Climate-tree-growth relationship of Quercus petraea Mill. stand in the forest of Bercé ("Futaie des Clos", Sarthe, France)

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Original article

Climate-tree-growth relationships of *Quercus petraea* Mill. stand in the Forest of Bercé ("Futaie des Clos", Sarthe, France)

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Abstract – The past history of a 300-year-old *Quercus petraea* stand (the "Futaie des Clos", 8 ha) located 20 km from the town of Le Mans in the Forest of Bercé in the western part of France (Sarthe) was analysed by a dendroecological approach. According to the number of healthy trees alive (> 400), the stand age (> 300 years), and the dimensions of the trees (dia: 92 cm; height: 45.2 m), this plot constitutes one of the most remarkable oak grove in France. High competition pressure between trees appeared to be the most important factor to explain the high-quality timber (high straight stems without wood defaults, narrow regular rings). After an initial 90-year period of decrease, this stand shows a 1 mm·year^{-1} growth increment from the 1810s to the present. The growth increase of 40–50% occurring for over than 20 years can be interpreted as a response to the increase of harvesting intensity. The influence of climate was evaluated by comparing earlywood, latewood and total ring indices with monthly climatic data collected at Le Mans over the period 1921–2001. Extreme growth years coincided with wet or dry springs (May–June) (± 40% of rainfall in relation to normal conditions) often associated with warm or fresh July. The climatic models accounted for between 18 and 26% of the variability of ring widths, and suggested that earlywood formation depended mainly on previous autumn hydric balance and winter temperature whereas the growth of the latewood band was maximum in early spring (positive effect of May hydric balance). The ecophysiological interpretations of the climatic correlations are discussed.

dendroclimatology / tree ring / radial growth / climate / response function / *Quercus petraea* / long term chronology / pointer years

Résumé – Dendroclimatologie du chêne sessile (*Quercus petraea* Mill.) en forêt de Bercé ("Futais des Clos", Sarthe, France). Une étude dendroécologique a été entreprise afin d'analyser l'évolution de la croissance radiale d'un peuplement âgé de chêne sessile (*Quercus petraea* Mill.) (la Futaie des Clos) localisé dans la forêt de Bercé à 20 km du Mans (Sarthe – France). En raison du nombre d'arbres présents (plus de 400 sur les 8 ha), de leur âge (> 300 ans en 2001) et de leur dimension (diamètre et hauteur moyens : 92 cm et 45,2 m), ce peuplement constitue une des plus remarquables chênaie sessiliflore de France. La sylviculture peu intensive pratiquée dans le peuplement explique en grande partie la très grande qualité des arbres (tronc très droit sans défaut, cernes fins réguliers). Après une période de décroissance de 90 ans, la largeur moyenne des cernes est d'environ 1 mm par an depuis 1810. L'augmentation de croissance observée depuis une vingtaine d'années (1980–2001) peut être interprétée comme l'expression de l'augmentation de l'intensité des éclaircies (diminution de la compétition entre les arbres). L'effet du climat a été analysé en comparant les variations du bois initial, du bois final et du cerne complet aux données climatiques du Mans sur la période 1921–2001. Les années de croissance extrêmes (années « caractéristiques ») coïncident avec des printemps pluvieux ou secs (mai–juin) (± 40 % de pluies par rapport aux conditions normales) souvent associés avec un mois de juillet frais ou très chaud. Les modèles climatiques expliquent entre 18 et 26 % de la variabilité des largeurs des cernes et suggèrent que la formation du bois initial dépend essentiellement du bilan hydrique de l'automne précédent et des températures hivernales alors que le bois final est fortement influencé par le bilan hydrique du printemps (rôle essentiel du mois de mai). Les interprétations écophysiologiques des corrélations climatiques sont discutées.

dendroclimatologie / cerne / croissance radiale / climat / fonctions de réponse / *Quercus petraea* / années caractéristiques

1. INTRODUCTION

Sessile oak (*Quercus petraea* L.) is one of the main tree species in France, both in terms of surface area and economic value. Sessile oak stands are mainly managed in high forests and regularly thinned to improve growth of selected trees. The harvest occurs mainly between 170 to 200 years [25]. The Forest of Bercé, which covers 5 380 ha in the western part of France (Sarthe), is well known for the production of high-quality sessile oak timber [12]. Among the different oak stands of this forest, "la Futaie des Clos", which covers 8 ha, has caught the attention of the foresters for many years [50]. Because of the particular characteristics of

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Table I. Evolution of the characteristics of the "Futaie des Clos" oak stand between 1888 and 2001. G: stand basal area (m^2/ha); Dg: quadratic mean diameter (at 1.30 cm). TSV: total stand volume over bark (m^3/ha). The mean height was estimated from measurements of 81 dominant oaks. RDI: Relative Density Index. Between 1888 and 1986, the stand age and the mean ring width were estimated according to the characteristics of the trees cored in 2001 (see text for details).

Year of inventory	1888	1895	1929	1947	1957	1986	2001
Stand age (years at 50 cm)	192	200	235	254	265	295	311
Nb of oak/ha	166	164	109	105	100	63	53
G (m^2/ha)	46.7	49.6	43.8	45.8	46	32.8	35.2
Dg (cm)	60	62	72	75	77	81	92
TSV (m^3/ha)	838	888	776	807	808	573	574
Mean tree volume (m^3)	5	5.4	7.1	7.7	8.1	9.1	10.9
Mean height (m)	–	–	–	–	–	–	45.2
RDI	1.02	1.07	0.92	0.95	0.94	0.64	0.67
Mean ring width (mm)	0.76	0.79	0.94	0.92	0.83	1.22	1.19

oak trees (high straight stems with diameters often above 90 cm), this plot is often considered as a "remarkable oak grove" [50]. However, a detailed survey of this site, especially of growth dynamic, has not been done yet. Thus, the coupling of old forest management plans analysis, dendroecology and climatic data should provide an improved understanding of past stand history. The objectives of this study were (1) to define the characteristics of this oak stand (age, growth rate, growth fluctuation), and (2) to ascertain the relationships between climate and total ring, early- and latewood radial growth. Such a study will allow to precise the time of the transition phase between both components and to partly assess the effect of climate on wood quality. The most prominent climatic factors affecting tree growth were identified (1) by distinguishing "pointer years", which correspond to abrupt changes in growth pattern and reveal the tree-growth response to extreme climatic events [46–48] and (2) by establishing the mean relationships between tree ring and climate through simple correlations and response-function analysis [18, 19].

