of pine was longer than that of the deciduous species. For both oak and pine, latewood was the component that was most sensitive to climatic variations and soil water deficits. According to the study findings, an increase in the frequency and the intensity of droughts could affect the three species. Maximum summer temperatures could have negative impacts for beech and pine growth. Dry and warm autumns could lead to long-term consequences and decrease the oak growth.

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1. Introduction

In the North of France, mean temperatures may increase from 2.5 to 3.5 °C in summer and from 2 to 2.5 °C in winter in 100 years (Christensen et al., 2007). In addition to global warming, the frequency and the intensity of droughts will probably increase in central and southern Europe. Drought may induce productivity decreases in temperate forests, as was observed for ecosystem CO₂ fluxes during the drought of 2003 (Ciais et al., 2005; Granier et al., 2007; Reichstein et al., 2007). The proportion of these

decreases could be linked to intensity of soil water deficits during droughts (Granier et al., 2007). Ecophysiological processes have been found to alter tree functioning immediately after a drought (such as related to crown condition declines, root mortality or cavitation) and for some years after an extreme event, which is mainly due to carbon reserve depletion (reviewed in Bréda et al., 2006). This may have future implications for carbon storage and species distribution areas (e.g. in France, Cheaib et al., submitted). Investigation of tree growth response to past climatic variations can allow anticipating the vulnerability of each species under future climate changes.

Dendroclimatic studies show the relationships between climatic data and standardised tree-ring width indices (e.g. Fritts, 1976). They highlight the growth sensitivity of each species to monthly temperatures and precipitation. Additional physiological

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indices, such as related to soil water deficits (Zahner and Stage, 1966), are used rather than climatic data to allow biological interpretations of the growth response to climate. These indices could be better correlated with radial growth than monthly climatic variables (Foster and Leblanc, 1993) because soil water availability is a major limiting factor for tree growth. Trees growing on sites with a low available water capacity could be more sensitive to climatic variations compared to trees growing on other sites (Lebourgeois et al., 2005).

Dendroecological studies are generally focused on one species growing under extreme environmental conditions where climate–growth relationships were strong, as in mountain ecosystems (e. g. Rigling et al., 2001; Wang et al., 2006). Fewer studies compared the growth of different species under the same temperate climatic conditions. Temperate forests represent 24% of the global forest area and exhibit carbon storage equally allocated between vegetation and soil (Robert and Saugier, 2003). Our study site is a French temperate forest where we compared the tree growth response of three species (*Fagus sylvatica* L., *Quercus petraea* (Matt.) Liebl. and *Pinus sylvestris* L.) to the same climatic variations. These species are widely distributed in European temperate forests, but dendroecological studies are scarce in the French plains (e.g. Lebourgeois et al., 2010; Mérian and Lebourgeois, 2011). Moreover, they have contrasting leaf phenology and wood anatomy. Common beech is a diffuse-porous species showing growth beginning after budburst (Suzuki et al., 1996) whereas Sessile oak is a ring-porous species characterised by growth beginning prior to budburst (Bréda and Granier, 1996). Scots pine is an evergreen species, so its needles can be photosynthetically active before and during radial growth and new needle expansion. As coniferous species, pine could thus exhibit photosynthesis in winter.

The objectives of this study are as follows: (i) to identify the stand characteristics explaining between-stand differences in dominant tree growth and climate–growth relationships from 1960 to 2007, (ii) to highlight the contrasting vulnerability of the species growth to climatic variations and soil water deficits (SWD) and (iii) to determine differences between earlywood and latewood growth responses to climatic variations and SWD for oak and pine. We discuss the species vulnerability in the context of climate change predictions.

2. Materials and methods

2.1. Study site and stand selection

The study was conducted in the Fontainebleau forest, which is a large forest extending over 17,000 ha southeast of Paris (48°25'N,

2°40'E, mean altitude 120 m). This national forest is managed by the French National Forest Office (Office National des Forêts, ONF). The temperate-type climate is homogeneous over the whole forest, with a mean annual temperature of 10.6 °C and mean precipitation of 750 mm that is fairly well distributed throughout the year. The soil texture is dominated by Stampian sand mixed with loam and clay at different depths. Nine monospecific stands (three per species) were selected with a maximal distance between stands of 9 km (Table 1). The soil profiles differed between stands which leads to differences in soil fertility (Robin, 1993). In April 2008, one core was sampled at breast height in 15 dominant healthy trees per stand. To limit ageing effects on growth, the selected stands were mature, excepting the beech stand B12 (43 years old in 1960) and the pine stand P3 (20 years old in 1960). For each species, the three stands were selected to have a gradient in available water capacity (AWC) which is representative of the range of AWC in the studied forest. These gradients allow testing the influence of AWC on growth response to climate.

2.2. Measurements of stand and tree characteristics

The stand dominant height, overstory basal area and understory proportion were obtained from forest inventories performed during winter in 1994–1995 (Le Dantec et al., 2000). The leaf area index (LAI) was estimated at each stand with a canopy analyser (LAI-2000, LI-COR Inc., Nebraska, USA). From 1994 to 2000, 40 to 150 measurements, according to stand area, were performed distributed along transects below the canopy on sunny days, 2 h after sunrise or before sunset. Linearly interpolated values of incident light on three zenith angles were used (from 0° to 43°, Dufrène and Bréda, 1995). For pine, measurements were divided by 0.57 to compute hemisurface leaf area (Stenberg et al., 1994). The mean of the maximal LAI measurements performed from 1994 to 2000 was chosen as the stand LAI parameter. AWC was calculated from soil samples collected every 2 ha in 1995 by the ONF. For each soil sample, all soil horizon depths and textures were determined. The field capacity and wilting point were calculated for each horizon according to the function of Saxton et al. (1986). AWC was the sum of the horizon differences between the field capacity and wilting point (Le Maire, 2005). Soil types (IUSS Working Group, 2007) and the C/N ratio were determined from soil pits dug in January and February 2004. Organic C and N were determined in the upper organo-mineral layer by oxidation, as soils are acid (pH ranging between 4 and 5) according to the normalised method (NF ISO 14235).

