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Original article

Short-term variations and long-term changes in oak productivity in northeastern France. The role of climate and atmospheric CO_2

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Summary — A dendroecological study was carried out in 2 forests in northeastern France with the aim of identifying and quantifying possible long-term trends in the radial growth of sessile oak (*Quercus petraea* (Matt) Liebl) and pedunculate oak (*Q robur* L). A total of 150 sites were selected to represent the ecological diversity of these forests. An index *Cd* was used to correct annual ring width in order to compensate for the effect of different competition situations. The data were standardized with reference to the mean curve 'basal area increment *vs* cambial age'. The growth index curves revealed a strong increase in sessile oak growth (+ 64% during the period 1888 to 1987) as well as in that of pedunculate oak (+40%). The growth increase in the 'young' rings (< 60 years) of sessile oak was + 81%, and that of young rings of pedunculate oak was + 49%. The corresponding increase in the 'old' rings (> 65 years) was + 48% and 15% respectively (not significant for the latter). It would thus appear that pedunculate oak has benefited to a lesser extent than sessile oak from the progressive changes in its environment. Years showing a strong growth decrease are more common for pedunculate oak than for sessile oak. These results are consistent with a recent hypothesis about a slow but general retreat of pedunculate oak, including severe episodic declines, in favour of sessile oak in many regions of France. A model was created using a combination of meteorological data (monthly precipitation and temperature) starting in 1881, and increasing atmospheric CO_2 concentrations. The model explains 78.3% of the variance for sessile oak and 74.3% for pedunculate oak. This includes some monthly parameters of year *y* (year of ring formation), and also some parameters of the years $y - 1$ to $y - 4$ for sessile oak and $y - 1$ to $y — 5$ for pedunculate oak. The models satisfactorily reproduce the long-term trends and the interannual variation. The climatic variables alone (*ie* excluding the CO_2 concentration) were insufficient to explain the trends observed. The possible direct and indirect effects of increasing CO_2 concentration on the growth of both species are discussed.

***Quercus robur* / *Quercus petraea* / France / tree growth / dendrochronology / dendroecology / climate / precipitation / temperature / CO_2 / global change**

Résumé — Variations à court terme et changements à long terme de la productivité du chêne dans le nord-est de la France. Rôle du climat et du CO_2 atmosphérique. *Une étude dendroécologique a été menée dans 2 forêts de chêne du nord-est de la France dans le but de mettre en évidence* *et de quantifier d'éventuels changements à long terme dans la croissance radiale du chêne sessile (*Quercus petraea *[Matt] Liebl) et du chêne pédonculé (*Q robur *L). Un total de 150 placettes ont été sélectionnées, représentatives de la diversité écologique de ces forêts. Les largeurs de cernes mesurées ont été corrigées à l'aide d'un index* Cd *afin de compenser l'effet des variations du statut de compétition entre les arbres. Ces données ont été standardisées par référence à la courbe moyenne des accroissements annuels en surface terrière en fonction de l'âge cambial. Les courbes d'indices de croissance révèlent une forte augmentation à long terme du niveau de productivité, aussi bien chez le chêne sessile (+ 64% entre 1888 et 1987) que chez le chêne pédonculé (+ 40%). L'augmentation est plus sensible pour les cernes «jeunes» (< 60 ans) : + 81% chez le sessile et + 49% chez le pédonculé. Pour les cernes «vieux» (> 65 ans), elle est respectivement de + 48% et 15% (non significatif pour la dernière). Il semble donc que le chêne pédonculé ait moins bénéficié que le chêne sessile des modifications progressives de son environnement. Les années caractéristiques d'une forte baisse relative de croissance sont beaucoup plus fréquentes chez le chêne pédonculé que chez le chêne sessile. Ces résultats sont cohérents avec l'hypothèse récente d'un déclin lent mais général du chêne pédonculé, au profit du chêne sessile, dans de nombreuses régions françaises, ponctué de dépérissements épisodiques sévères. Deux modèles climatiques ont été élaborés, sur la base de données météorologiques mensuelles de précipitations et de températures disponibles depuis 1881 ; l'augmentation progressive de la teneur en* CO_2 *atmosphérique a également été prise en compte. Ces modèles expliquent 78,3% de la variance pour le chêne sessile, et 74,3% pour le chêne pédonculé. Ils incluent non seulement certains paramètres climatiques de l'année* y *(année de formation du cerne), mais aussi divers paramètres des années* y – *1 à* y – *4 pour le chêne sessile et* y – *1 à* y – *5 pour le chêne pédonculé. Ces modèles reconstruisent de façon très satisfaisante aussi bien les tendances à long terme que les variations interannuelles. Les variables climatiques seules, sans la teneur en* CO_2 *atmosphérique, sont insuffisantes pour expliquer les tendances observées. Les effets possibles, directs et indirects, de l'augmentation du* CO_2 *sur la croissance des 2 espèces sont discutés.*

Quercus robur / Quercus petraea / *France / croissance des arbres / dendrochronologie / dendroécologie / climat / précipitations / température /* CO_2 */ changements globaux*

INTRODUCTION

Recent dendrochronological studies suggest that a long-term increase has taken place in the wood production rates of various forest ecosystems. This has been observed in boreal forests in Europe (Hari *et al*, 1984) and North America (Payette *et al*, 1985; d'Arrigo *et al*, 1987; Jozsa and Powell 1987), and also in the mountain forests of the temperate zones in Europe (Becker, 1989; Briffa, 1992) and North America (Lamarche *et al*, 1984; Graumlich *et al*, 1989; Peterson *et al*, 1990). Fewer studies have been carried out in the plain forests of temperate zones (Wagener *et al*, 1983).

In addition to these dendrochronological studies, Kenk *et al* (1989) reported a similar result in the Black Forest in Germany after directly comparing the production of 2 successive generations of Norway spruce on the same site.

A similar growth increase has been found in the case of silver fir (*Abies alba* Miller) in the Vosges mountains (France), in studies started in 1984 as a part of the national research program Deforpa (forest decline and air pollution). In these studies, forest decline at altitudes ranging from 400 to 1 000 m has proved to be one of the main episodic crises which affect the growth and vitality of trees as a consequence of unfavourable meteorological conditions (Becker, 1987). On the other hand, on the century time-scale, a clear long-term increase in the average radial growth level was demonstrated (Becker, 1989). Moreover, the monthly precipitation and temperature data for the year of ring formation and the 6 preceding years explained a high proportion (almost 80%) of the observed variation during the episodic crises as well as the long-term trend, *ie* the average in the production rate over more than a century.

In contrast to these results, there was no significant increasing trend in the average radial growth rate found in a preliminary analysis using the same methodology in northeastern France using oak at low altitudes (200–250m) (Nieminen, 1988). A number of possible explanations have been proposed:

(1) Different species react differently to changes in the environment. This could be the case between silver fir and oak but this could also be due to differences on a larger scale between conifers and broadleaved trees.