2. MATERIALS AND METHODS

2.1. Study site

The "Futaie des Clos" is located 20 km from the town of Le Mans, included in the Forest of Bercé (5 380 ha – Sarthe). The "Futaie des Clos" has an area of 8 ha, and is located on a plateau, with an altitude below 100 m asl. Forest ecological type was identified using ground vegetation and soil description and chemical analysis [12]. The soil is deep sandy-loam to loam-clay brown earths, with parent material of flint clay formed in the Turonian. Soil is relatively acidic and poor (pH = 4.2 and C/N = 18.2 in the first mineral horizon). The maximum extractable soil water was calculated from simple soil profile observations: depth of each soil horizon, texture, percentage of stones and rooting patterns. Soil water reserve averages 150 mm on a depth of 1 m which corresponds to a relatively wet site. From the phytosociological point of view, the study site belongs to *Quercion robori-petraea* alliance. The station type is defined as an acidicline oak grove of plateau and corresponds to a good class of fertility [25].

Mature sessile oak (*Quercus petraea* L.) is the dominant tree species in the forest canopy and European beeches (*Fagus sylvatica* L.) are present under the dominant oaks. For several centuries up to late 1800s, the "Futaie des Clos" was managed by the French Forest Office. The forest management plan of 1843 planned the regeneration of oaks between 1903 and 1933. In 1895, due to the high quality of the oak wood [50], it was decided to preserve this remarkable stand. The "official" protection of the "Futaie des Clos" dates from 1930 following the creation of the "artistic parcels" at the national scale [50].

Oak is managed in high forest and seven inventories was available from the period 1888–2001 (Tab. I). At each date, mean diameter, stand basal area, total stand volume and stand density were calculated [12]. To define the competition pressure, the Relative Density Index (RDI) was calculated. This index takes into account the mean quadratic circumference (Dg) and the stand density (N). The formulae is: RDI = N × Dg^1.701/171582. The value leads to zero when the competition pressure between trees is low. Values around 1 correspond to maximal competition pressure [15, 16].

2.2. Climatic records

Climatic data were used from the meteorological station of Le Mans (47° 56' 49.3'' N, 00° 11' 40.5'' W) located at 51 m above sea level, 20 km from the study site. For the period 1961–1990, the mean annual precipitation was 678 mm and the number of rainy days averaged 170 (Tab. II and Fig. 1). The annual temperature averaged 11.1 °C, 6.6 °C and 15.6 °C for mean, minimum and maximum temperature respectively. Snow-covered winters and late frosts in spring were rare. The growing season rainfall (May to September) averaged 255 mm with 60% of rainless days and 26% of days with a maximum temperature above 25 °C.

2.3. Sampling, measurements, and computation of chronologies

Because of the exceptional quality of the timber and the high commercial value of the trees, only 18 dominant oaks were bored to the pith at 0.50 cm (one core per tree) and measured (diameter at breast height over bark). The 5 483 rings were measured microscopically for earlywood, latewood and total ring width to the nearest 0.01 mm using a digitizing tablet connected to a micro-computer and the tree-ring program SAISIE (Becker, unpublished). Early- and latewood transitions

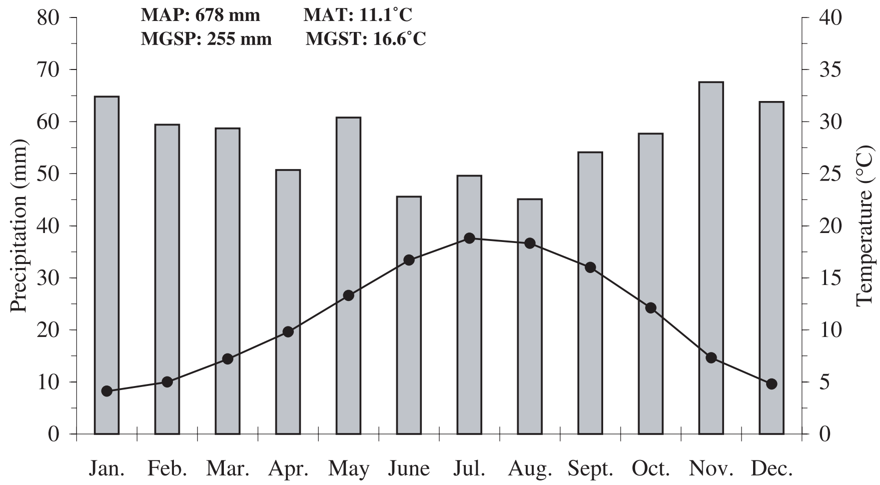

Figure 1. Climatic diagram for Le Mans (47° 56' 49.3'' N, 00° 11' 40.5'' W, 51 m). Mean monthly temperatures (°C; line) and precipitations (mm; bars) were calculated for the period 1961–1990. MAP, MGSP, MAT and MGST = Mean Annual or Growing Season (May to September) Precipitation and Temperature.

Table II. Mean climatic conditions in Le Mans (47° 56' 49.3'' N, 00° 11' 40.5'' W, 51 m). Means were calculated for the period 1961–1990. GS: growing season (May to September, 153 days).

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Year	GS
Nb of days with P > 0 mm	17	15	16	14	16	12	11	11	11	14	17	16	170	61
T_{min} (°C)	1.2	1.5	2.8	4.9	8.2	11.3	13.1	12.6	10.5	7.6	3.8	1.9	6.6	11.1
T_{max} (°C)	7.1	8.5	11.6	14.7	18.4	22.0	24.5	24.0	21.5	16.6	10.8	7.7	15.6	22.1
Nb of days with T_{min} < 0 °C	12	10	9	3	1					2	7	11	55	1
Nb of days with T_{max} > 25 °C				2	3	7	13	11	6	2			44	40

within the annual rings were defined according to qualitative aspects. Earlywood is of low density, because of a high proportion of large vessels, whereas latewood, which is made small vessels and fibres, is of high density [53, 54]. To reduce bias in the tree-ring measurements, early- and latewood data were collected by only one person. The individual ring-width series were crossdated after progressively detecting regional pointer years. When growing conditions are less favourable, the annual ring is narrower than normal and is commonly narrow for most trees falling under the influence of this environmental factor [43, 46–48]. The pointer years were defined for each ring component as those calendar years when at least 75% of the rings were at least 10% narrower or wider than the previous year. Thus, each pointer year was expressed as a relative growth changes in % [2, 30]. Absolute dating was checked by program COFECHA [24] which identifies all locations within each ring series that may have erroneous cross-dating. Climatic factors acting on pointer years were analysed for the period 1921–2001.

For each tree, ring characteristics were calculated from the common period 1715–2001 (287 years). 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 upon the current year's growth [18]. Series intercorrelation was estimated according to formulae given in Briffa and Jones [7]. The statistics of expressed population signal (EPS) and signal-to-noise ratio (S/N ratio) are calculated to quantify the degree to which the chronology signal is expressed when series are averaged. Both parameters are an expression of the strength of the observed common signal among trees [52]. Though a specific range of EPS values which constitutes acceptable statistical quality cannot be given, Wigley et al. [52] suggest a threshold of 0.85 as reasonable. The signal-to-noise ratio (SNR) is defined as SNR = N $r/(1 - r)$ where r is the average correlation between trees and N is the number of trees within a site chronology.