With respect to tree characteristics, the diameter at breast height (DBH) was measured in the 15 sampled trees per stand in

Table 1
Mean stand characteristics: stand area, dominant height (Hd) in 1995, overstory basal area (BA) and understory proportion of the total stand basal area in 1995, maximal leaf area index (LAI) during 1994–2000, available soil water capacity (AWC), soil type and C/N of the organic layer (soil horizon A) in 2004. Mean characteristics of the sampled trees in 2008: age and diameter at breast height (DBH).

Mean stand characteristics									Sampled tree characteristics		
Stand	Species	Stand area (ha)	Hd (m)	BA (m ² ha ⁻¹)	Understory (%) ^a	LAI (m ² _{leaf} m ⁻² _{soil})	AWC (mm)	Soil type	Soil C/N	Age (years)	DBH (cm)
B4	<i>F. sylvatica</i>	8.6	33	29.4	7.8	5.6	141	Entic Podzol to Luvisol	27.0	114	66.2
B9	<i>F. sylvatica</i>	11.8	33	29.8	9.2	4.1	136	Luvisol	20.0	142 ^b	61.7
B12	<i>F. sylvatica</i>	10.4	23	17.7	12.0	5.5	101	Haplic Albeluvisol	18.7	92	49.1
O3	<i>Q. petraea</i>	9.8	30	35.5	11.7	6.3	125	Haplic Albeluvisol	18.7	179 ^b	63.9
O4	<i>Q. petraea</i>	10.2	32	27.8	11.3	6.5	115	Haplic Albeluvisol	18.7	151 ^b	63.8
O19	<i>Q. petraea</i>	6.6	34	41.3	14.4	5.5	180	Endostagnic Luvisol	14.5	199 ^b	70.8
P3	<i>P. sylvestris</i>	4.7	23	25.6	1.3	3.7	118	Albic Podzol	20.1	68	40.2
P8	<i>P. sylvestris</i>	5.0	23	33.4	0.6	3.8	100	Ortsteinic Albic Podzol	32.3	84	45.2
P13	<i>P. sylvestris</i>	6.6	24	26.2	23.5	4.6	144	Albic Podzol	32.3	115	50.4

^a Proportion of the total stand basal area.

^b Data obtained from a previous study (Barbaroux, 2002).

April 2008. After cross-dating, the mean pine age was estimated from 8 to 15 trees per stand in the sampled cores. To have more realistic estimates of tree ages, the number of missing rings between the first ring measured and the “missed” pith at the centre of the tree were estimated by using the curvature of the innermost measured rings (Villalba and Veblen, 1997) and comparing them to concentric circles with different radii. For the other stands, the mean age of the trees was obtained using data from previous studies (Barbaroux, 2002; E Silva, 2010).

2.3. Tree-ring data and pointer years

Tree rings were measured microscopically in the sampled cores for earlywood, latewood and total ring width to the nearest 0.01 mm from 1960 to 2007 (i.e., the period of climatic data measurements) using a digitising tablet connected to a micro-computer and the tree-ring program SAISIE (Becker, unpublished). As beech is a diffuse-porous species, only the total ring widths were measured for this species. After cross-dating, 45 individual ring series for oak (15 trees in three stands), 45 for beech and 41 for pine were used. Thinning information was available for each stand from 1970 to 2007 (ONF). The lowest thinning rate was observed for the stand O3 with no thinning from 1970 to 2000. Some thinning impacted the stand tree-ring series and led to stand pointer years, especially for beech. Thus, the pointer years were identified for each species to limit the number of non-climatic pointer years. They were calculated separately for each ring component, i.e., earlywood, latewood and total ring. Relative growth variation (RGV) was calculated for each n year in each individual ring series as follows:

$$RGV = \left(\frac{W_n - W_{n-1}}{W_{n-1}} \right) * 100 \quad (1)$$

where W is the width of the considered ring component. The mean RGV by species was calculated for each ring component. The pointer years were defined for each ring component as those calendar years when at least 75% of the cross-dated trees presented the same sign of growth change (at least 10% narrower or wider than the previous year).

2.4. Tree basal area increment chronologies

The basal area increment (BAI) of earlywood, latewood and total ring were calculated for each tree using ring data and DBH from 1960 to 2007. BAI was preferred to ring width because it provides a more accurate quantification of wood production due to the continually increasing diameter of a growing tree (Rubino and McCarthy, 2000). Chronology statistics were calculated for each

stand BAI series from 1960 to 2007 (Table 2) with the COFECHA v6.06P program (Holmes, 1994). The mean sensitivity (MS) is a measure of year-to-year variability, and the first-order autocorrelation coefficient (AC) assesses the influence of the previous year's growth on the current year's growth (Fritts, 1976). Standardisation of each individual BAI series was performed using the program ARSTAN v6.05P (Cook, 1985). For all series, we used a 60-year cubic spline with a 50% frequency response, which preserved 99% of the variation within individual series at a wavelength of 19 years. Subsequently, first-order autoregressive modelling of the residuals and bi-weight robust estimation of the mean were applied (Cook and Peters, 1981).

