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ORIGINAL ARTICLE

F. Lebourgeois · N. Bréda · E. Ulrich · A. Granier

Climate-tree-growth relationships of European beech (*Fagus sylvatica* L.) in the French Permanent Plot Network (RENECOFOR)

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Abstract The influence of climate on the radial growth of *Fagus sylvatica* was investigated using 15 chronologies developed from mature stands of the French Permanent Plot Network (RENECOFOR) growing under different climatic and soil conditions. The relationships between climate and ring widths were analyzed using extreme growth years, simple correlations and response functions analysis. Monthly climatic regressors were derived by a physiological water balance model that used daily climatic data and stand parameters to estimate soil water deficits. The three most frequent negative pointer years (1959, 1989, 1976) result from a particularly intense and durable drought, whereas positive years (1977, 1958) coincide with wet conditions. The total ring chronology variance attributable to climate averages 34.1% (15.8% –57%). Current early-summer soil water deficit enters in 10 models and the deficit in June explains alone a large part of the radial growth variability (mean value: 26.6%). Temperature or soil water deficit for the other months and weather conditions during the previous season were of little consistency across stands. The response pattern of earlywood is very similar and the percentage of variance explained is higher (16.2% –57.8%). Latewood widths present a different response pattern. High minimum temperature in August and/or September often favour wide latewood widths and monthly water deficits play a secondary role. The percentage of variance explained ranges from 8.8% to 67.4%. Soil water capacity strongly modulates ring characteristics and climate-growth relationships. Mean sensitivity, expressed population signal, signal-to-noise ratio and the strength of growth-climate correlations increase with decreasing soil water capacity.

Keywords *Fagus sylvatica* · Tree ring · Water balance · Drought · Pointer years

Introduction

In 1992, a forest network was created by the French National Forest Office (ONF) to complete the existing French forest health monitoring activities. The main objective of this French Permanent Plot Network for the Monitoring of Forest Ecosystems (RENECOFOR), covering the entire country of France, is to detect possible long-term changes in the functioning of a great variety of forest ecosystems, selected as regionally representative stands, and to determine as far as possible the reasons for the changes. It consists of 102 permanent plots (ten different species), which are to be monitored for at least 30 years. Each plot has a surface of about 2 ha, the central 0.5 ha of which is fenced. In 1997, a dendrochronological study was carried out to learn about the growth history of the RENECOFOR stands before the network was established (Lebourgeois 1997). To provide a view of the behavior of beech under a large range of climate and site conditions, and to explain the determinism of growth crisis observed in the stands, the relationships between beech tree-ring widths and monthly climate were studied. Commonly used procedures for studying relationships between tree growth and climatic constraints are based on correlations between standardized tree-ring width indices and monthly climate data (Fritts 1976). Radial growth is assumed to reflect physiological processes, and monthly mean temperature and total

F. Lebourgeois (✉)
UMR INRA-ENGREF 1092, Laboratoire d'Etude des Ressources Forêt-Bois (LERFOB), Equipe Ecosystèmes Forestiers et Dynamique du Paysage,
54042 Nancy Cedex, France
e-mail: lebourgeois@engref.fr
Tel.: +33-3-83396874
Fax: +33-3-83396878

N. Bréda · A. Granier
UMR INRA-UHP 1137, Ecologie et Ecophysiologie Forestières, INRA,
54280 Champenoux, France
e-mail: breda@nancy.inra.fr
e-mail: agranier@nancy.inra.fr

E. Ulrich
Office National des Forêts, Département Recherche,
77300 Fontainebleau, France
e-mail: Erwin.Ulrich@onf.fr

precipitation are assumed to correlate with climatic phenomena that influence tree physiology. Regression analyses commonly model linear growth-climate relationships at time scales of months or longer, but physiological responses of trees to climatic phenomena occur at time scales from seconds to days and may include threshold effects (Foster and LeBlanc 1993). Different studies have used daily climatic parameters to define "physiological" indices such as potential evapotranspiration, soil-moisture stress. (Zahner and Stage 1966; Zahner and Donnelly 1967; Giles et al. 1985; Wickramasinghe 1988; Roberston et al. 1990). In their physiological approach to dendroclimatic modeling of oak radial growth, Foster and LeBlanc (1993) clearly showed that individual physiological response indices were better correlated with radial growth than were monthly climatic variables, and were more amenable to biological interpretation than models using monthly climate variables. They also showed that the physiological approach reduced the number of predictor variables.