(2) Different climates are present on the plain and in the mountains, even though the distance between these areas is only about 100 km. More precisely, these were differences in climate modification that took place in these areas during the last century.

(3) The skewed structure of the data resulting from the different silvicultural history of the stands could cause artifacts. About 150 years ago the treatment in some parts of the forest changed from coppice-with-standards to that of an even-aged high forest. As a consequence, most of the older sampled trees grew at a lower stand density during their early stage of development than the younger trees sampled. This difference in competition has a strong influence on height and tree-ring width development.

In order to test this third hypothesis, an index of competition (*Cd*) was created to compensate for the effects of different competition status experienced by the trees throughout their lifetime (Becker, 1992). The data set, which has since been enlarged by additional sampling, has been reprocessed using corrected tree ring widths.

In addition, we have used the basal area increment (BAI), instead of the widely used tree ring width, partly because BAI is more directly related to the production rate that is of interest to foresters, but especially because it is less dependent on the cambial age, or current age, *ie* the age of a tree at the time of annual ring formation (Federer *et al*, 1989; Briffa, 1992; Jordan and Lockaby, 1990).

The main aim of this study was to establish the presence or absence of a long-term trend in the radial growth rate of oak growing on the plain. If it were shown to exist, then quantifying the trend, as well as modelling the response of radial growth to climatic factors and atmospheric CO_2 concentrations, were additional aims. Moreover, a comparison between the 2 oak species that grow on the plains of northeastern France was an important objective in itself. Pedunculate oak (*Quercus robur* L) is known to be more sensitive to abnormal weather conditions than sessile oak (*Q petraea* (Matt) Liebl). Pedunculate oak is very sensitive to successive years of drought, and, in France, it has suffered from severe episodic declines during the 20th century (Becker and Lévy, 1982).

MATERIALS AND METHODS

Study area

The forest area under study is situated in northeastern France (48° 45'N, 6° 20' E, 250 m elevation) in the region of Lorraine, in 2 state forests located close to each other: the forest of Amance (972 ha) and the forest of Champenoux (467 ha). The climate type is semi-continental, although there is fairly regular rainfall throughout the year. Annual precipitation is about 700 mm, and the average annual temperature 9.1°C. The most typical soil type is 'leached brown earth', which is developed on marls covered with loam of varying depth. Exceptions are the 'pelosol' and 'pseudogley' soils in certain valley bottoms where drainage is insufficient.

Pedunculate and sessile oaks are the major tree species with a varying admixture of beech

(*Fagus silvatica* L) and hornbeam (*Carpinus betulus* L). Prior to 1826, the forests were treated as coppice-with-standards stands for centuries. From 1867 until 1914, most of the stands were regenerated to form even-aged high-forest stands, but the old coppice-with-standards stands are still to be found in some parts of the forests.

Sampling

The study sites were chosen to represent the complete ecological diversity in the forest areas, although mixtures of both oak species were favoured. Five dominant trees of both species were bored to the pith on every sample plot whenever possible. However, the total number of sample trees on many of the plots was less than 10 owing to the low abundance of 1 of the 2 species, and in some rare cases codominant trees had to be chosen as sample trees. Special attention was paid to the ecological homogeneity of the sample plots. The homogeneity of the ground vegetation was also taken into account.

The topographic position and the drainage conditions on each sample plot were recorded in order to characterize the availability of water in the soil. A complete floristic 'relevé' according to the method of Braun-Blanquet was also produced. The total height (H) and the stem diameter at breast height (D) of the sample trees were also measured.

Two cores were taken from each sample tree at a height of 2.80 m (to minimize the negative effects on the wood quality of the butt log), one from the northern side of the trunk and the other from the southern side. Throughout the text, age refers to that determined at this height. The total number of sample plots was 150. Sessile oak was present on 121 plots (529 sample trees) and pedunculate oak on 115 plots (505 trees). Both species were present on 85 plots. The average age of sessile oak was 86 years, giving a total of about 91 000 measured tree-ring widths. The average age of pedunculate oak was 80 years, with about 80 800 measured tree-ring widths.

Data processing

The annual ring widths of 2 068 cores were measured with a binocular microscope fitted with a 'drawing tube' and a digitizing tablet coupled to a computer. The individual ring-width series were crossdated using a moving graphic program after progressive detecting of so-called 'pointer years'. The mean ring-width series (the average of 2 cores per tree) was calculated and used in the following data-processing stages. The 'pointer years' were defined as those calendar years when at least 70% (or 80% for the 'special pointer years') of the rings were at least 10% narrower or wider than the previous year.

Two competition indices, *Cd* for ring width and *Ch* for tree height, were defined in order to compensate for the effect of the different competition situations among the trees. The methods used for calculating these indices has been published separately (Becker, 1992). It is based on the hypothesis that the *H/D* ratio of a tree depends on its average competition status in the past, but is largely independent of the ecological site conditions. *H/D* is also closely related to age, in accordance with the following model:

$$\mathrm{LN}\ (H/D) = a - b \times Age \qquad [1]$$

The indices *Cd* and *Ch* are determined from the relationships: $Cd \times D = Dr$ and $Ch \times H = Hr$, where *Hr* and *Dr* are the dimensions of a reference tree that would be of the same age and characterized by an average competition status. *Hr* and *Dr* are unknown, but the *Hr/Dr* ratio can be calculated according to [1]. Thus, *Cd/Ch* is well defined, and called *alpha*. A simple model is used to obtain the competition indices: $Cd = alpha^{0.7}$ and $Ch = alpha^{-0.3}$. Coefficients *a* and *b* were determined separately for sessile oak and pedunculate oak. The *Cd* index was then calculated for each sample tree and used to compensate the BAI series. Each tree is assumed to always have been subject to the same degree of competition, given that the trees are the same age in the whole sample. This is generally the case with the dominant trees in an even-aged high forest and with the standards in a coppice-with-standards. Although the whole BAI series of a tree is multiplied by a constant, given that the present age of the trees in the whole sample is very varied, the mean chronologies calculated subsequently may be more or less strongly affected.

Two methods were used to detect possible long-term trends in radial growth.

Firstly, for a given cambial age class, the average radial growth was calculated for all those calendar years when at least 4 annual BAIs were available. It was then plotted *vs* calendar year. This was repeated for 10 cambial age classes from 10 (±2) to 100 (±2) years. The drawback to this method is the low number of tree rings corresponding to each date for a given cambial age. On the other hand, it can reveal possible long-term trends directly from the raw data (Becker, 1987; Briffa, 1992) without preliminary 'standardization', which is a more complicated and somewhat disputable operation.

Secondly, the effect of cambial age on BAI was taken into account using the following standardization method (Becker, 1989). The average BAI curve according to the cambial age (current age) was constructed for both species. As varying site conditions and varying calendar years of formation of the annual rings corresponded to every current year in the curve, the effects of the various environmental conditions tended to cancel each other out. In addition, the curve was balanced so as to take into account the different number of available annual rings for every pair 'cambial age–calendar year', and this balanced curve was fitted to a curvilinear model [2]. The model had to be as simple as possible and convincing from a biological point of view. Growth indices (*IC0*), expressed in %, were calculated for each individual radial growth series as the ratio of each actual BAI *versus* the reference value of model [2].