The raw ring-widths were standardized by means of a two-step procedure using the program ARSTAN [24]: the series were first fit to a negative exponential or straight line and then to a cubic smoothing spline with a 50% frequency response of 50 years, which is flexible enough to reduce considerably non-climatic variance [11, 44]. Autoregressive modeling of the residuals and biweight robust estimation of the mean were used to calculate chronology indices for each ring component [11, 44]. These master chronologies were used to evaluate the radial growth-climate relationships.

2.4. Dendroclimatological analysis

Monthly averaged minimum (T_{min}) and maximum (T_{max}) temperatures (°C), monthly sums of precipitation (mm) and hydric balance

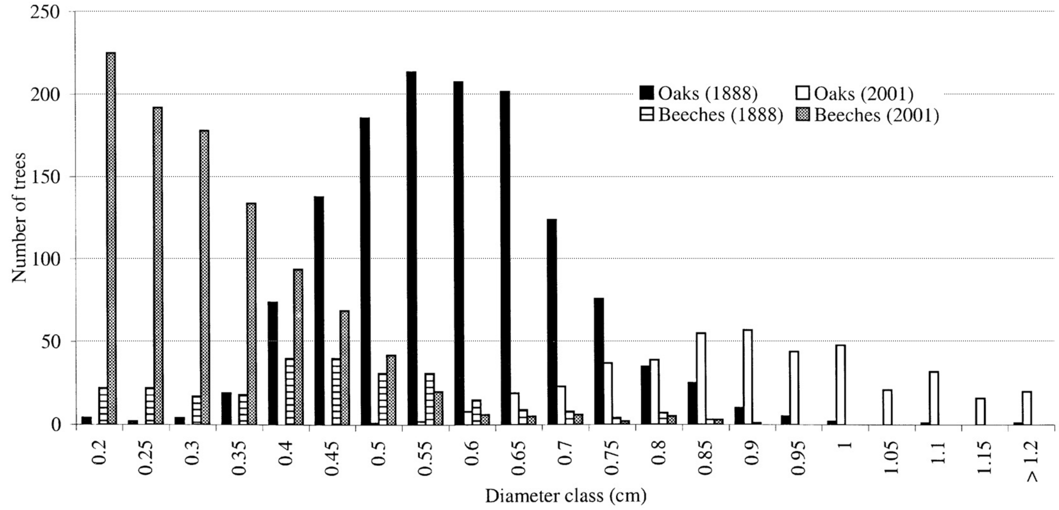

Figure 2. Number of oak and beech trees in 1888 (first available inventory) and 2001 (last inventory) in the "Futaie des Clos" according to the diameter classes (in cm at 1.30 cm). The indicated values correspond to the highest diameters of the classes (example: 0.6 = 0.55–0.6).

(BH = P–ETP) from the period 1921–2001 were used as explanatory variables. ETP was calculated using Turc's formula; it has the advantage of taking into account only temperature, global radiation and average day length, which are the data available for the whole period (1921–2001). BH is a monthly synthetic variable, positive or negative, that is related to soil moisture variations [2]. Climatic parameters were considered from October of the previous year to September of the current year. For each ring component, the effect of climate on growth was investigated in three steps. First, pointer years were compared with climatic data. Second, simple correlation analyses were performed for the whole period 1921–2001 between monthly climatic data arranged as previously defined and the master index chronologies. Third, bootstrapped response functions were calculated using the 24 monthly climatic parameters as regressors and the mean chronologies as a dependent variable [20]. For each ring component, four response functions were established taking into account as predictors the (P-T_{min}), (P-T_{max}), (BH-T_{min}) and (BH-T_{max}) combinations [49]. The bootstrap procedure provides an interesting method to simultaneously test the regression coefficients and the stability of the response function. The idea is to replace the lack of information on the statistical properties of the data by a great number of estimates, each based on different subsamples of data [20, 34, 49]. The comparison of these estimates shows the variability of the estimates. The subsampling is done by random extraction with replacement from the initial data set. The size of each subsample is the same as that of the initial data set (n = 81 in our study) to avoid bias. Each subsample forms a bootstrap test useful for cross-validation. For each pseudo-data set, the regression coefficients and the multiple correlation are computed on the observations randomly selected (calibration years). Some observations of the initial data set are used repeatedly while others are omitted. The verification years are those that are omitted from the subsample. Repeated 200 times, this procedure yields 200 sets of regression coefficients, 200 multiple correlations, and 200 independent verification correlations. A mean regression coefficients set with standard deviations is computed on these 200 estimates. Means (R) and standard deviations (S) are also computed for the multiple correlation and the independent correlation sets. The R value and the R/S ratio for the verification years give an estimation of each bootstrapped regression coefficient. When the ratio ranges from 1.65–1.95, 1.96–2.57, 2.58–3.29 and > 3.29 the significance of the corresponding regression coefficients reaches 90%, 95%, 99%, 99.9% of probability respectively [20, 34, 49].

3. RESULTS

3.1. Stand characteristics

In 2001, oak trees represented more than 75% of the total stand basal area (Tab. I and Fig. 2). Stand density was 53 oaks/ha and stand basal area averaged 35.2 m^2/ha. The total stand volume over bark was 574 m^3/ha. Oak tree diameters ranged from 0.50 to 1.60 m and more than 30% of the trees presented a diameter over bark (at 1.30 m) above 100 cm (Fig. 2). Trunks were straight with a mean height without branches of 23 m. The total tree volume ranged from 3.5 to 15 m^3 and averaged 10.9 m^3. According to the ages of cored oaks (Tab. III), it might be suggested that the current stand age ranged between 300 and 330 years. Frost crack was observed for only 8% of the trees. According to the standard sylvicultural practices defined for sessile oak [25], this stand appeared very dense. The forest management plan of 1888 (Tab. I) indicated a mean diameter of 60 cm for a stand density of 166 trees/ha. For a similar range of ages (190–200 years), the standard sylviculture recommended a stand density of 80 trees/ha for a mean diameter of 75 cm [25]. Sylvicultural interventions have been effectively scarce before the 1900s [12, 50] causing a high competition pressure between trees throughout their life (high values of RDI) (Tab. I). From the 1900s up to now, the growing conditions of the trees have varied. Between 1920 and 1929 a total amount of about 1 500 m^3 of wood was harvested (190–200 m^3 per ha). Between 1929 and 1947, only the dead trees were harvested. The forest management plan of 1957 followed by the harvesting of the storm damage of 1967, 1968 and 1990 (1700–2000 m^3) resulted in an important decrease of stand oak density (–40%) causing a lower competition pressure (RDI values below 0.7) and a rapid development of beech. Between 1947 and 1986, the number of beech stems was multiplied by 6.5 (16 to 103 stems/ha). In 2001, diameters below 30 cm represented more than 60% of the beech stems (Fig. 2).