2.5. Climatic data and simulations of soil water deficit

Mean, maximum and minimum temperatures (°C) and mean relative air humidity (%) were recorded daily at the Melun–Villaroche meteorological station (Météo-France network). Precipitation (mm) was recorded at the Fontainebleau station. The monthly means of the minimum and maximum temperatures (T_{min} , T_{max}) and monthly sums of precipitation (P) were calculated for each year from 1960 to 2007.

The daily water balance model BILJOU© (Granier et al., 1999) was used to calculate each water-flux component and the resulting daily soil water content. The intensity (I_s), starting date and duration of SWD were calculated each year for each stand. The input climatic data were daily precipitation and potential evapotranspiration (PET) calculated according to the Penman formulation (Penman, 1948). The budburst day was fixed at 20 April for oak and 25 April for beech, according to observations made by Dufrière (unpublished data), and the leaf fall day was fixed at 27 October for these two species. Pine was assumed to maintain a constant LAI and to be able to transpire throughout the year, including winter, depending on PET. Detailed soil parameterisation was performed for each stand based on descriptions from deep soil pits dug in 2004. According to the observed soil properties and the fine root distribution, two layers were defined, including 75% of fine roots for the top soil layer and 25% for the deeper one. AWC and soil density were calculated for the two soil layers based on the properties of the corresponding pedological horizons. For each stand, daily relative extractable soil water (REW) was calculated from 1960 to 2007 as:

$$REW = \frac{W_e}{AWC} \quad (2)$$

where W_e is daily extractable water. A soil water deficit is assumed to occur when REW drops below a critical threshold of 0.4 (REW_c), under which transpiration is gradually reduced due to stomatal closure (Granier et al., 1999).

Table 2

Chronology statistics of tree basal area increment (BAI) series: number of sampled trees (N), mean BAI per tree (SD), series intercorrelation (IC), average mean sensitivity (MS) and first-order autocorrelation (AC). Means were calculated for each tree from 1960 to 2007 and averaged per stand and species.

Stand	N	Total ring				Earlywood				Latewood			
		BAI (cm ²)	IC	MS	AC	BAI (cm ²)	IC	MS	AC	BAI (cm ²)	IC	MS	AC
B4	15	38.4 (11.1)	0.723	0.308	0.566								
B9	15	30.8 (6.7)	0.787	0.398	0.422								
B12	15	27.7 (6.2)	0.698	0.334	0.603								
Beech mean	45	32.3 (5.5)	0.736	0.347	0.530								
O3	15	26.3 (4.6)	0.724	0.194	0.470	10.8 (1.7)	0.220	0.185	0.417	15.4 (3.7)	0.715	0.326	0.348
O4	15	29.8 (6.7)	0.771	0.218	0.547	10.8 (2.8)	0.356	0.206	0.455	19.0 (4.8)	0.746	0.338	0.455
O19	15	30.9 (8.3)	0.693	0.209	0.550	12.8 (3.1)	0.307	0.178	0.519	18.1 (5.8)	0.685	0.348	0.430
Oak mean	45	29.0 (2.4)	0.729	0.207	0.522	11.5 (1.2)	0.294	0.190	0.464	17.5 (1.9)	0.715	0.337	0.411
P3	14	21.8 (4.7)	0.619	0.271	0.690	14.7 (3.6)	0.518	0.289	0.658	7.1 (1.5)	0.658	0.434	0.440
P8	14	17.9 (5.2)	0.584	0.272	0.674	11.9 (3.1)	0.444	0.285	0.640	6.0 (2.4)	0.601	0.489	0.377
P13	13	15.9 (4.2)	0.711	0.326	0.671	10.7 (3.2)	0.655	0.327	0.630	5.2 (1.4)	0.709	0.545	0.471
Pine mean	41	18.5 (3.0)	0.638	0.290	0.678	12.4 (2.0)	0.539	0.300	0.643	6.1 (1.0)	0.656	0.489	0.429

The intensity of SWD (I_s), which accumulates the difference between REW and REW_c , was calculated monthly or annually:

$$I_s = \frac{\sum(0.4 * AWC - W_e)}{0.4 * AWC} \quad (3)$$

2.6. Statistics and dendroclimatic analyses

All statistical analyses were performed using a statistical software package (Statistica; Statsoft, Tulsa, OK, USA). The coefficient of variation (CV, ratio of standard deviation to mean) was calculated from 1960 to 2007 to compare the mean BAI of earlywood and latewood for oak and pine. Analysis of variance was conducted to determine whether “species” was a factor that significantly influenced the mean species BAI from 1960 to 2007. Comparisons between the stand or species mean BAI, MS or AC were checked with a *t*-test at the 95% confidence level. The homoscedasticity assumption and the comparison of the interannual variation amplitudes between the species BAI were checked by a Levene-test.

Bootstrapped correlation coefficients were calculated between monthly climatic data (Tmax, Tmin and P) and the residual chronology of each stand (earlywood, latewood and total ring) with the software package DENDROCLIM2002 (Biondi and Waikul, 2004). This software calculates the statistical significance of the coefficients by calculating 95% quantile limits based on 1000 bootstrap re-samples of the data. Correlations were performed from August of the previous year ($n-1$) to August of the current year (n) from 1961 to 2007 (47 years). Analyses were conducted for two periods: 1961–2007 (47 years) and the pointer years for each species (22 years for beech, 28 for oak and 21 for pine). The bootstrapped correlation coefficients were also calculated between SWD indices and the residual chronology of each stand from 1961 to 2007. The SWD indices were I_s from June to October ($n-1$ and n) and annual SWD duration ($n-1$ and n).