The average curve of these growth indices according to calendar years was calculated with the aim of determining the progression of radial growth over time and detecting possible growth crises, long-term trends, *etc*. Other kinds of curve could also be calculated, *eg*, separate curves for the growth indices of the 'young' (< 60 years) and the 'old' (> 65 years) rings (cambial age).

In the final stage, the curve of the growth indices *IC0* was modelled according to the available meteorological parameters, using a linear regression model. The meteorological data consisted of monthly precipitation values (P) and average monthly temperatures (T) from a meteorological station in Nancy-Essey. This station is situated only 12 km from the forests under study, and meteorological data have been collected there since 1881. Inclusion of the change in atmospheric CO_2 concentration over time (Neftel *et al*, 1985; Keeling, 1986) has also proved useful. The dependent variable was the growth index, *IC0*, of year y. In addition to the predictors P, T and CO_2, the growth index *IC1* of year ($y - 1$) was included when studying the autocorrelation problems that are common in time series analyses (Monserud, 1986). A standard method was used involving stepwise multiple linear regression, which provides correlation functions (Fritts, 1976; Cook *et al*, 1987; Peterson *et al*, 1987). The explained variance is calculated in each step k, and the residuals of the regression are analysed using the F ratio:

$$F = (SCR_k - SCR_{k-1}) / S^2$$

where SCR_k = sum of square residuals in step k; SCR_{k-1} = sum of square residuals in step $k - 1$; $S^2 = SCR_k/(n - k - 1)$; and n = number of years analysed. F is then compared with Snedecor's table levels.

RESULTS

Pointer years

Practically speaking, there were no real missing rings in the initial data, although some rings were very narrow and especially hard to distinguish. This was rather surprising when we consider the situation for silver fir in a nearby region, where 31% of the trees had real missing rings (Becker, 1989).

The years with a strong relative growth increase or decrease are presented in table I. These pointer years reveal the great similarity between the 2 species. They are more common in the case of sessile oak, but most of the additional years occur prior to 1870, and thus must be related to the structure of the sample; old trees (more than 150 years) are more common in the case of sessile oak (n = 71) than in the case of pedunculate oak (n = 33). However, there is a clear difference between the 2 species when the number of 'special pointer years' for an increase and those for a decrease are compared. The ratio of special pointer years *versus* all pointer years is 57% (increase) and 48%

Table I. Calendar years characterized by a strong relative increase or decrease in radial growth.

	Sessile oak	*Pedunculate oak*
Years with increase	1834 (1846) (1847) (1856) 1869 1871 (1875) (1883) 1888 (1894) 1906 1910 (1912) 1916 1922 1927 (1935) 1946 1948 1955 1958 (1969) (1980)	(1869) 1871 (1875) (1882) (1888) (1897) (1906) (1910) (1912) 1916 1922 1927 (1946) (1955) 1958 (1969) (1985)
n	13 (10)	5 (12)
Years with decrease	1839 (1844) (1865) 1870 1876 1880 (1900) (1904) 1911 (1926) 1928 (1940) (1944) 1947 (1952) (1953) (1962) 1964 1972 1976 (1983)	(1868) 1870 1876 1880 (1896) (1900) (1904) (1911) (1926) 1928 1952 1964 1972 1976 1983
n	10 (11)	9 (6)

The years and numbers *n* in parantheses refer to such an occurrence found in 70 to 79% of the trees ('pointer years'), otherwise such an occurrence found in 80% or more of the trees ('special pointer years').

(decrease) for sessile oak, and 29% (increase) and 60% (decrease) for pedunculate oak.

The competition correction index

The estimates of model [1] are:

Sessile oak

$$LN(H/D) = 4.744 - 4.940 \times 10^{-3} \times Age$$

Pedunculate oak

$$LN(H/D) = 4.708 - 5.001 \times 10^{-3} \times Age$$

The averages of *Cd* are close to unity: 0.974 (*sd* = 0.096) for sessile oak (extremes: 0.68 and 1.31) and 0.986 (sd = 0.083) for pedunculate oak (extremes: 0.66 and 1.32).

The development of radial growth in different cambial age classes

Ten figures were constructed for the following cambial classes (± 2 years): 10, 20, ... 100 years. The number of rings older than 100 years was too small for determining possible trends. Most of these figures indicated a clear increase during the last century, especially for sessile oak (figs 1 and 2).

A linear regression was performed for each cluster of points in order to quantify this increase. The mean relative increase in BAI during the last 100 years is 67% for sessile oak and 40% for pedunculate oak (table II). Moreover, it tends to be lower for higher cambial ages. However, this primarily concerns pedunculate oak, in which growth increase is no longer significant at cambial ages higher than 60 years.