Table III. Tree-ring characteristics of the18 sessile oak trees. Diameter was measured at breast height over bark (cm). TRW, EWW, LWW: total ring, earlywood and latewood tree-ring widths (mean and standard deviation). MS and AC: mean sensitivity and first-order autocorrelation coefficient of the ring widths. SW: sapwood width (mm). NSR: number of sapwood rings. WS: mean tree-ring width in the sapwood. *r*: series intercorrelation. EPS: expressed population signal. SNR: signal-to-noise ratio. The ring characteristics were calculated for the common period 1715–2001 (287 years) on the unfiltered series.

Total ring								Earlywood						Latewood						Sapwood			
		r: 0.453		EPS: 0.937		SNR: 14.9		*r*: 0.292		EPS: 0.881		SNR: 7.42		*r*: 0.422		EPS: 0.929		SNR: 13.1					
Dia.	Age	TR_W	std	Min	Max	MS	AC	EW_W	Std	Min	Max	MS	AC	LW_W	Std	Min	Max	MS	AC	S_W	N_{SR}	W_S	Std
96.1	300	1.03	0.27	0.40	2.14	0.209	0.42	0.52	0.16	0.23	1.11	0.229	0.55	0.51	0.23	0.05	1.63	0.360	0.39	67.1	62	1.08	0.24
82.8	311	0.93	0.38	0.34	2.30	0.183	0.83	0.45	0.12	0.21	0.80	0.227	0.44	0.48	0.31	0.05	1.82	0.297	0.83	33.3	35	0.95	0.25
83.4	308	0.93	0.35	0.30	2.53	0.176	0.77	0.50	0.16	0.16	1.20	0.215	0.57	0.43	0.25	0.11	1.41	0.286	0.75	31.7	20	1.59	0.46
86.9	288	1.07	0.43	0.31	2.67	0.228	0.72	0.46	0.14	0.18	0.91	0.247	0.49	0.61	0.35	0.10	1.99	0.335	0.67	35.8	22	1.63	0.45
73.5	315	0.95	0.40	0.25	2.50	0.211	0.75	0.40	0.13	0.13	0.77	0.239	0.58	0.55	0.32	0.11	1.97	0.321	0.65	27.4	41	0.67	0.15
78.9	317	1.01	0.41	0.32	3.63	0.226	0.67	0.38	0.13	0.12	0.95	0.260	0.56	0.63	0.34	0.07	2.89	0.328	0.60	48.2	36	1.34	0.41
80.5	288	1.20	0.57	0.37	3.63	0.256	0.76	0.49	0.16	0.12	1.20	0.238	0.60	0.70	0.46	0.13	2.82	0.382	0.69	42.5	37	1.15	0.37
77.0	311	0.99	0.35	0.28	2.30	0.213	0.7	0.43	0.12	0.13	0.75	0.235	0.42	0.56	0.28	0.10	1.63	0.299	0.68	28.5	25	1.14	0.30
75.1	320	0.73	0.32	0.20	1.81	0.265	0.67	0.27	0.07	0.11	0.51	0.235	0.36	0.46	0.27	0.05	1.47	0.366	0.67	22.9	36	0.64	0.20
81.5	326	0.99	0.42	0.22	2.63	0.207	0.8	0.42	0.16	0.12	0.96	0.227	0.72	0.57	0.30	0.04	1.99	0.309	0.73	33.1	24	1.38	0.33
75.4	320	0.86	0.45	0.26	2.82	0.255	0.74	0.35	0.12	0.15	0.90	0.250	0.56	0.52	0.36	0.06	2.02	0.349	0.72	20.8	35	0.59	0.21
89.8	308	1.04	0.48	0.33	2.81	0.225	0.77	0.42	0.15	0.13	0.83	0.247	0.62	0.61	0.38	0.10	2.09	0.326	0.74	37.6	32	1.17	0.41
82.4	308	0.92	0.47	0.36	2.82	0.196	0.81	0.41	0.14	0.16	0.86	0.219	0.62	0.51	0.38	0.11	2.24	0.294	0.76	37.9	27	1.41	0.53
74.8	315	0.86	0.38	0.20	2.76	0.177	0.86	0.37	0.12	0.1	0.79	0.222	0.62	0.49	0.29	0.08	2.08	0.274	0.82	19.9	21	0.95	0.14
77.0	326	1.08	0.49	0.48	3.20	0.201	0.79	0.45	0.15	0.19	1.29	0.224	0.53	0.63	0.40	0.17	2.41	0.308	0.76	22.9	20	1.14	0.20
86.6	311	1.02	0.48	0.33	2.89	0.219	0.79	0.42	0.13	0.17	0.98	0.260	0.38	0.61	0.41	0.09	2.36	0.326	0.76	19.8	27	0.73	0.17
69.7	321	0.92	0.36	0.30	2.74	0.186	0.73	0.46	0.16	0.15	1.04	0.250	0.57	0.46	0.26	0.12	1.83	0.310	0.65	52.7	36	1.46	0.44
67.2	300	0.97	0.38	0.35	3.08	0.199	0.74	0.44	0.14	0.19	0.97	0.234	0.53	0.52	0.28	0.09	2.11	0.306	0.69	30.4	22	1.38	0.54

3.2. Ring characteristics of cored oaks

The age of cored trees ranged from 288 to 326 years in 2001 (Tab. III). Sapwood width averaged 34 mm with a mean number of sapwood rings of 31 which was consistent with previous observed values of this species [31]. Total ring, earlywood and latewood ring-widths averaged 0.97, 0.42 and 0.55 mm, respectively. As previously known [14, 22, 53, 54], latewood proportion ranged from 80 to 50% of total ring width according to cambial age (between 10 and 320 years) (Fig. 3) and there was a strong positive correlation between the total tree-ring width and latewood width ($r^2 = 97\%$). The latewood width mainly determined the total tree-ring width and the earlywood is more constant in time. For the period 1715–2001, mean sensitivity (MS) of total ring width ranged from 0.176 to 0.265 (mean value: 0.213) (Tab. III). The higher MS values suggested that latewood was more sensitive to climate than earlywood. EPS-values exceeded the suggested threshold of 0.85 suggesting a strong climate signal in each chronology. Lower EPS and S/N values in earlywood suggested that the climate signal chronologies is lower in this ring component. There was also a high correlation between current earlywood widths and previous latewood widths ($r^2 = 25.8\%$; $p < 0.001$).

Total ring and latewood ring-width chronologies exhibited a similar growth pattern (Fig. 4). After an initial decrease during 90 years (age-related trend), both chronologies showed a long period of relative stability (1810–1910) followed by a slow increase from the 1910s to the present. For both chronologies, a more pronounced growth increase occured after the 1980s. Earlywood growth pattern appeared different with a stable initial growth, but also a slow increase from the beginning of the 20th century. Between 1910 and 2001, ring-width has increased of about 50%. The growth pattern of the sampled trees was in agreement with the stand growing conditions, especially from the 1900s to the present. Thus, the increase of tree ring widths during the last century was closely linked to decreasing competition (Tab. I).