Bootstrapped response function coefficients (Guiot, 1991) were calculated between monthly climatic data (Tmax or Tmin and P) and the residual chronology of each stand (EW, LW and total ring). Climatic parameters were considered from August $n-1$ to July n for the deciduous species and from September $n-1$ to August n for pine. Analyses were performed using 12 monthly Tmax or Tmin and 12 P from 1961 to 2007. Response function analyses were also

performed between monthly temperatures (Tmax or Tmin) and SWD indices and the residual chronology of each stand. The SWD indices were I_s from June to October ($n-1$ and n) and annual SWD duration (n and $n-1$). Analyses were thus performed using 12 monthly Tmax or Tmin and 12 SWD indices. Linear multiple regressions were finally performed between the significant climatic data or SWD indices resulting from the response function analyses and the residual chronology of each stand from 1961 to 2007. The adjusted R^2 obtained from these regressions accounted for the percent of the interannual variations in dominant tree growth explained by climatic (Tmax, P) or bioclimatic (Tmax, SWD indices) models.

3. Results

3.1. Interannual growth variations

The growth of the three species responded similarly to dry years (e.g. 1964, 1976, 1996), which induced a decrease in growth (Fig. 1). The interannual variations were more pronounced for beech (Levene-test, $p < 0.001$). The pointer years were different between species (Fig. 2). Considering the total ring, the proportion of pointer years was higher for oak (28) than for beech (22) and pine (21) from 1961 to 2007. There were only two pointer years for beech from 1961 to 1973 because the pointer years were different between the three beech stands (data not shown). For oak, a low growth level was observed during the 7 years from 1972 to 1978, with a lack of a positive pointer year in 1975 compared to the other species. The drought in 2003 had an impact on pine, resulting in a decrease of 25% in RGV in that year (negative pointer year), whereas the impact was delayed by one year, to 2004, for oak and beech (decreases of -26% and -49% , respectively).

The number of pointer years was higher in latewood than in earlywood for pine (22 vs. 15) and particularly for oak (29 vs. 2). The proportion of earlywood in the total ring width from 1960 to 2007 was significantly higher for pine ($68.2 \pm 5.1\%$) than for oak ($41.8 \pm 6.1\%$, *t*-test, $t = 23.0$, $p < 0.001$). The interannual growth variations for oak were mainly due to latewood growth variations rather than earlywood variations because earlywood variations were extremely low from 1960 to 2007 ($CV_{EW} = 14\%$ vs. $CV_{LW} = 26\%$, Fig. 3a). Oak earlywood growth was significantly correlated with latewood growth variations from 1960 to 2007

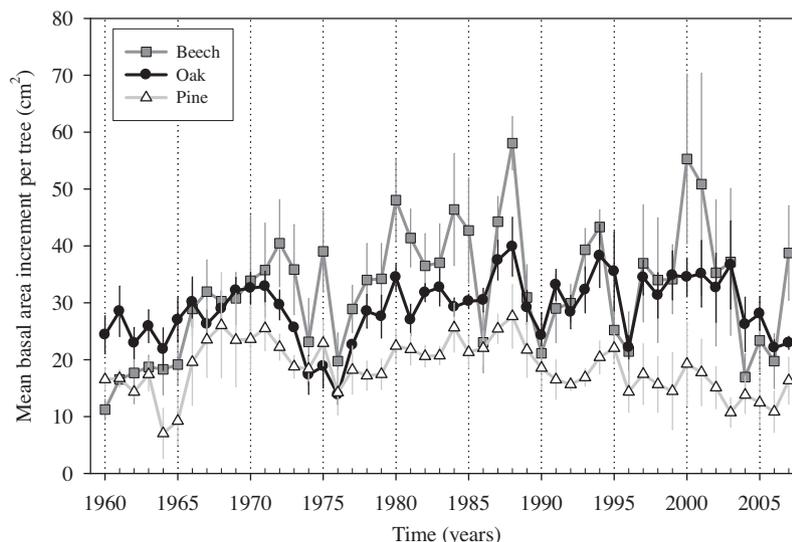


Fig. 1. Interannual variations in the mean basal area increment per tree from 1960 to 2007 for beech, oak and pine. Error bars represent ± 1 SD ($N = 3$ stands per species).

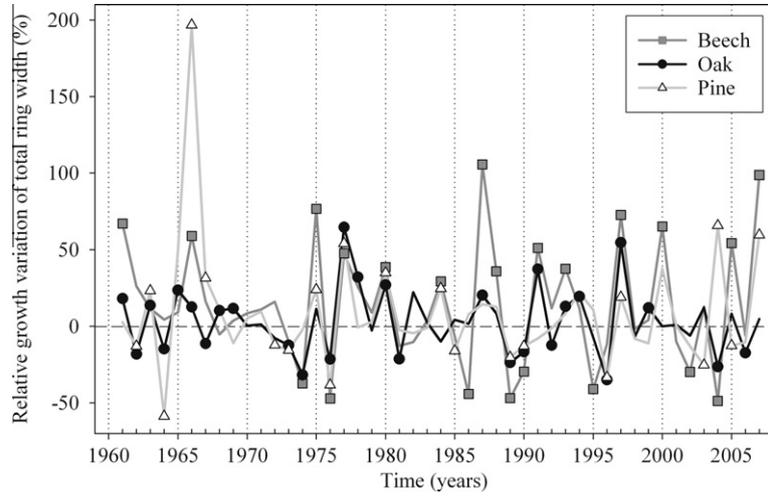


Fig. 2. Relative growth variation (RGV) of total ring width (Eq. (1)) for each species from 1961 to 2007. Pointer years (i.e., when at least 75% of the cross-dated trees presented the same sign of change in RGV between two consecutive years that was at least of 10%) are represented by a symbol ($41 \leq N$ trees per species ≤ 45).