The effects of droughts on annual tree-ring of beech have been reported in different areas throughout Europe (Dittmar et al. 2003), but in France dendroclimatological investigations of beech are scarce and have been mainly reported in the northeastern calcareous plain (Badeau 1995). The aim of this study is to ascertain the relationships between climate and total ring, early- and latewood radial growth of European beech trees growing under different sites and climatic conditions (low and high altitudes, dry-mesic and moist soils) in the French Permanent Plot Network for the Monitoring of Forest Ecosystems network (RENECOFOR). 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 (Schweingruber et al. 1990; Desplanque et al. 1999), and (2) by establishing the mean relationships between tree ring and climate through simple correlations and response-function analysis (Fritts 1976). Soil water deficits calculated from a retrospective daily soil water deficit modelling were used as climatic variables (Granier et al. 1999). This approach involves a soil iterative water balance model that calculates daily changes of soil water content, and soil water deficit during phenologically defined periods of the growing season. Climatic input data are daily potential evapotranspiration and daily rainfall. Site and stand requested parameters are soil water capacity, rooting depth and vertical distribution, maximum leaf area index and global radiation extinction coefficient. Model outputs include soil water deficit indexes, which integrate both duration and intensity of drought constraints in forest stands.

Materials and methods

Site characteristics

The 15 European beech stands were sampled in different French bioclimatic areas, between 43° and 49.3° N and 3.3° W and 6.4° E (Fig. 1). Plots were selected to obtain a wide range of site conditions (Tables 1 and 2). The general topography is gently rolling (slope$<$20% in most stands) with elevation ranging from 50–1,300 m above sea level. The examined forests are naturally regenerated beech monocultures (*Fagus sylvatica* L.) composed of even-aged stands from 54 to 160 years old. In the selected stands, beech is managed in high forests with regular thinnings (Cluzeau et al. 1998). The site type was identified using the species composition of the ground vegetation (Dobremez et al. 1997), and pedological properties were observed on two trenches per plot (Brêthes and Ulrich 1997).

Table 1. Site description and characteristics of selected stands. *BZ* Bioclimatic zone, *N* north, *NE* northeast, *SE* southeast, *SW* southwest, *W* west. *Topo* Topography, *P* plateau, *R* ridgetop, *S* slope. *H* and *DBH* Tree height and diameter at breast height, mean values (SD). *LAI* Maximum Leaf Area Index. *N* number of trees per hectare. *Age** Age at breast height, mean values (SD) maximum

Site Code	Latitude	Longitude	BZ	Topo	Aspect	Slope (%)	Alt. (m)	H (m)	DBH (cm)	LAI (m^2/m^2)	N (No./ha)	Age*(years)
HET 02	49°12′21″ N	3°07′36″ E	N	P	–	0	145	29.2 (2)	42 (6)	10.2	318	54 (4)/66
HET 03	46°11′37″ N	2°59′54″ E	NE	R	N	15	590	28.9 (1.7)	39 (6)	7.8	261	87 (23)/117
HET 04	44°07′52″ N	5°48′00″ E	SE	S	N	50	1300	25.5 (1.3)	38 (5.1)	7.8	350	85 (2)/156
HET 09	42°55′53″ N	1°16′56″ E	SW	S	SW	32	1250	21.4 (1.4)	37 (4.7)	7.5	413	152 (9)/166
HET 14	49°10′57″ N	0°51′23″ W	W	P	–	4	90	25.2 (1.8)	44 (4.8)	9	260	83 (4)/97
HET 21	47°48′50″ N	4°51′18″ E	NE	P	NE	3	400	28.6 (1.5)	44 (4.8)	7.3	231	128 (13)/156
HET 29	47°50′16″ N	3°32′34″ W	W	P	–	0	50	23.1 (4.5)	29 (4.9)	8.8	537	64 (4)/70
HET 52	47°47′46″ N	5°04′17″ E	NE	P	–	0	440	30.2 (1.5)	42 (4.4)	8.4	282	106 (4)/113
HET 54a	48°30′35″ N	6°42′23″ E	NE	S	E	5	325	29.1 (1.8)	44 (6.6)	8.5	278	95 (13)/127
HET 54b	48°38′57″ N	6°04′04″ E	NE	P	–	2	390	28.3 (1.6)	44 (4.2)	9	242	99 (15)/158
HET 55	49°10′15″ N	5°00′17″ E	NE	P	–	0	250	29.3 (1.7)	46 (5.2)	7.8	210	88 (8)/108
HET 60	49°19′27″ N	2°52′34″ E	N	P	–	0	138	26.6 (1.2)	34 (4.2)	9.2	633	62 (3)/70
HET 64	43°09′01″ N	0°39′29″ W	SW	S	NW	44	400	28.4 (2)	41 (7.9)	7.2	485	67 (7)/83
HET 65	43°01′36″ N	0°26′12″ E	SW	S	NW	25	850	29.5 (1.9)	50 (5.1)	5.4	201	160 (4)/169
HET 88	48°06′21″ N	6°14′50″ E	NE	R	W	3	400	24.7 (2.4)	32 (4.1)	8.6	764	68 (7)/78