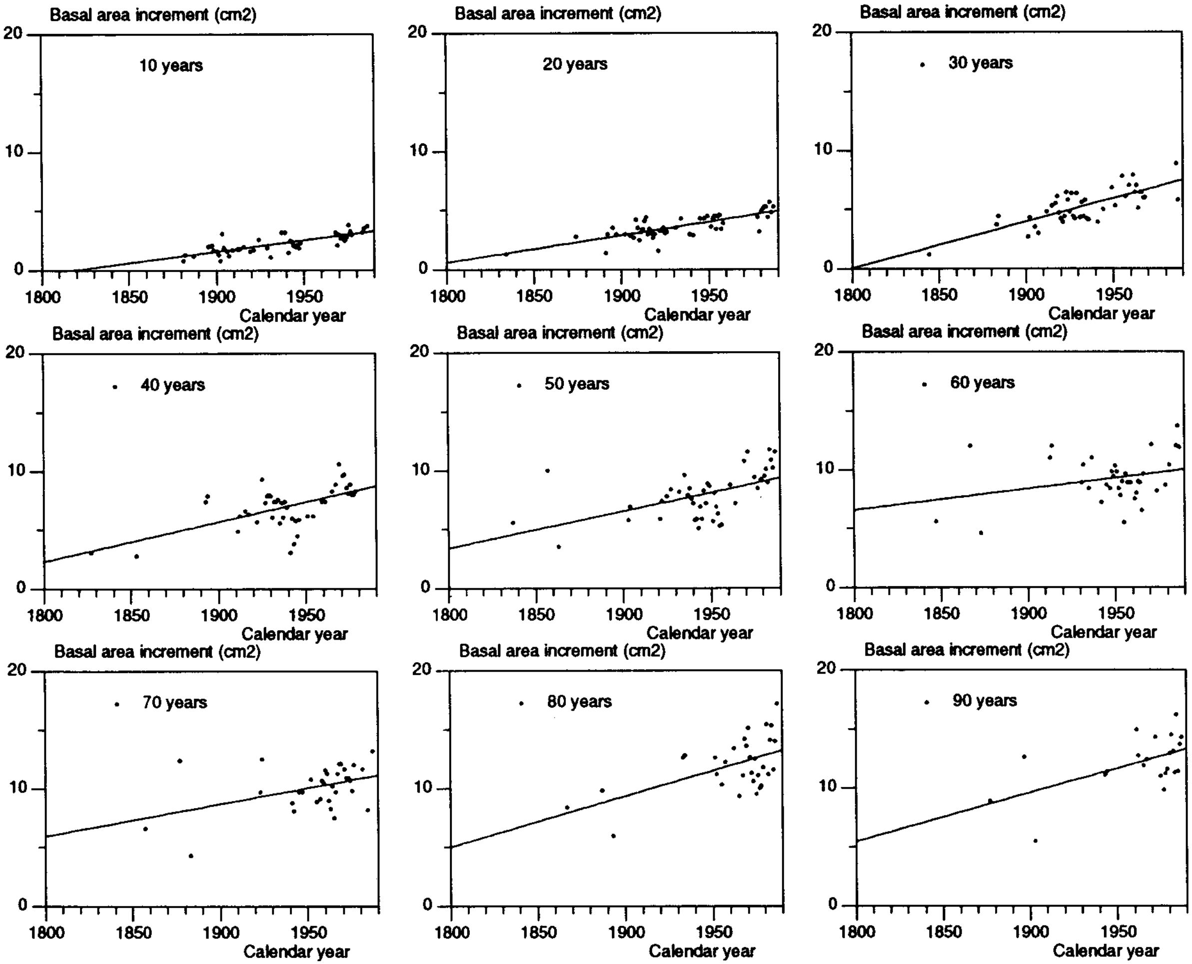

Fig 1. Annual basal area increment (BAI) of sessile oak *vs* calendar years, according to the cambial age of the rings.

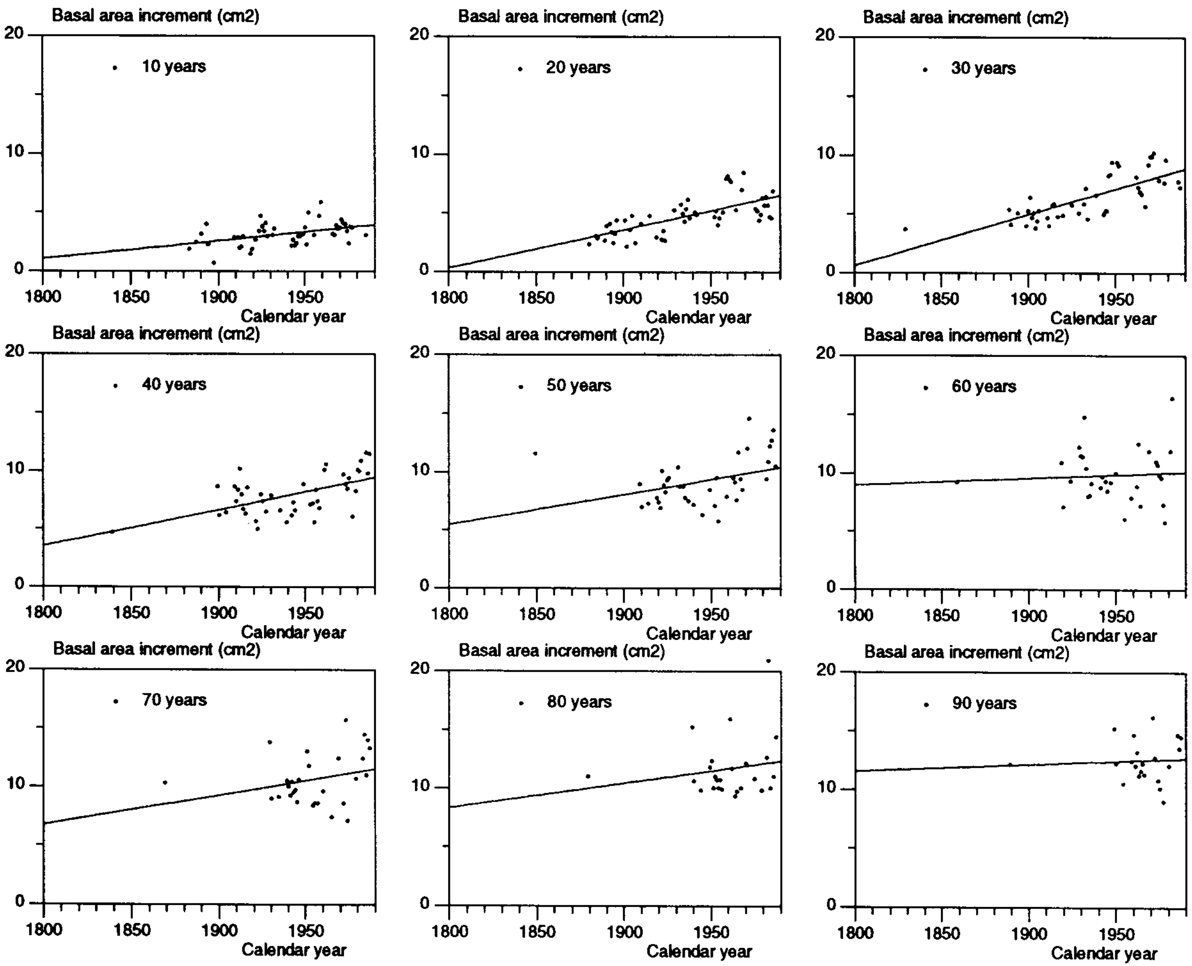

Fig 2. Annual basal area increment (BAI) of pedunculate oak *vs* calendar years, according to the cambial age of the rings.

In 1980, the mean BAI of pedunculate oak was higher than that of sessile oak for cambial ages of 10 to 70 years (+ 16% on average), but then decreased (fig 3). At the age of 100 years, the BAI of both species was still increasing.

Table II. Increase in annual basal area increment (BAI) during the last 100 years according to the cambial age class of the rings.

Cambial age (± 2 years)	*1987 BAI – 1888 BAI* (cm^2)	
	Sessile oak	*Pedunculate oak*
10	1.91 (+ 139%) **	1.50 (+61%) **
20	2.27 (+ 88%) **	3.25 (+103%) **
30	3.94 (+ 109%) **	4.34 (+95%) **
40	3.36 (+ 64%) **	3.15 (+ 50%) **
50	3.13 (+ 51%) **	2.59 (+ 33%) *
60	1.80 (+ 22%) *	0.62 (+ 7%) ns
70	2.74 (+ 33%) **	2.49 (+ 27%) ns
80	4.34 (+ 49%) **	2.13 (+ 21%) ns
90	4.16 (+ 46%) **	0.58 (+ 5%) ns
100	6.16 (+ 70%) **	–0.01 (0%) ns

* Significant at $p = 0.10$; ** significant at $p = 0.05$; ns not significant (test made on the correlation coefficient r of the linear trend, *eg*, fig 1).