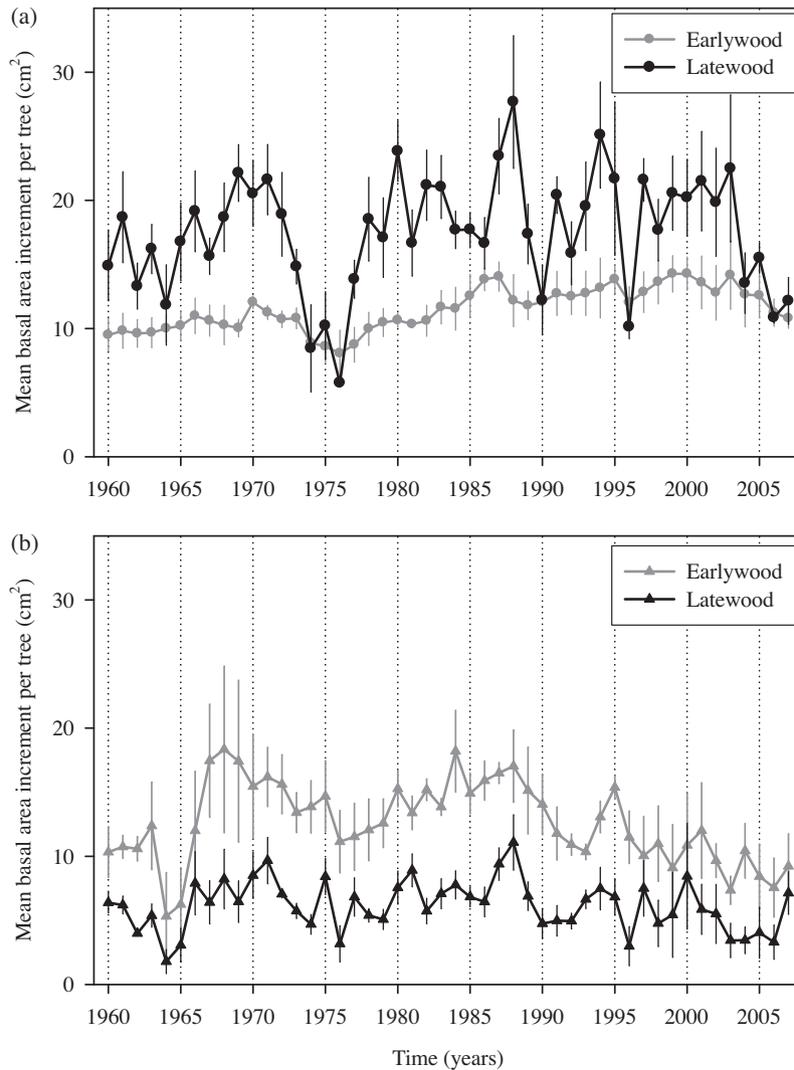


Fig. 3. Interannual variations in the mean earlywood and latewood tree basal area increment from 1960 to 2007 for oak (a) and pine (b). Error bars represent ± 1 SD ($N = 3$ stands per species).

($R^2 = 0.29$, $p < 0.001$). Contrary to what was seen in oak, for pine, the interannual variations of earlywood and latewood growth were close from 1960 to 2007 ($CV_{EW} = 25\%$ vs. $CV_{LW} = 32\%$, Fig. 3b). Pine earlywood growth was also more correlated with latewood growth variations from 1960 to 2007 ($R^2 = 0.45$, $p < 0.001$) compared to oak.

3.2. Tree BAI chronology statistics

The stand mean BAI from 1960 to 2007 was significantly different among the three species (ANOVA, $F = 100$, $p < 0.001$, Table 2). The mean BAI of pine was significantly lower than that of oak (18.5 ± 3.0 vs. 29.0 ± 2.4 ; t -test, $t = -10.0$, $p < 0.001$). Among the beech stands, the mean BAI was significantly highest in B4 (t -test, $p < 0.01$). For oak, the mean BAI was lowest in O3 (t -test, $p < 0.05$, after a logarithm transformation to homoscedasticity). Considering the pine stands, the mean BAI was highest in P3 and lowest in P13 (t -test, $p < 0.05$). The mean sensitivity (MS) of the beech total ring BAI (0.347) was significantly higher than that of oak (0.207) and pine (0.290; t -test, $p < 0.001$, after a log transformation). The first-order autocorrelation (AC) of the pine total ring BAI (0.678) was significantly higher than that of beech (0.530) and oak (0.522; t -test, $p < 0.001$). For oak and pine, MS of the earlywood BAI was significantly lower than that of the latewood BAI (0.190 vs. 0.337 for oak and 0.300 vs. 0.489 for pine; t -test, $p < 0.001$, after a log transformation for pine).

3.3. Climatic effects on total ring growth

The effects of monthly temperatures and precipitation on the stand total ring chronologies were quantified by bootstrapped correlations for each species from 1961 to 2007 (Fig. 4). The differences in AWC between stands did not seem to influence the strength of climate–growth relationships. The growth of the three species was positively correlated with precipitation from May to July, with a higher sensitivity for beech compared to that of oak and pine. The between-species comparison of climatic effects on growth also revealed major differences. Beech growth was affected by warm temperatures in previous August and current June and July. The climate–growth relationships were quite similar between the beech stands. Among the oak stands, the growth in O3 was sensitive to climate in the current year, particularly to temperatures and precipitation in June. In contrast, the growth in the other oak stands was more affected by warm temperatures in the previous August and September and promoted by precipitation in the previous August and October, rather than by temperatures in the current growing season. Pine growth was negatively correlated with temperatures in current August and positively with precipitation in current August, contrary to that of the deciduous species. Moreover, pine growth was positively influenced by warm temperatures in the previous December. The temperatures in spring and summer were negatively correlated with the pine growth but these relationships were different between stands.