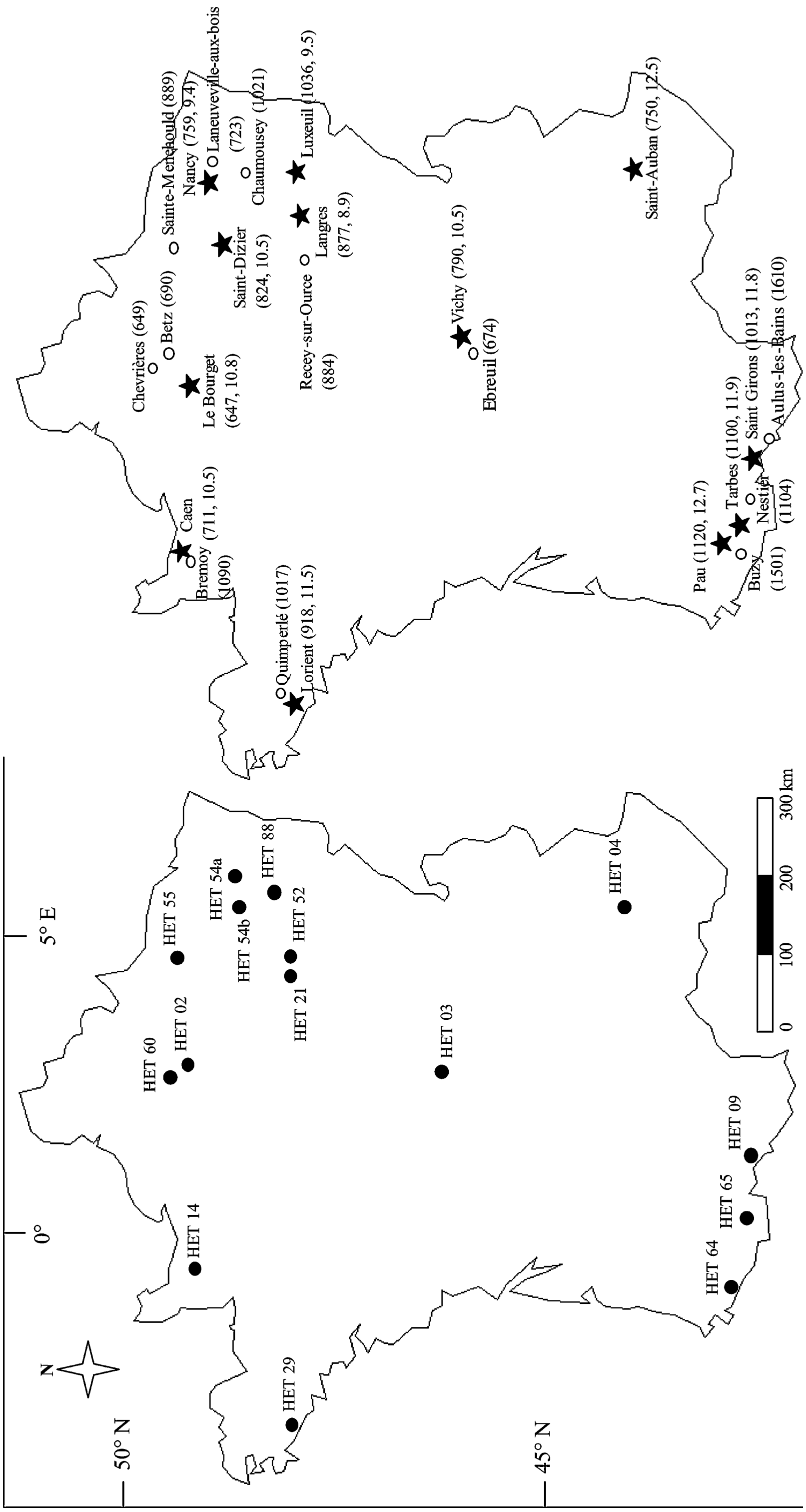


Fig. 1 Geographical location of the 15 studied European beech stands (HET, *filled circles*) and the 24 meteorological stations (source: Météo France network). *Filled stars* stations with daily temperature (°C, min and max), precipitation (mm), cumulative global radiation [J/m^2], mean wind speed [m/s] and mean vapour pressure deficit (Pa) data. *Open circles* stations with only daily precipitation data. The first value in brackets corresponds to the mean annual precipitation (P in mm) and the second to the mean annual temperature (T in °C) (reference period 1961–1990). For each plot, the number indicates the sampling department

Standard dendrochronological methods

A total of 450 dominant trees were cored to the pith with an incremental borer at breast height (30 trees per plot). The 33,810 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 data). Early- and latewood transitions within the annual rings were defined according to qualitative aspects. The individual ring-width series were crossdated after progressively detecting regional pointer years. For each site, the pointer years were defined for each ring component as those calendar years when at least 75% of the 30 cross-dated trees