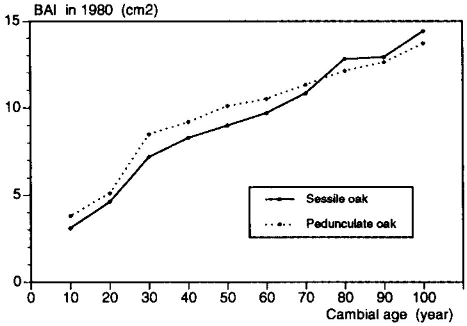

Fig 3. Basal area increment (BAI) of sessile oak and pedunculate oak in 1980 *vs* cambial age of the rings.

Mean annual BAI according to cambial age

The mean evolution of BAI as a function of cambial ring age is very similar for both species (fig 4), although the BAI of pedunculate oak is consistently slightly higher (from 2 to 3 cm^2). The relatively important fluctuations observed after the age of 150 years are due to a rapid decrease in the number of very old tree rings. The same type of exponential model has been defined using a curvilinear regression on both species:

Sessile oak

$$\mathrm{LN}(BAI) = 8.522 + 0.708 \times \mathrm{LN}\ (Age) - 1.095 \times 10^{-3} \times Age$$

Pedunculate oak

$$\mathrm{LN}(BAI) = 8.555 + 0.742 \times \mathrm{LN}(Age) - 1.945 \times 10^{-3} \times Age$$

These 2 adjustments have been used to standardize the raw data, *ie* to convert them into growth indices that can be studied without reference to their cambial age.

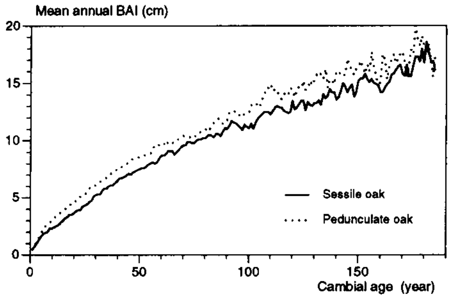

Fig 4. Mean annual basal area increment (BAI) of sessile oak (solid line) and pedunculate oak (dashed line) *vs* cambial age of the rings.

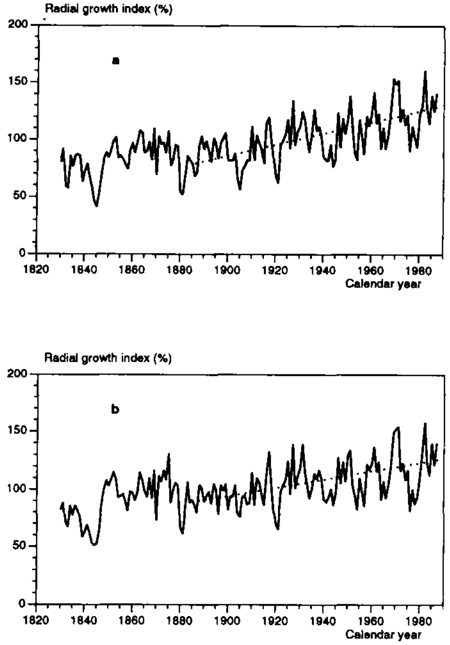

Fig 5. Mean radial growth index of sessile oak **(a)** and pedunculate oak **(b)** *vs* calendar years.

Development of growth indices according to the calendar year

The growth indices clearly confirm the preceding results, *ie* a strong increase for sessile oak (fig 5a) as well as for pedunculate oak (fig 5b). The growth increase of sessile oak (+64% between 1888 and 1987, significant at $p = 0.05$) is always stronger than that of pedunculate oak (+40%, significant at $p = 0.05$). There are strong interannual fluctuations, among which can be found all of the pointer years discussed earlier. Moreover, some 'crises', *ie* longer or shorter periods (from 5 to 10 years) of steeper or slighter growth decline, are apparent, *eg*, 1838–1848, 1879–1898, 1899–1910, 1917–1924, 1938–1946, and, especially, 1971–1982.

The difference in behaviour of the 2 oak species with regard to cambial age shown in table II suggests a separation in the growth indices of 'young' rings, *ie* less than 60 years (fig 6), and 'old' rings, *ie* more than 65 years (fig 7). The increase in the young rings of sessile oak is + 81% (significant at $p = 0.05$), and that of pedunculate oak + 49% (significant at $p = 0.05$). The increase in the old rings is respectively + 48% (significant at $p = 0.05$), and only + 15% (not significant at $p = 0.05$).

Modelling the annual growth index

As the long-term increase in radial growth is approximately linear for both species and the increase in atmospheric CO_2 is practically exponential, the logarithm of CO_2, LN*(CO_2)* has been used as a predictor in the regressions. Moreover, preliminary calculations have shown that low (below 0°C) temperatures in wintertime depress growth during the next vegetation period. In order to gain a better picture of this phenomenon, already detected for silver fir in northeastern France (Becker, 1989), a variable LN (T + 10) was utilized in the following calculations for January and February.

The autocorrelation, which is largely expressed by the correlation between *IC0* and *IC1*, was strong for both oak species, $r = 0.583$ for sessile oak and $r = 0.612$ for pedunculate oak. This has encouraged us to search for and quantify the possible lag effects of certain meteorological events that occur before the formation of a tree ring (year *y*). In fact, such lag effects have been verified back until year $y - 4$ for sessile oak and $y - 5$ for pedunculate oak. The existence of these lag effects multiplies the number of potential predictors. It thus becomes highly probable that a certain number of apparently statistically significant correlations will occur by chance even though they

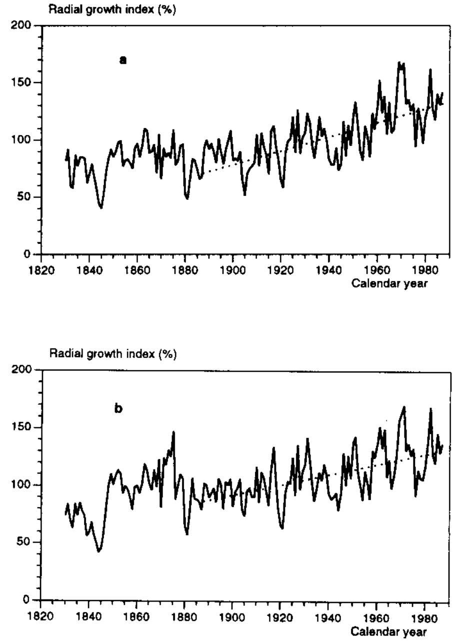

Fig 6. Mean radial growth index of sessile oak **(a)** and of pedunculate oak **(b)** *vs* calendar years. Only rings less than 60 years (cambial age).