3.3. Pointer years

For the period 1715–2001 (287 years), a total of 60 years were defined as pointer years, either for total ring, earlywood or latewood. A total of 24 corresponded to low-growth years and 36 to high-growth years (Tab. IV).

A total of 33 pointer years were defined for total ring (20 positive years). The frequency of pointer years was significantly higher

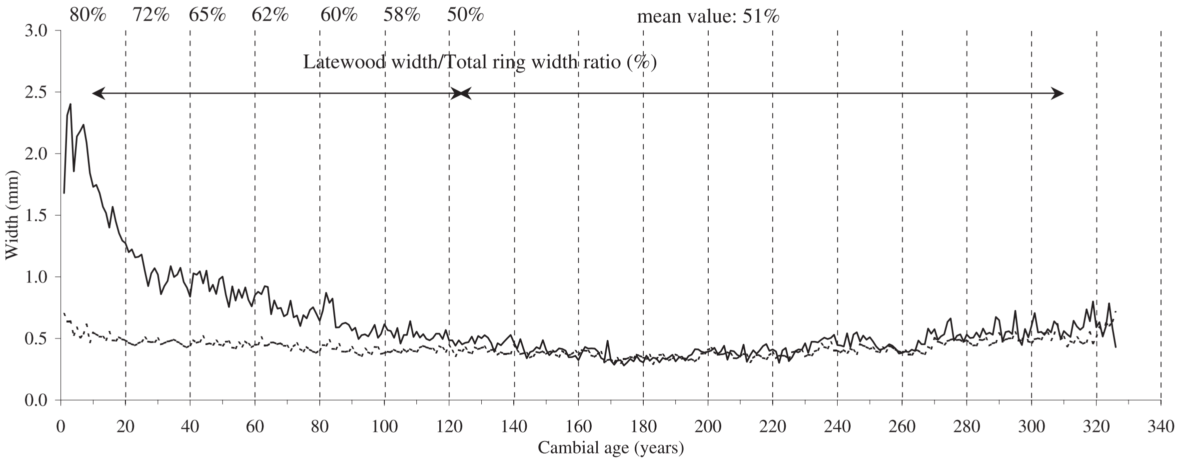

Figure 3. Earlywood (dotted line) and latewood width (solid line) in relation to cambial age. For each ring, the cambial age corresponds to the age of the tree when the ring was formed (period 1690–2001). After 100 years, LW/TR ratio is relatively stable around 51%.

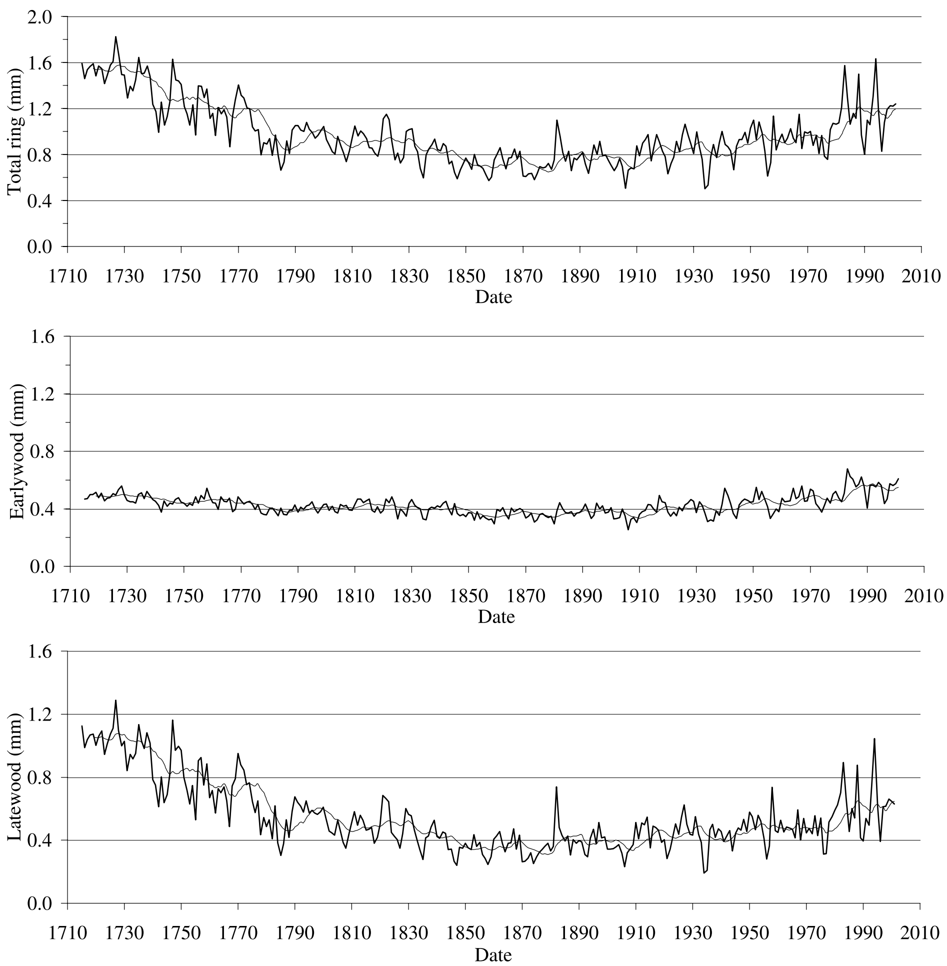

Figure 4. Raw tree-ring ring mean chronologies for total ring, earlywood and latewood from the "Futaie des Clos". Thin line represents a 10-year running average. The number of trees per year is 18 (period 1715–2001; 287 years).

Table IV. Calendar years characterized by a strong relative decrease (negative pointer years) or increase (positive pointer years) in radial growth for each ring component. TR: total ring; EW: earlywood; LW: latewood. The years refer to a strong relative increase or decrease (> 10%) found in at least 75% of the 18 crossdated trees (period 1715–2001).

Negative pointer years (relative decrease in %)							
Year	TR	EW	LW	Year	TR	EW	LW
1996	–27	–18	–33	1915	–22		–31
1995	–22		–29	1906	–26	–23	–26
1989	–30		–41	1892			–18
1985			–22	1887			–26
1984			–11	1883			–22
1976			–31	1870	–23		
1968	–26		–31	1824			–25
1959	–23		–34	1784			–32
1956	–25		–28	1778	–16		
1952		-16		1755	–20		–20
1944	–17		–23	1722		–16	
1934	–29		–40				
1921			–22				
				Total	**13**	**4**	**20**

Positive pointer years (relative increase in %)							
Year	TR	EW	LW	Year	TR	EW	LW
1998		30		1897			31
1997	32		73	1894	20		41
1994	28		41	1882			109
1993	26		59	1881		32	
1991		45		1865		25	
1988	37		68	1848			44
1983	32	35	34	1829	30		41
1978	40		91	1821	28		39
1973			41	1789	27		46
1967	28	22	46	1787	23		40
1958	52		104	1786			39
1937		32		1783			59
1936	47		169	1769		26	
1931		25		1768	36		63
1924		18		1763	26		
1916			47	1756	56		94
1917		34		1747	28		38
1907	38		58	1743	32	25	49
				Total	**20**	**12**	**26**

for latewood (46 years) than for earlywood (16 years). The negative years 1996, 1906 and the high-growth years 1983, 1967 and 1743 appeared for each ring component. There were many points of agreement between total ring and latewood whereas earlywood component reacted more individually. Among the 33 pointer years defined in total ring, only 2 did not appeared in latewood (1870 and 1778). For earlywood, 11 of the 16 pointer years appeared only in this ring component. There were three relatively long periods when no signature years occured: 1715–1739; 1790–1819; 1830–1869. From the 1930s to the present, at least one pointer year was observed for each decade (1 to 5; mean: 2.4/10 years). The recent period 1990–2001was characterized by the highest number of pointer years ($n = 5$).