Table 2 Soil description of selected stands. Soil types were defined according to the French pedological reference. Humus type: *E* eumull, *M* mesomull, *D* dysmull, *O* oligomull, *Dy* dysmoder, *Mo* moder, *H* hemimoder. Soil texture: *L* loam, *S* sand, *C* clay. Soil depth according to root maximal extension, used for soil water content (EWm) calculation

Site code	Soil type	Humus type	Dominant texture	Soil depth (cm)	Soil water content (mm)	Phytosociological community
HET 02	Luvisol-redoxisol	Mo-H	L	130	274	*Galio odorati-Fagenion*
HET 03	Alocrisol typique	Dy-O	L-S-C	100	154	*no data*
HET 04	Calcisol colluvial	O	L-C	100	150	*Geranio nodosi-Fagenion sylvaticae*
HET 09	Podzosol ocrique	H	L-S	120	115	*Luzulo sp. pl. - Fagion sylvaticae*
HET 14	Alocrisol typique leptique	Mo-Dy	L-S	110	100	*Carpinion betuli*
HET 21	Rendosol	E-M	L-C	100	84	*Cephalanthero-Fagion*
HET 29	Calcisol	Dy	L-S	120	199	*Quercenion robori-petraeae*
HET 52	Rendosol	E-M	C	50	77	*Cephalanthero-Fagion*
HET 54a	Neoluvisol redoxique	M-D	L	70	93	*Lonicero periclymeni-Carpinenion betuli*
HET 54b	Calcosol	M	C-L	100	87	*Daphno laurealae-Carpinenion betuli*
HET 55	Podzosol ocrique	H	L-S	120	98	*Lonicero periclymeni-Carpinenion betuli*
HET 60	Calcisol redoxique	O	S-L	100	109	*Galio odorati-Fagenion*
HET 64	Calcisol	O	L-C-S	100	119	*Fagio sylvaticae*
HET 65	Alocrisol typique	Mo-Dy	L-C-S	150	188	*Luzulo sp. pl. - Fagion sylvaticae*
HET 88	Alocrisol typique	M	L-S-C	120	151	*Quercenion robori-petraeae*