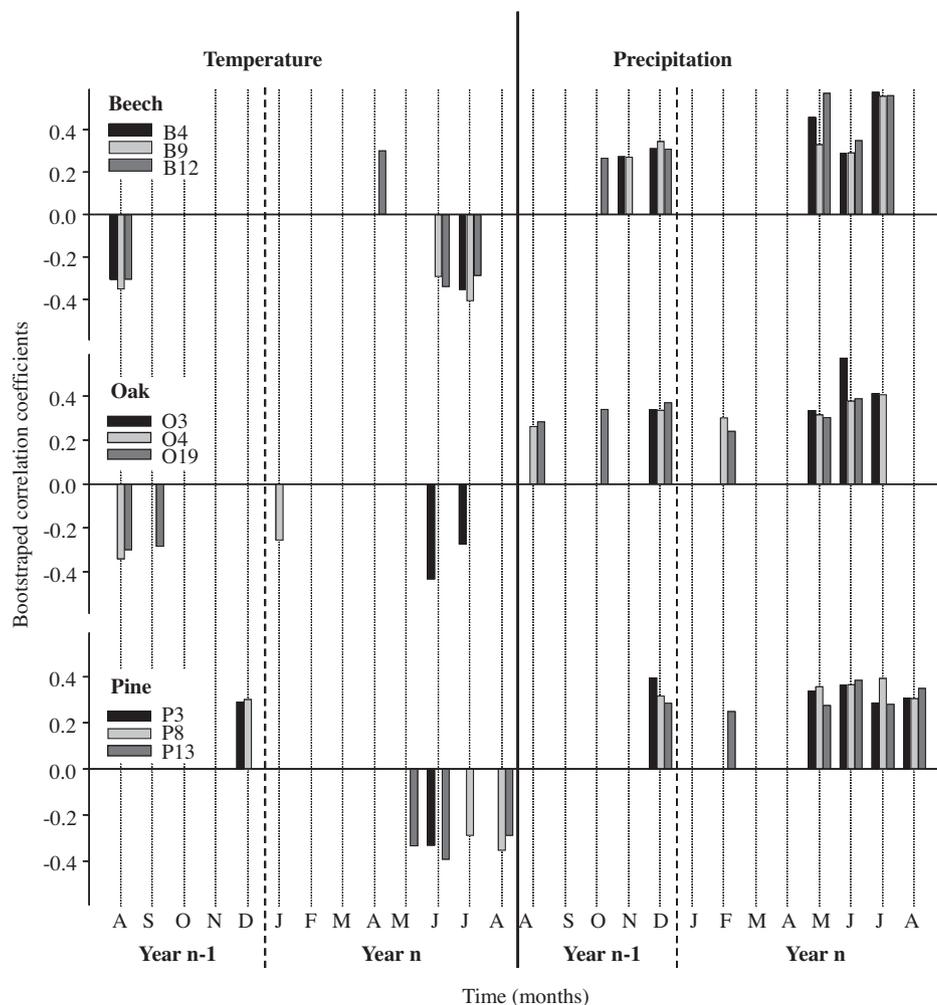


Fig. 4. Significant bootstrapped correlation values (95% level) calculated between each stand's total ring chronology and the monthly maximal temperatures and precipitation. Correlations were performed from 1961 to 2007 from the previous August ($n-1$) to the current August (n).

Climate–growth relationships were also quantified by bootstrapped correlations considering only the pointer years of each species. During pointer years, beech growth was strongly affected by warm temperatures in July and positively correlated with precipitation in May and July. For oak, the effect of the previous year's climate on growth was stronger during pointer years than that over all the considered period. The growth of the three oak stands was negatively correlated with minimal temperatures in previous August and September and positively with precipitation in previous October and December. For pine, the growth of all stands was negatively correlated with maximal temperatures in June and July during pointer years (data not shown).

3.4. Climatic effects on earlywood and latewood growth

The earlywood growth of both oak and pine was slightly sensitive to climate, and its response was different between stands (Fig. 5). Oak earlywood growth was negatively influenced by temperatures of the current January and positively correlated with precipitation in the current April and June. Pine earlywood growth was positively correlated with temperatures and precipitation in the previous December and was negatively influenced by the maximal temperatures in May and June. In contrast, oak and pine latewood growth were very sensitive to climate for all stands. Oak latewood growth was positively correlated with the precipitation in the previous August, October and December and from current May to July. Pine latewood growth was negatively correlated with maximal temperatures in June and July and positively correlated with precipitation in February and from May to August.

3.5. Growth response to soil water balance

Bootstrapped correlations coefficients were quantified between each earlywood and latewood stand chronology and SWD indices. Oak earlywood growth was only significantly negatively correlated with I_s in June, whereas its latewood growth was sensitive to I_s from June to August. For pine, both earlywood and latewood growth were significantly correlated with I_s from June to September, but the correlation values were lower for earlywood compared to latewood (data not shown).

Response function analysis was performed between the stand total ring indices and 24 bioclimatic regressors (T_{max} , monthly I_s and SWD duration from 1961 to 2007 (Table 3). Beech growth was influenced by SWD duration and I_s in the current July and August. The oak growth was sensitive to I_s from June to August. Pine growth was positively influenced by warm temperatures in the previous December and I_s in August. However, the between-stand difference in the bioclimatic growth response was stronger for pine compared to that of beech and oak.