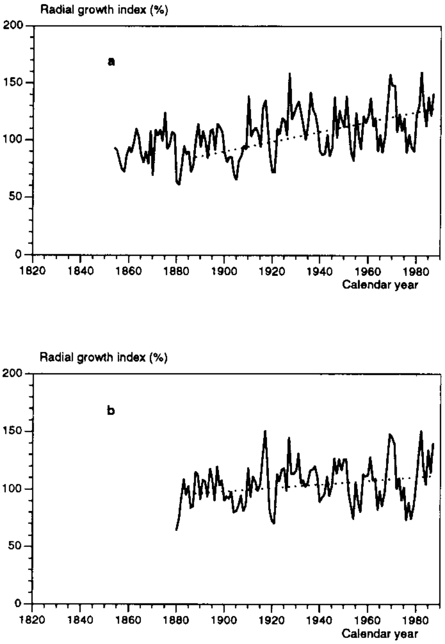

Fig 7. Mean radial growth index of sessile oak **(a)** and of pedunculate oak **(b)** *vs* calendar years. Only rings more than 65 years (cambial age).

are not biologically meaningful (Verbyla, 1986).

First, we employed a somewhat empirical approach to distinguish 'significant' variables. This consisted of evaluating the biological relevance and the overall consistency of the variables in the final model, especially when lag effects were detected. The case of July is special, and is discussed later. The variance explained amounts to 78.3% for sessile oak with 21 predictors (table III), and to 74.3% for pedunculate oak with 24 predictors (table IV). Figure 8 shows the estimated growth indices compared with the actual indices for sessile oak. The corresponding curve for pedunculate oak was essentially similar.

We then attempted to validate the models. This was done by dividing the total available period (1881–1987) into a calibration period (1881–1960) and a verification period (1961–1987) (Cook *et al*, 1987). The first period made it possible to elaborate a temporary version of the model, using the same variables as in the previous one, and this second model was then applied to the second period. This procedure resulted in a satisfactory similarity between the 2 models; before 1960 as well as after 1960, and for sessile oak (fig 9) as well as for pedunculate oak.

The proportion of variance explained increases progressively as the years prior to *y* are taken into account in the models (fig 10) , although more rapidly for sessile oak than for pedunculate oak. Simultaneously, the weight of *IC1* (autocorrelation) decreases and tends towards 0 for both species.

Table III. Model explaining the mean radial growth indices of sessile oak from 1886 to 1987 (102 values) according to atmospheric CO_2 and 21 monthly climatic parameters.

ICO	Partial F	Relative weight
$-1120.4 + 202.77 \times \ln(CO_2)$	47.9	9.3
$+ 19.299 \times \ln 0T1 + 10)$	19.5	5.4
$- 0.0720 \times 0P3$	2.7	−2.1
$+ 0.1349 \times 0P5$	10.6	4.2
$+ 0.1943 \times 0P6$	26.7	6.7
$+ 0.1679 \times 0P7$	16.6	5.6
$+ 0.1542 \times 0P8$	18.2	5.2
$- 0.0607 \times 1P3$	1.9	−1.7
$+ 2.0126 \times 1T4$	6.3	3.3
$+ 0.1666 \times 1P5$	16.2	5.1
$- 2.0126 \times 1T7$	14.5	−4.7
$+ 0.0915 \times 1P8$	6.7	3.1
$- 0.1599 \times 2P3$	13.5	−4.5
$+ 2.0594 \times 2T4$	6.4	3.3
$+ 0.0045 \times 2P5$	0.1	0.1
$+ 3.1696 \times 2T7$	13.8	5.0
$+ 0.0764 \times 2P8$	4.8	2.6
$+ 2.2978 \times 3T4$	8.4	3.7
$+ 0.1128 \times 3P5$	7.4	3.5
$- 2.4324 \times 3T7$	9.4	−3.9
$+ 0.0309 \times 3P8$	0.7	1.0
$- 3.3684 \times 4T8$	11.8	−4.9

CO_2 (atmospheric CO_2 concentration) is expressed in ppm; P (precipitation) in mm, and T (temperature) in °C. aPb and aTb are total precipitation and average temperature, respectively, of year $y - a$ (y is the year of ring formation) and month b. Relative weight (of a predictor) is the variation in ICO when the variable increases by the value of its standard deviation.

Table IV. Model explaining the mean radial growth indices of pedunculate oak from 1886 to 1987 (102 values) according to atmospheric CO_2 and 23 monthly climatic parameters.

ICO	Partial F	Relative weight
$-548.9 + 106.99 \times \ln(CO_2)$	12.7	4.9
$+ 13.547 \times \ln(0T1 + 10)$	9.4	3.8
$- 0.0497 \times 0P3$	1.2	−1.4
$+ 0.0779 \times 0P5$	3.3	2.4
$+ 0.1739 \times 0P6$	21.4	6.0
$+ 0.0916 \times 0P7$	4.7	3.1
$+ 0.1593 \times 0P8$	19.5	5.4
$- 0.9397 \times 1T3$	1.7	1.7
$+ 2.0523 \times 1T4$	6.4	3.3
$+ 0.1865 \times 1P5$	18.6	5.8
$- 2.0608 \times 1T7$	6.9	−3.3
$+ 0.0866 \times 1T8$	6.0	2.9
$- 0.1527 \times 2P3$	12.6	−4.3
$+ 1.5526 \times 2T4$	3.8	2.5
$+ 0.0408 \times 2P5$	0.8	1.3
$+ 3.8421 \times 2T7$	19.9	6.1
$+ 0.1054 \times 2P8$	9.0	3.5
$+ 2.4179 \times 3T4$	9.2	3.9
$+ 0.1268 \times 3P5$	8.4	3.9
$- 1.2425 \times 3T7$	2.3	−2.0
$+ 0.0239 \times 3P8$	0.4	0.8
$- 0.0955 \times 4P7$	6.6	−3.3
$- 3.5913 \times 4T8$	13.6	−5.2
$- 2.7710 \times 5T8$	7.8	−4.0

CO_2 (atmospheric CO_2 concentration) is expressed in ppm; P (precipitation) in mm and T (temperature) in °C. aPb and aTb are total precipitation and average temperature, respectively, of year $y - a$ (y is the year of ring formation) and month b. Relative weight (of a predictor) is the variation in ICO when the variable increases by the value of its standard deviation.

DISCUSSION

The mean annual basal area increment (BAI) according to cambial age of both oak species continues to increase after an age of 150 years, when it amounts to about 15 cm^2. This result is significantly different when compared to coniferous tree species, especially silver fir, in which BAI was found to reach a maximum at the age of 50 and then to decrease slowly (Bert and Becker, 1990). This simple observation provides support for the usual French silvicultural practice of planning the final felling of oak for an age of 150–200 years or more, while that of silver fir is much earlier (100–120 years).