presented the same sign of change (at least 10% narrower or wider than the previous year). Thus, each pointer year was expressed as a relative growth change in percent (Becker et al. 1994; Lebourgeois 1997). Absolute dating was checked by program COFECHA (Holmes 1994), which identifies all locations within each ring series that may have erroneous cross-dating. Standardization of measurement series was done using the program PPPBase (Guiot and Goeury 1996). Each individual ring-width series were standardized by removing low- and intermediate-frequency variations, using the appropriate Auto-Regressive Moving-Average procedure (Box and Jenkins 1976; Guiot 1986). At each site, the residuals were averaged by year to develop a mean chronology that represented the common high-frequency variation that existed in the individual series. A mean chronology was calculated for each ring component separately. Statistic parameters were calculated for the maximum period common to all cores (1949–1994; 46 years) (except HET02, 1952–1994). The mean sensitivity (MS) and the first-order autocorrelation coefficient (AC) of the ring widths were calculated for each tree and averaged per plot. MS is a measure of year-to-year variability and AC assesses the influence of the previous year's growth upon the current year's growth (Fritts 1976). Series intercorrelation was estimated according to formulae given in Briffa and Jones (1990). The statistics of expressed population signal (EPS) and signal-to-noise ratio (SNR 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 (Wigley et al. 1984; Oberhuber et al. 1998). Though a specific range of EPS values which constitute acceptable statistical quality cannot be given, Wigley et al. (1984) suggest a threshold of 0.85 as reasonable. The signal-to-noise ratio (SNR) is defined as SNR $= Nr/(1-r)$ where$r$ is the average correlation between trees and N is the number of trees within a site chronology.

Regional climate

Beech stands cover various climatic conditions, distributing from west to east in the northern area (11 stands) and in the southern mountain region (4 stands) (Fig. 1, Table 3). The climate of the western zone is mild oceanic with mild, humid winters and fresh, humid summers. The north-eastern zone presents a semi-continental climate with cold, humid winters and mild, humid summers. The south-western zone presents wet, mild winters and dry, warm summers.

Table 3 Mean climatic characteristics of each sampling bioclimatic area. *DJF* winter (December–February); *MAM* spring (March–May); *JJA* summer (June–August); *SON* autumn (September–November). *Fd* number of frost days ($T_{\min}<0^\circ$C); *Wd* warm days ($T_{\max}>25^\circ$C); *Rd* rainy days ($P>0$ mm) (reference period: 1961–1990)

Bioclimatic zone	No. of stations	No. of stands	Rd	Precipitation (mm)					Mean Temperature (°C)					Jan	July	Fd	Wd
				Annual	DJF	MAM	JJA	SON	Annual	DJF	MAM	JJA	SON				
West	4	2	179	933	294	210	164	265	11.0	5.8	9.7	16.5	11.9	5.4	17.3	38	26
North	3	2	160	662	160	166	163	173	10.8	4.1	9.9	17.7	11.5	3.5	18.5	55	41
Northeast	10	7	166	848	213	210	213	212	9.8	2.2	9.1	17.4	10.4	1.5	18.3	83	45
Southwest	6	3	167	1,242	337	362	254	289	12.1	6.0	10.7	18.6	13.2	5.5	19.5	50	61
Southeast	1	1	111	750	168	187	172	221	12.5	4.9	11.2	20.7	13.1	4.3	22.0	60	94

A daily soil water balance model was used to quantify retrospectively drought intensity and duration in forest stands (Granier et al. 1999). This model was already used to relate the effects of soil drought on radial growth of oak stands (Bréda 1994), and for beech trees growing in the northeastern calcareous plain (Badeau 1995). The model simulated accurately the dynamics of soil water depletion and recharge, and predicted the main components of forest water balance. This model is iterative and the variation in soil water content are calculated at a daily pace as: $\Delta W = P - \mathrm{In} - T - \mathrm{Eu} - D$, where ΔW is the change in soil water content between two successive days, P = rainfall, In = rainfall interception, T = stand transpiration, Eu = Evaporation from understorey plus soil, and D = drainage.