3.6. Comparison between climatic and bioclimatic models

For each stand BAI chronology, multiple linear regressions were performed between growth indices and significant monthly climatic (T_{max} , P) or bioclimatic (T_{max} , I_s and SWD duration) variables resulting from the response function analysis (24 regressors). The adjusted determination coefficient values obtained with the climatic and bioclimatic models were compared and showed in Fig. 6. The bioclimatic models explained significantly more of the interannual growth variations of pine than the climatic models (t -test, $p < 0.05$; mean adjusted $R^2 = 34\%$ vs. $R^2 = 7\%$, respectively). This difference between models was smaller with respect to latewood growth (mean adjusted $R^2 = 31\%$ vs. 42% , data not shown). For oak, the bioclimatic models explained slightly more of the interannual growth variations than the climatic models (mean adjusted $R^2 = 40\%$ vs. 34%). The difference in the adjusted R^2 between the bioclimatic and climatic models clearly increased when considering latewood growth (mean adjusted $R^2 = 39\%$ vs. 25% , data not shown). However, for beech growth, the use of a bioclimatic model did not improve the percent of explained variance compared to a climatic model (mean adjusted $R^2 = 33\%$ vs. 40%). The interannual growth variations were the best explained by both the climatic and bioclimatic models in the stands B12 and O3.

4. Discussion

4.1. Between-stand growth

For the three species, the mean BAI from 1960 to 2007 was probably linked to the soil profile of the stand. Trees growing on

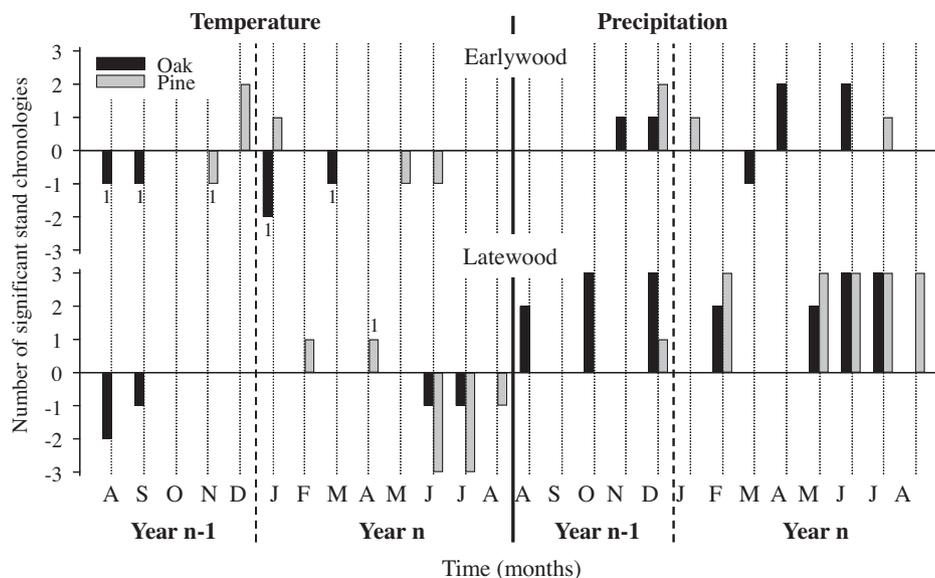


Fig. 5. Number of stand chronologies with significant bootstrapped correlation values (95% level) calculated between each stand's chronology and the monthly maximal temperatures (except 1 minimal temperatures) and precipitation. Correlations were performed for earlywood and latewood from 1961 to 2007 from the previous August ($n-1$) to the current August (n). The stand numbers are indicated as negative for negative correlations and positive for positive correlations.

the pointer years, the oak growth was also more sensitive to the climate of the previous year compared to beech and pine (data not shown). Oak growth was sensitive to cold temperatures and low precipitation in the previous autumn and December, as described at other French sites by Lebourgeois (2006). The temporal dynamics of soil water recharge for recovering field capacity appears to be a water balance pattern pre-conditioning the next ring. Large earlywood vessels of oak are sensitive to embolism generated by winter frosts (Hacke and Sauter, 1996). Therefore, the production of new earlywood before leaf expansion for the spring recovery of hydraulic conductivity largely depends on the use of carbon reserves. Dry autumnal conditions could affect carbon reserve storage because the accumulation of non-structural carbohydrates in temperate sessile oak continues after growth cessation until leaf fall (Barbaroux and Bréda, 2002; Hoch et al., 2003). Carbohydrate depletion could explain long term consequences of climate on oak growth, such as our results from 1972 to 1978 with a time lag of more than one year (Becker et al., 1994). As for beech, oak growth was positively correlated with the precipitation of the growing season over the all considered period, but the months with the strongest climatic impact were June and July. The June–July period corresponded to latewood formation (see Michelot, 2011). Latewood was the ring component that most influenced the total ring width variations. The growth response to I_s in June and July highlighted the vulnerability of oak growth to SWD during this period.