According to an opinion widely held in France, the use of dendrochronology in ecophysiological studies (dendroecology) is mainly applicable to mountain coniferous species, especially in the case of open stands in which competition among the trees is low. The high number of pointer years found in the present study, and the strong climatic determinism of these years, emphasize that broadleaved species, even in dense stands, can be fruitfully investigated by dendroecological methods. This is particularly true for oaks (both sessile and

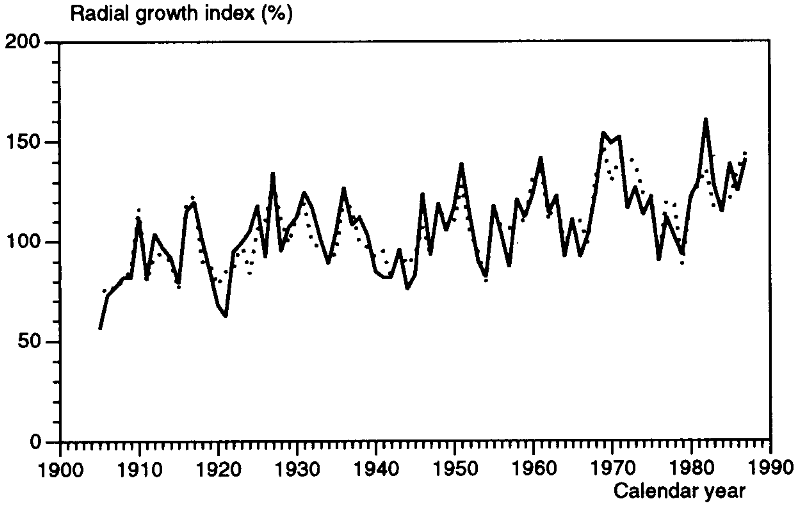

Fig 8. Actual radial growth indices of sessile oak (solid line) and indices estimated according to the climatic model (dashed line). Calibration period: 1887–1987.

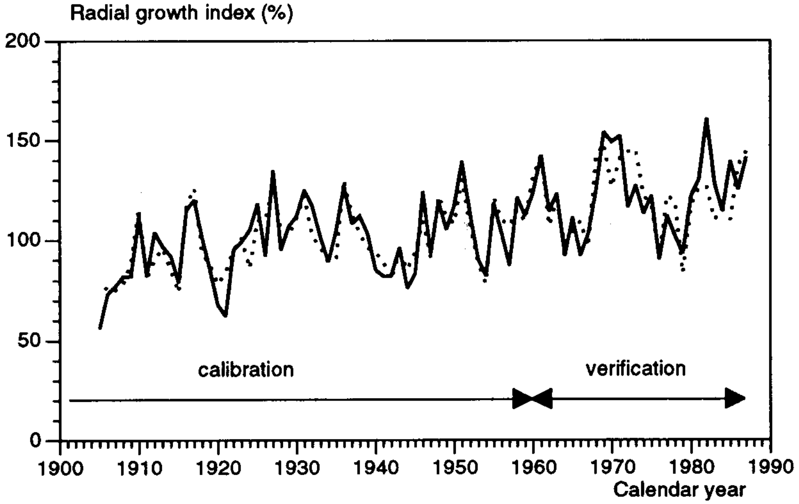

Fig 9. Validation of the climatic model constructed for sessile oak using a calibration period (1887–1960) and a verification period (1961–1987). Solid line represents actual growth index; dashed line represents estimated growth index.

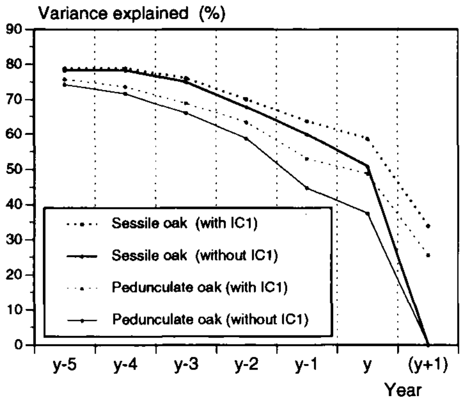

Fig 10. Proportion of explained variance in the growth index *(IC0)* of year *y* according to the number of years taken into account starting from year *y* for the climatic predictors. Thick lines represent sessile oak; thin lines represent pedunculate oak; solid lines represent only climatic variables in the model; dashed lines represent climatic variables plus ring of year *y* – 1 *(IC1)* in the model.

pedunculate), which rank among the major broadleaved trees used for timber production in western Europe.

In the case of pedunculate oak, the number of pointer years highly characteristic of a growth decrease was about twice that for a growth increase. In contrast, the respective numbers were approximately equal for sessile oak. This suggests that sessile oak is able to recover more rapidly than pedunculate oak after stresses that lead to a growth decrease. Such a difference between the 2 species is consistent with the longer and stronger after-effects of unfavourable climatic events found for pedunculate oak compared to sessile oak (fig 10). Unfavourable events of this sort (mainly hot and dry periods), responsible for severe growth decreases, occurred during the last century, principally in 1917–1924, 1938–1946 and 1971–1982 (fig 5). In fact, these crises fit precisely the main declines which old oak stands (more than 80–100 years) suffered from in many regions in western Europe (Delatour, 1983), but which only proved fatal to pedunculate oak (Becker and Lévy, 1982).

Irrespective of the method used for processing the data, there is clear evidence of a long-term increase in radial growth in both species for more than a century (table II, fig 5). However, this increase is higher for sessile oak (+64%) than for pedundulate oak (+40%). Moreover, the difference between the 2 species is even clearer when we compare the BAI of the 'old' rings, *ie* more than 65 years (fig 7), which show that the increase is no longer significant in pedunculate oak, while it is still high (+48%) in sessile oak. It thus appears that, unlike sessile oak, pedunculate oak (more precisely the mature trees) have not benefited from the progressive environmental changes of the last 100–150 years. This last result seems to be consistent with the greater susceptibility of pedunculate oak to growth declines. Furthermore, it reinforces a recent hypothesis suggesting a slow but general retreat of pedunculate oak in favour of sessile oak in many regions of France (Becker and Lévy, 1982).

Except for the precipitations in year *y* – 4 and the temperatures in year *y* – 5, which express the longer lag effects discussed above for pedunculate oak, the significant predictors retained are the same in both models (tables III and IV).

The case of July appears somewhat disconcerting because the related parameters from years *y*, *y* – 1 and *y* – 3 on the hand, and years *y* – 2 and *y* – 4 on the other, can be given opposing biological meanings. This could be an artifact due to the large number of potential predictors. However, the corresponding values of the partial *F* rank among the more significant in the models. An alternative explanation could involve specific patterns for shoot and root growth: the poor water supply conditions in July of year *y* (low precipitation and/or high temperature) would result in decreased shoot growth during years *y* and *y* + 1. In contrast, these conditions would stimulate root growth during year *y* which, in turn, would result in increased shoot growth during year *y* + 2. This sort of alternate effect would persist until year *y* + 3 in sessile oak, and *y* + 4 in pedunculate oak. It was eventually decided to keep these variables in the models.

The interpretation of the other climatic variables is much easier. A very low temperature in January has a negative influence on the growth during the following growing season, but there are no longer lag effects. Sessile oak is more sensitive to this variable, which is consistent with its reputation as a slightly more thermophilous species.

High precipitation in May, June and August (or low temperatures, which correlate positively with precipitation during these months) are favourable for growth. Lag effects are apparent for May and August only, but not for June, for which no clear explanation was found. The case of July was discussed above.