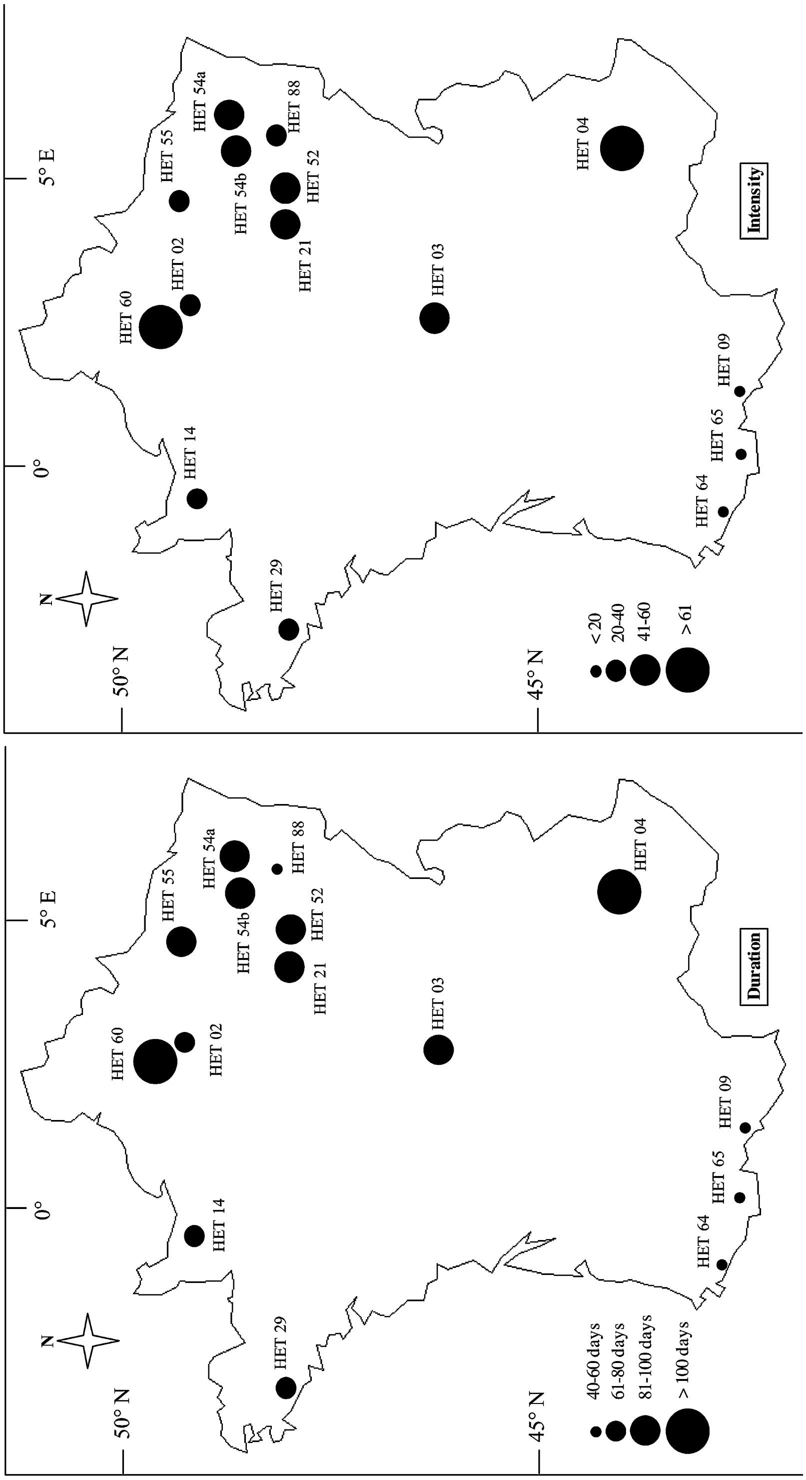
Required input climatic data are daily potential evapotranspiration and rainfall. For this study, sampled meteorological stations were selected based on their homogeneity and location in order to be the most representative and the nearest climatic data. Daily temperature ($T_{\min}$, $T_{\max}$; °C), precipitation (mm), cumulated global radiation (J m^{-2}), mean wind speed (m s^{-1}) and mean vapour pressure deficit (Pa) were available for 12 stations (Météo-France network, Fig. 1). To reduce the effect of the spatial variability of precipitation, the sample was completed with 12 stations with only daily precipitation data (mean distance from stands = 11 km, Fig. 1). The Penman equation was used to calculate the daily potential evapotranspiration (PET) from the raw data. This equation is considered as an index for evapotranspiration rather than a model, because it does not take into account surface resistance of vegetation, and aerodynamic resistance is calculated using a unique relationship, independent of canopy structure. Moreover, different simulations showed that Penman equation as compared to Penman Monteith formula did not modify water stress indexes to a large extent (Granier et al. 1999).