Pine was the only evergreen species included in our study, and its growth increased in the case of warm temperatures in the previous December. Warm conditions in December could improve carbohydrate storage because photosynthesis occurs in conifers during mild winters (Guehl, 1985; Lebourgeois et al., 2010). This factor, in combination with abundant precipitation in the previous December, which increases extractable soil water, promoted earlywood formation during spring. Pine growth was also affected by maximal temperatures in June (as in Rigling et al., 2002), July and August, especially during pointer years (data not shown) and positively correlated with abundant precipitation from May to August. Therefore, pine was the only species sensitive to the climate of August. The observed pine growth response to I_s in August also highlighted the key role of the soil water status at the end of the growing season. This could be explained by the longer growing season of pine in Fontainebleau (until September) compared to beech and oak over a mean climatic year (Michelot et al., submitted). Warm and dry climatic conditions from June to August could lead to quick stomatal closure in Scots pine, and thus, photosynthesis is reduced during the early stage of drought (Cochard, 1992; Zweifel et al., 2009). We found that the use of SWD indices, rather than precipitation to predict the interannual growth variations of pine greatly improve model quality. These indices include the accumulated SWD during the growing season and thus the water constraints of the previous months, contrary to monthly precipitation. A major effect of summer SWD on Scots pine ring formation has been observed in other European sites (reviewed in Lebourgeois et al., 2010): in Mediterranean forests (e.g. Andreu et al., 2007) and Alpine valleys in Switzerland and Austria (e.g. Bigler et al., 2006; Weber et al., 2007).

In the context of climatic changes, droughts will be more intensive and frequent, and maximal temperatures will increase in central and Southern Europe, both in summer and winter (IPCC, 2007). The high sensitivity of beech to maximum temperatures in June and July and the precipitation of the current growing season could make this species highly vulnerable to future drought events, as suggested by the results of Gessler et al. (2007). In the case of summer droughts, reserve depletion due to soil water deficits could lead to long-term consequences on oak growth. Bréda et al. (2006) have already shown the impact of drought in 2003 via the

amount of carbohydrate reserves on the crown vitality of oak during the following year. Pine could be the species that is less vulnerable to expected climate changes among the investigated species because its growth could be stimulated by warm December. However, recent studies have shown that its great sensitivity to maximum summer temperatures and summer SWD, as we found, could have an opposite effect. A decrease in pine growth and survival was observed in central and southern Europe (Reich and Oleksyn, 2008) and a probable decrease of future distribution area of pine was predicted in the west of France (Cheaib et al., submitted).

4.3. Differing responses between earlywood and latewood growth

As beech is a diffuse-porous species, the beech earlywood and latewood widths were not separately measured in our study. For oak, interannual earlywood growth variations were buffered compared to latewood growth. The mean sensitivity and the number of pointer years were therefore extremely low for the earlywood chronologies. In most years, oak earlywood develops over April to mid-May (Bréda and Granier, 1996; Gricar, 2010; Michelot, 2011) before leaf maturity occurs. Consequently, SWD intensity is low during its formation. Moreover, carbohydrate reserves are used as the main substrate for earlywood formation, as shown by the severe depletion of total non-structural carbohydrates during this period in Barbaroux and Bréda (2002) and by studies on the intra-ring carbon isotopic composition (Eglin et al., 2010; Helle and Schleser, 2004; Michelot et al., 2011). Thus, as in Bréda and Granier (1996), we showed that earlywood growth was less dependent on the climate and SWD of the current year than latewood growth, which was significantly correlated with many climatic variables. Concerning latewood growth, our results showed a large influence of precipitation, rather than the temperatures of the current growing season. However, latewood growth was more influenced by the previous autumn–winter conditions than was that of earlywood, contrary to the findings of most dendrochronological studies in Europe (reviewed in Dolezal et al., 2010). Like earlywood, latewood also appeared to be affected by carbon reserve depletion due to unfavourable conditions in the previous autumn.

In contrast to what was seen in oak, the interannual earlywood growth variations of pine were close to those of latewood. The number of pointer years was smaller for earlywood compared to latewood growth, but the decrease was much smaller than for oak. During a mean climatic year, the growth rate of pine earlywood was higher than that of latewood (Michelot, 2011; Michelot et al., submitted), which could explain the observed proportion of earlywood in total ring width (68%). Pine earlywood growth was sensitive to temperatures and precipitation during winter but was only slightly influenced by the climate of the current growing season as in Lebourgeois et al. (2010). Contrary to what was seen for oak, earlywood growth was sensitive to I_s in the growing season as in Eilmann et al. (2009) and Lebourgeois et al. (2010). Latewood growth was very sensitive to the climate of the current growing season and was greatly reduced when the I_s values of SWD in July and August were strong. Latewood formation occurred from June to September, which corresponded to the period when the soil water deficit was the strongest.

5. Conclusions

Comparison of the growth response to climatic variations and SWD of each species highlighted a common response to precipitation from May to July but also differences in species vulnerability. Beech was the species that was most sensitive to the climatic conditions of the current growing season. Oak exhibited long-term

consequences of autumnal droughts on growth, particularly during pointer years. Unfavourable climatic conditions in the previous autumn affected current oak growth, probably due to the resulting storage reserve depletion. Pine was positively influenced by warm and wet conditions in the previous December and was vulnerable to temperatures and SWD in the growing season. The climate of August influenced pine growth, contrary to what was seen for the deciduous species, probably because the growing season of pine was the longest. In contrast to what was observed for oak, the earlywood growth of pine was sensitive to soil water deficits in the growing season. For both oak and pine, latewood was the component that was most sensitive to climatic variations and soil water deficits. An increase in the frequency and the intensity of droughts, as predicted by the IPCC (2007), could affect the three species differently, with negative impacts of maximal summer temperatures for beech growth and long-term consequences of tree carbohydrate storage depletion for oak. Although the warm winters could promote the pine growth, it could be largely affected by global warming in summer. These specific growth responses to climatic variations highlight the necessity of understanding and integrating the functioning of each species to improve future simulations of carbon storage and to adapt forest management practices under conditions of climate change.

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