There were many points of agreement between latewood pointer years and extreme spring precipitation and maximum July temperature (Fig. 5). Thus, 9 of the 12 low-growth years were characterized by both spring drought ($P < 60$ mm) and warm summer (+0.5 to +4.5 °C above normal conditions). By contrast, the positive pointer years often corresponded to the “coldest” summers. This was particularly true for the four positive years 1936, 1978, 1993 and 1958 characterized by a very wet spring ($P > 120$ mm) and “fresh” summer (–2.5 °C below normal value). The similar pattern was observed for total ring (data not shown). The growth depression centred on the negative pointer year 1934 was not correlated to exceptional weather conditions, but was a consequence of an important defoliation caused by an oak defoliating caterpillar during the two consecutive years 1933–1934 [12].

The low number of earlywood pointer years (only 9 for the period 1921–2001) made climatic analysis difficult. High minimum temperature in September and low maximal temperature values in Spring seemed to play a major role in producing earlywood signature years (data not shown).

3.4. Simple correlations and response functions analysis

For total ring and latewood, correlations between growth and climate appeared slightly higher when hydric balances (BH) and minimal temperatures (T_{min}) were taken into account as predictors. Correlations with maximal temperatures were never significant excepted for July in latewood ($r = –0.220$; $p = 0.048$). For both components, simple correlations and response function analysis appeared consistent and showed that each chronology was more closely correlated to hydric balance than temperature (Fig. 6). Climatic models found four months to be significant. Previous October hydric balance, current May hydric balance and minimal May temperature entered in both models with positive regression coefficients. For both ring component, the highest correlation was observed for current May hydric balance ($r = 0.301$ and 0.363 for total ring and latewood, respectively; $p < 0.001$). Total ring also showed a positive association with previous November hydric balance. The positive effect of current June hydric balance was also significant for the latewood growth. The percentage of the climatic variance accounted for by total ring and latewood chronologies was 21.4% and 25.1%, respectively (Fig. 7).

The response function obtained for earlywood series was different and the percentage variance explained was weaker

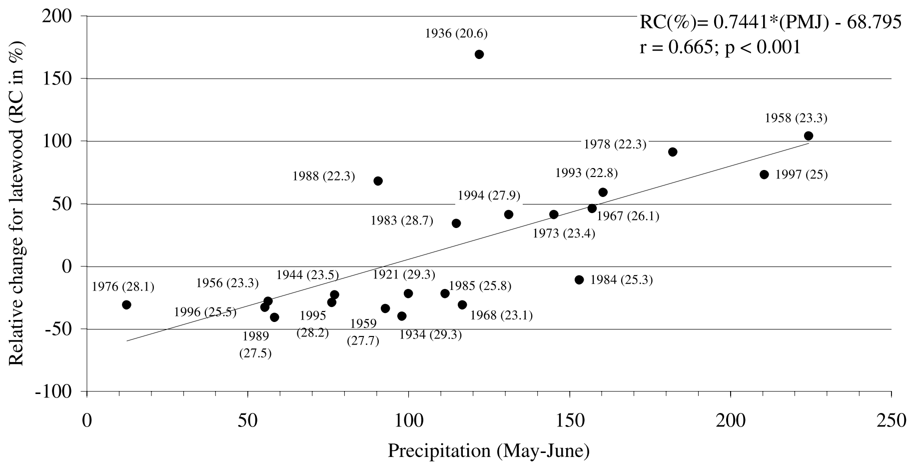

Figure 5. Correlation between the 22 latewood pointer years observed for the period 1921–2001 and spring precipitations (May–June, in mm). The values in brackets correspond to the mean maximum July temperature (°C) (Average maximum July temperature: 24.8 °C). Each pointer year is expressed as a relative growth change in % (see text for details).

(r^2 = 18.2%). The effect of temperature became more pronounced (Fig. 6). The influence of previous autumn weather conditions increased: positive influence of both October-November hydric balance and minimal November temperature. The current hydric balance influence shifted to late winter (March) instead of spring (May–June) in the case of total or latewood (Fig. 6). In addition, minimum January and August temperatures negatively influenced earlywood growth. For January and March, a negative influence of maximum temperature was also observed at the 95% and 90% level, respectively. Adding the previous latewood indices to the regressors resulted in a significant increase in the global significance of response function. The response function included 4 regressors: previous latewood indice (positive effect; +), previous November hydric balance (+), minimum temperature in January (–) and August (–). This model explained 25.7% of the variance. For total ring and latewood series, response functions were similar when ring parameters were involved in the calculation.

4. DISCUSSION

According to the number of healthy trees alive (more than 400 on the 8 ha), the stand age (> 300 years), the dimensions of the trees (dia: 92 cm; height: 45.2 m), indeed the "Futaie des Clos" constitutes a remarkable oak grove [9, 36]. The range of observed ages suggests that the regeneration of this stand started before 1700. High stand density and high competition pressure between trees appear to be the most important factor to explain the formation and the quality of this stand (high straight stems without wood defaults, narrow regular rings). After an initial 90-year period of decrease, this stand shows a 1 mm·year^{-1} growth increment from the 1810s to the present. The growth increase of 40–50% occuring for over than 20 years can be interpreted as a response to the decrease of stand oak density. The high harvesting intensity has created canopy gaps and has stimulated a pulse beech establishment. The oak ring width is usually considered as a good indicator of wood quality because wood properties (density, shrinkage, machinability…) are closely correlated with ring widths [39–41]. Thus, wide rings (> 1.5–2 mm) correspond to denser wood which is less favourable to veneer production (the main use of oak wood) because denser wood in this species is associated with higher shrinkage and machinability [14, 53, 54]. Thus, from this point of view, this oak grove can be considered as a high quality stand for veneer production.