To calculate the daily water balance, required site and stand parameters are maximum extractable soil water ($\mathrm{EW_M}$), growing season duration and leaf area index (LAI), the latter controlling (I) global radiation extinction coefficient (k), (ii) stand transpiration; (iii) forest floor evapotranspiration; and (iv) rainfall interception. A detailed parameterization was made at each sampled site. The extractable soil water of each soil horizon was estimated according to textural properties, depth and coarse element percentages. Soil depth averaged 110 cm except if physical or pedological constraints to root penetration were observed in at least one of the two trenches (Table 2). Vertical root distribution was split in two layers, including 75% or 25% of fine roots respectively. Soil extractable water was calculated for each of the two root layers as the cumulated volume of the corresponding pedological horizons. Soil types vary from rendosol with low maximum extractable soil water ($\mathrm{EW_M}$) (77 mm) to deep luvisol with high $\mathrm{EW_M}$ up to 250 mm (French pedological reference) (Table 2). Leaf area indexes were estimated from an average value of leaf falls during 1996 (Bréda 2003). The range of LAI is 5.4 to 10.2 $\mathrm{m^2/m^2}$ and the mean value is 9 $\mathrm{m^2/m^2}$ (Table 1). The growing season corresponds to the period between budburst and leaf yellowing dates. For each beech stands, this period was estimated according to the phenological data available in the network (Lebourgeois et al. 2002).

Rainfall interception was calculated in the model from functions proposed by Aussenac (1968), and interception was reduced during 30 days of leaf expansion and of leaf fall. If rainfall was less than 1 mm, interception was assumed to be 100%. When water is not limiting, understorey and soil evapotranspiration (Eu) mainly depends on available energy below trees (Granier et al. 1999). Available energy below trees is proportional to global radiation above the canopy, and dependent on LAI of the tree layer. In the model, available energy below the canopy was calculated from the Beer-Lambert function and a light coefficient of extinction (k=0.5). During water stress, Eu was assumed to decrease linearly with relative extractable water in the upper soil layer.

Work done at stand level (but also at tree level) showed a strong dependency of transpiration (T) from potential evapotranspiration (PET), LAI and soil water content (Bréda et al. 1995; Granier et al. 1999). Under non-limiting soil water content and high LAI ($\geq$6), the ratio (r) T/PET averages 0.75 (Granier et al. 1999). Below this level of LAI, a linear relationship exists between r and LAI. Under water stress conditions, r decreases linearly as soon as relative extractable water (REW) drops below a threshold of 0.4 (critical REW, REWc) of maximum extractable water ($\mathrm{EW_M}$). REWc is basically a physiological threshold at which regulation of transpiration begins to occur due to stomatal closure. In the model, two stress indices are calculated if REW<REWc (see Fig. 4). Both indices can be monthly, seasonally or annually cumulated. The first index corresponds to the number of days of water stress, i.e. the number of days during which $\mathrm{REW}<0.4\times\mathrm{EW_n}$. The second index

Fig. 2 Mean annual soil water deficit duration (number of days of water deficit) and intensity calculated for the 15 beech stands. Size of the symbols is proportional to drought duration and intensity (see Materials and methods)



is the water stress index, which cumulates the difference between REW and REWc (corresponding to the dashed area in Fig. 4). Water balance model was applied for different periods according to available daily climatic parameters (shortest period: 1968–1994; longest period: 1949–1994). The mean characteristics of soil water deficits (intensity and duration) observed at each site are presented in Fig. 2. Mean annual water stress duration lasted more than 1 month in all sites with the exception of two sites (HET09, HET64), while maximum drought duration at four sites lasted over 3 months.