The negative effect of high precipitation (or low temperatures) in March and low temperatures in April may be explained by 2 complementary theories: firstly the related shortening of the growing season; secondly, and more importantly, the unfavourable effects of an excess of water on the soil structure and on the rooting of the trees owing to the impermeability of the subsoil.

Of the recent dendroecological studies that demonstrate a long-term increase in the wood production rate of forest ecosystems, some tend to dismiss the direct role of atmospheric CO_2 (Becker, 1989; Graumlich *et al*, 1989). On the other hand, they cannot exclude the indirect role of CO_2 on climate (Wigley *et al*, 1984). In the present study, the climate variability alone appears to be insufficient to explain the trends observed, especially in sessile oak. Moreover, CO_2 appears to be the most important predictor principally explaining the long-term growth increase observed. However, caution is necessary in interpreting this result, which, strictly speaking, does not prove a pure causal relationship. CO_2 could be partly responsible for the trends observed, but some other variables which vary in time in a similar manner to CO_2 may also be important. It may not be possible to include these in the models because of the lack of historical data: for example, atmospheric anthropogenic deposits, especially of nitrogen compounds (Kenk and Fischer, 1988).

Recent studies conclude that the CO_2 concentration will probably double by the year 2050, which might lead to increased wood productivity in boreal and temperate forest ecosystems (Pastor and Post, 1988). In the case of sessile oak in western Europe (and assuming that the model in table III is real and can be extrapolated), the growth rate could rise from 140% in 1988 (fig 5a) to 280% in 2050, *ie* exactly double. However, such a long-term forecast appears rather unlikely because the climatic conditions will probably change as well and become incompatible with the ecological requirements of oak. Perhaps the first signs of this incompatibility are already perceptible in pedunculate oak, through its present response to climatic factors and atmospheric CO_2.

REFERENCES

Becker M (1987) Bilan de santé actuel et rétrospectif du sapin (*Abies alba* Mill) dans les Vosges. Étude écologique et dendrochronologique. *Ann Sci For* 44, 379-402

Becker M (1989) The role of climate on present and past vitality of silver fir forests in the Vosges mountains of northeastern France. *Can J For Res* 19, 1110-1117

Becker M (1992) Deux indices de compétition pour la comparaison de la croissance en hauteur et en diamètre d'arbres aux passés sylvicoles variés et inconnus. *Ann Sci For* 49, 25-37

Becker M, Lévy G (1982) Le dépérissement du chêne en forêt de Tronçais. Les causes écologiques. *Ann Sci For* 39, 439-444

Becker M, Lévy G (1982) Le point sur l'écologie comparée du chêne sessile et du chêne pédonculé. *Rev For Fr* 42, 148-154

Bert GD, Becker M (1990) Vitalité actuelle et passée du sapin (*Abies alba* Mill) dans le Jura. Étude dendroécologique. *Ann Sci For* 47, 395-412

Briffa KR (1992) Increasing productivity of 'natural growth' conifers in Europe over the last century. *In: Tree rings and Environment Proc Intern Dendrochronological Symp*, Ystad, Sweden, 3-9 Sept 1990. *Lundqua Report* 34, 64-71

Cook ER, Johnson AH, Blasing TJ (1987) Forest decline: modeling the effect of climate in tree rings. *Tree Physiol* 3, 27-40

d'Arrigo R, Jacoby GC, Fung IY (1987) Boreal forests and atmosphere-biosphere exchange of carbon dioxide. *Nature (Lond)* 239, 321-323

Delatour C (1983) Les dépérissements de chênes en Europe. *Rev For Fr* 35, 265-282

Federer CA, Tritton LM, Hornbeck JW, Smith RB (1989) Physiologically based dendroclimate models for effects of weather on red spruce basal-area growth. *Agric For Meteorol* 46, 159-172

Fritts HC (1976) *Tree rings and climate.* Academic Press, New York

Graumlich LJ, Brubaker LB, Grier CC (1989) Long-term trends in forest net primary productivity: Cascade Mountains, Washington. *Ecology* 70, 405–410

Hari P, Arovaara H, Raunemaa T, Hautojärvi A (1984) Forest growth and the effects of energy production: a method for detecting trends in the growth potential of trees. *Can J For Res* 14, 437-440

Jordan DN, Lockaby BG (1990) Time series modelling of relationships between climate and long-term radial growth of loblolly pine. *Can J For Res* 20, 738-742

Jozsa LA, JM Powell (1987) Some climatic aspects of biomass productivity of white spruce stem wood. *Can J For Res* 17, 1075-1079

Keeling CD (1986) Atmospheric CO_2 concentrations. Mauna Loa Observatory, Hawai 1958-1986. NDP-001/R1. *Carbon Dioxide Information Analysis Center.* Oak Ridge National Laboratory, Oak Ridge, TN, USA

Kenk G, Fischer H (1988) Evidence from nitrogen fertilization in the forests of Germany. *Env Poll* 54, 199-218

Kenk G, Rommel WD, Spiecker H (1989) Weitere Ergebnisse zum aktuellen und früheren Wachstumsverhalten von Fichten *KfK-PEF 50*, 117-126

Lamarche VC, Graybill DA, Fritts HC, Rose MR (1984) Increasing atmospheric carbon dioxide: tree ring evidence for growth enhancement in natural vegetation. *Science* 225, 1019-1021

Monserud RA (1986) Time-series analyses of tree-ring chronologies. *For Sci* 32, 349-372

Nertel A, Moor E, Oeschger H, Stauffer B (1985) Evidence from polar ice cores for the increase in atmospheric CO_2 in the past two centuries. *Nature (Lond)* 315, 45-47

Nieminen, TM (1988) Étude dendroécologique du chêne (pédonculé et sessile) et du hêtre dans une forêt de la plaine lorraine. Diplôme d'Études Approfondies, Université de Nancy

Pastor J, Post WM (1988) Response of northern forests to CO_2-induced climate change. *Nature (Lond)* 334, 55-58

Payette S, Filion L, Gauthier L, Boutin Y (1985) Secular climate change in old growth tree-line of northern Québec. *Nature (Lond)* 315, 135-138

Peterson DL, Arbaugh MJ, Wakefield VA, Miller PR (1985) Evidence of growth reduction in ozone-injured Jeffrey pine (*Pinus jeffreyi* Grev and Balf) in Sequoia and Kings Canyon national parks. *J Air Poll Control Assoc* 37, 906-912

Peterson DL, Arbaugh MJ, Robinson LJ, Derderian BR (1990) Growth trends of whitebark pine and lodgepole pine in a subalpine Sierra Nevada forest, California, USA. *Arct Alp Res* 22, 233-243

Verbyla D (1986) Potential prediction bias in regression and discriminant analysis. *Can J For Res* 16, 1255-1257

Wagener K, de Luca Rebello A, Hollstein E (1983) Increasing productivity in recent European oak trees. *Radiat Environ Biophys* 22, 303-310

Wigley TM, Briffa KR, Jones PD (1984) Predicting plant productivity and water resources. *Nature (Lond)* 312, 102-103