The calculation of response functions provides readily accessible information about the dominant mode of linear response between tree-ring and climate variables of many years. Thus, response function analysis allowed us to determine the common mesoclimatic factor which makes the series comparable with each other [18, 19]. As a disadvantage, however, response functions and also correlation analysis are unable to render evidence about less frequent and time-dependent growth limiting factors. The pointer years analysis provides information on an individual year basis and can be considered as a supplement to the calculation of linear regression models [43, 48]. The combination of these different procedures gives the most comprehensive dendroclimatological information [30]. In this study, the three methods clearly showed that the radial growth of old sessile oak trees, growing at low elevation on acidic soil in the Forest of Bercé, is mainly controlled by current spring hydric balance and previous autumn conditions. A deficient water balance negatively influences annual growth as a result of low precipitation and high temperature. Climatic models reflect only between 18–26% of the variance. To explain this relatively weak response of global growth to climate, it might be suggested that the environmental conditions in the forest under study are usually not restrictive for tree growth: low altitude and temperate climate associated with deep soil. For the later point, soil water reserve is estimated to 150 mm on a depth of 1 m. Because of the high capacity of soil prospection by the roots of oak species [4, 5, 33], it may be suggested that rooting depth is superior to 1 m which increases the maximum extractable soil water reserve and leads to minimize the effects of drought. It might

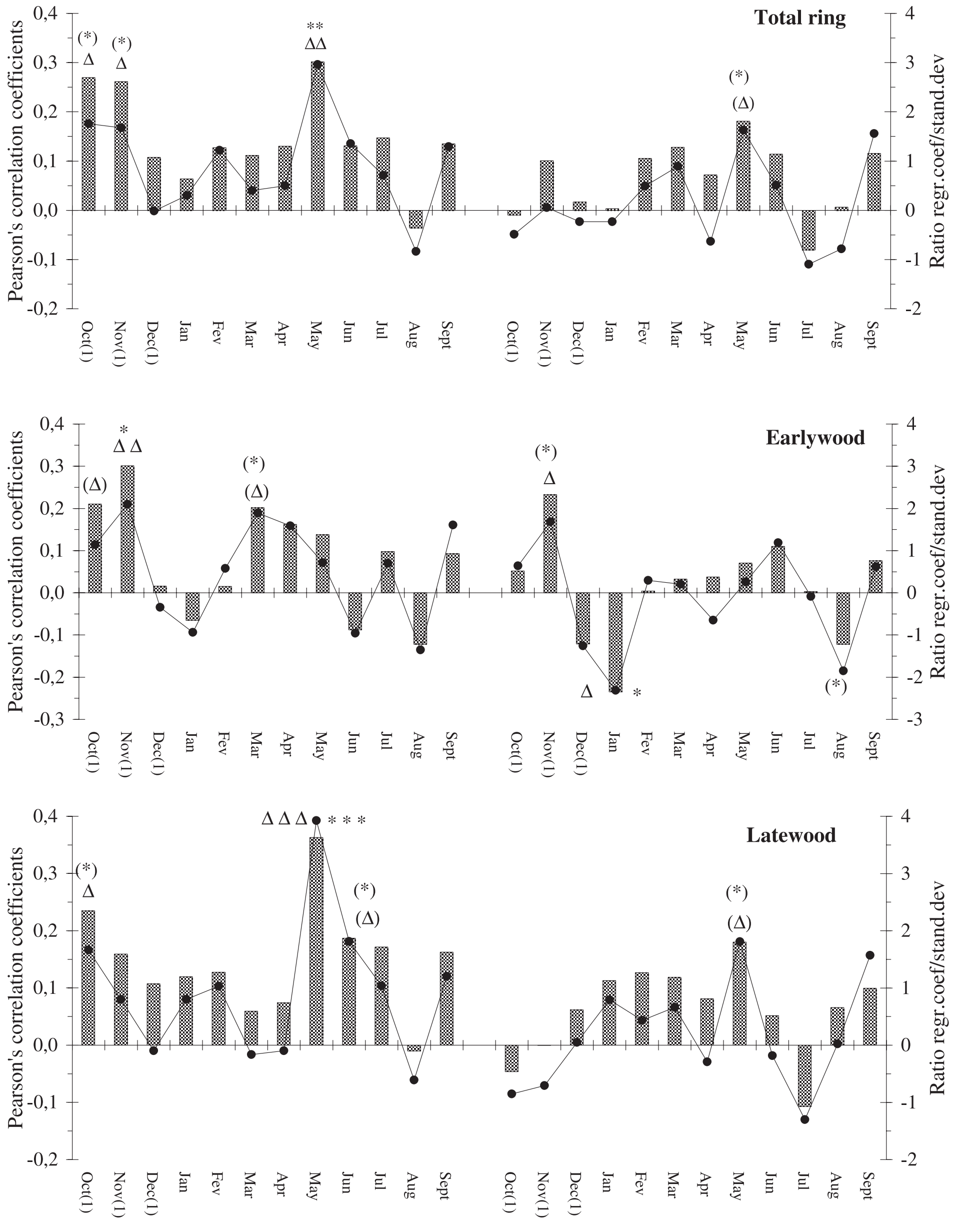

Figure 6. Simple Pearson's correlation (r) coefficients (bars) and response function coefficients (lines) for monthly minimum temperature and hydric balance (P-ETP) from previous October to current September for each ring component (period 1921–2001; $n = 81$). The number of stars (for response function) and triangles (for correlation function) indicates significance at the 90%, 95%, 99% and 99.9% levels.

be also suggested that the oak growth on this site is too "complex" to be explained only by monthly climatic parameters. A stronger correlation can probably be achieved by using daily climatic data grouped into periods of different lengths [5, 17, 29]. Even if low, the percentage of explained variance is within the usual range in other Europe localities [5, 8, 27, 35, 38, 44, 49].

The same clear pattern for spring weather conditions is visible for extreme years which result from extreme May–June precipitations. Thus, the majority of pointer years coincides with dry or wet spring (+40% or –40% of rainfall in relation to mean conditions) often associated with warm or fresh July. This type of relation, however, cannot always be found. For example, the years 1949 and 1962 were expected to be negative pointer years, due to severe droughts, but this was not the case. These years present narrow rings (Fig. 4) but the calculation of the relative growth change shows that the different thresholds fixed by the method were not attained (data not shown). A similar remark can be done for the rainy years 1950 and 1951. These years present wide rings but there are not defined as pointer years because only 50% of the trees present the same positive change of growth.

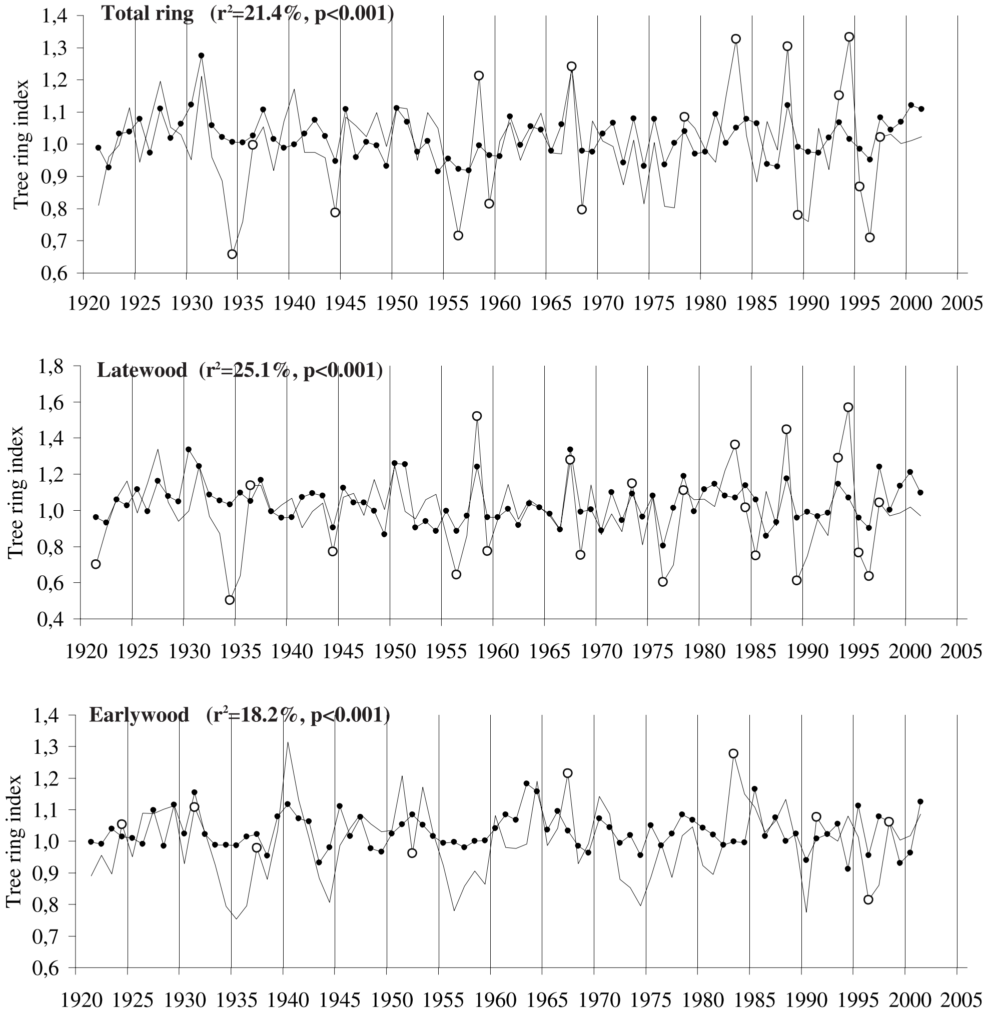

Figure 7. Actual growth index (solid line) and estimated growth index (closed symbols) of sessile oak for each ring component at the "Futaie des Clos", Forest of Bercé (Sarthe) (Period 1921–2001). The open symbols correspond to the pointer years (see text for details). The variance accounted for by the significant climatic variables is given by the r^2 value.

Our results agree with previous studies done throughout Europe which showed that signature years in European oaks were mainly linked to growing season precipitation anomalies; temperature anomalies playing no or a secondary role in determining the pointer years [3, 6, 26, 32, 43]. Few pointer years observed in this old oak stand are in agreement with previous observations done throughout France, where the most frequent pointer years observed in the sessile oak stands of the French network RENECOFOR are the rainy years 1958 (+) and 1946 (+) and the dry years 1976 (–) and 1989 (–) [32]. The years 1976 (–), 1958 (+) and 1989 (–) seem to be very important throughout Europe because they have also been observed in north-eastern France in the region of Lorraine [3], in the plain of Alsace [5] and in a wide range of taxa in England [6].

Latewood appears to be more sensitive to current climate variations than earlywood and the response pattern obtained for latewood is very similar to the one defined from total ring series. The reliability of the climatic response of early- and latewood widths confirms that both parameters can be used to obtain subseasonal climatic information [35]. This kind of quantification may be considered as an intermediate step between classical measures of ring widths and methods based on wood structure. This method is easily applicable in the case of ring porous species (abrupt transition between earlywood and latewood) and takes into account wood-structural features. Earlywood formation seems to be mainly controlled by previous autumn conditions, latewood widths of the preceding years and January temperature. This positive link has been previously observed in other studies [35, 37, 45] and could be ecophysiological meaningful. It could be the consequence of a trade-off between allocation to vessels or leaves at bud burst time. In oak trees, carbohydrate storages (starch and sugars) mainly occur in autumn (October to December) and spring mobilization is especially high [1, 28]. This seasonal dynamic of stored carbohydrates corresponds to the typical phenology and anatomy pattern of this ring-porous species where about 30% of the total annual stem increment (mainly earlywood formation) is added before bud burst [1, 4, 23]. Spring mobilization of carbohydrates reserves in oak may be related to its hydraulic properties. The large vessels in oaks are very sensitive to winter embolism [21, 51]. A large part of the previous year's earlywood vessels are embolized by frost events in winter; therefore, the production of new earlywood large vessels before leaf expansion is necessary for the spring recovery of hydraulic conductivity [10, 13]. The large vessels in oaks are very sensitive to winter embolism, and so spring reactivation of growth is very dependent on stored carbon. This ecophysiological pattern could explain the climatic correlations observed in our study between autumn and winter conditions and earlywood formation. The high negative influence of low temperature in January was also observed in north-eastern France by Becker et al. [3]. Another explanation could be that roots will continue to grow at the end of the growing season if they have a sufficient supply of nutrients and water, until the soil temperatures become too low [42]. As a result, if it rains during this period the roots will grow and when the new growth cycle begins, the following year, the tree will have a much larger root structure and will therefore be in a position to grow more [45]. For earlywood formation, the related shortening of the growing season due to deficient hydric balance in March could partially explain the correlation (only significant at the 0.10 level) observed with this month.

To ensure wide latewood and total ring widths the trees need an important supply of water in May and June. The above growth pattern of oak is organized in successive fluxes and, during the growing season, the same axis can produce several buds consecutively. Therefore, an ample water supply during this period is essential to ensure foliar development and thus to ensure that growth can continue. A decrease in spring precipitation (SP) also leads to a decrease of the latewood-to-total-wood ratio of about 12% (48% for SP below 70 mm to 54% for SP above 150 mm; period 1921–2001; $r = -0.383$***). Thus, by modifying the latewood ratio, spring drought also changes wood density and thus wood quality characteristics.

In conclusion, this study has revealed the past and the current level of radial growth of a 300-year-old *Quercus petraea* stand located at low altitude in a wet acidic station in the western part of France. Mean radial growth and extreme growth years appeared to be more sensitive to spring and autumn precipitation than temperature which coincides with the radial growth-climate relationships for this species in Atlantic, Mediterranean and Central European localities (positive response to precipitation during May to July) [3, 5, 35, 38, 44, 45]. Both ring components can be successfully used for dendroclimatological purposes and to obtain subseasonal climatic information.

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