Response function analysis

For each ring component, the effect of climate on growth was investigated in three steps. First, pointer years were compared with climatic data (seasonal and monthly cumulated water balance indexes). Second, simple correlation analyses were performed between the annual water balance index, the annual number of days with soil water deficit and the master index chronology. Third, bootstrapped response functions were calculated using 12 monthly water balance indexes (Def) (May to October for the year and for the previous year) and 12 maximum or minimum monthly temperature [from November to the previous growing season ($t-1$) to October of the year in which the ring was formed] as regressors. The master chronology of residuals, resulting from ARMA modeling of ring sequences, was used as dependent variables (Guiot 1991). At each site and for each ring compartment, two response functions were established taking into account as predictors the (Def-$T_{\min}$) and (Def-$T_{\max}$) combinations. 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 (Tessier 1989; Guiot 1991). 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 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 (Guiot 1991). Means (R) and standard deviations (S) are also computed for the multiple correlation and the independent correlation sets. When the ratio R/S 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 (code 1, 2, 3 and 4 in Table 6) (Tessier 1989; Guiot 1991). The variance accounted for by the climatic variables is given by the r^2 value. According to the available daily climatic series, response functions were calculated on sequences of 27–46 years (1968–1994; 1949–1994).

A cluster analysis was performed on response functions to detect beech populations which respond in a similar way to prevailing environmental factors (Tessier 1989; Oberhuber et al. 1998). The (dis)similarity between sites was measured as Euclidean distance as: distance $(x, y) = \{\sum_i (x_i - y_i)^2\}^{1/2}$ and the hierarchy computed according to Ward's method. This method uses an analysis of variance approach to evaluate the distances between clusters and attempts to minimize the Sum of Squares (SS) of any two (hypothetical) clusters that can be formed at each step.

Results

Ring characteristics

Selected trees show different levels of growth. Narrow ring-widths are observed for the old stands growing at high elevations (HET09, HET65) and on dry soils (HET21, HET52) (Tables 2 and 4). Earlywood represents between 70 and 90% of the total ring according to cambial age (data not shown). For the period 1949–1994, mean sensitivity (MS) of total ring width ranges from 0.199 to 0.319 (mean value: 0.266) (Table 4). Values of MS are higher for earlywood-width than for total ring-width at all sites (0.235–0.385; mean value: 0.317). For latewood-width, MS is higher at 9 sites (0.198–0.328; mean value: 0.278). MS is higher for earlywood than latewood at 11 sites. The difference between both compartments suggests that earlywood is more sensitive to climate than latewood. First-order autocorrelation coefficients averaged 0.523, 0.504 and 0.253 for total ring, earlywood and latewood, respectively. For earlywood, this high coefficient indicates a strong dependence of current growth on the previous year's growth. Because of its lower autocorrelation, latewood seems to be the least deterministic part of the ring. All total ring and earlywood EPS-values exceed the suggested threshold of 0.85 suggesting a strong climate signal in site chronologies (Table 4). Lower EPS and S/N values in latewood suggest that the climate signal chronologies are lower in this ring component.

Analysis of pointer years

The number of pointer years for total ring-width ranges from 8 to 23 (mean: 14) from 1949 to 1994 (Table 5). Positive pointer years are more frequent than negative years. The number of pointer years increases with decreasing maximum extractable soil water ($\mathrm{EW_m}$) and autocorrelation (AC), and increasing mean sensitivity (MS) (Fig. 3). Below 100 mm of EW_m, the frequency of pointer years exceeds the threshold of 40% (more than 20 pointer years during the period 1949–1994); MS and AC values being above 0.3 and below 0.5, respectively. Beech trees reacted strongly and negatively in 1959 (with 60% of reactive stands), 1976 (80%), and 1989 (67%). For these years, the relative growth decrease averages −34%, −43%, and −35%, respectively. There were many points of agreement between these negative pointer years and extreme droughts (Fig. 4). Depending on stands, the year 1959 is the first or the second driest year from 1949 to 1994. This year is characterized by above annual water stress intensity (+51% to +260%, mean: +120%) and duration (+28% to +100%, mean: +57%) compared to the long-term mean. The years 1976 and 1989 are the third and the fourth driest years in most stands. The differences of annual water stress intensity and duration are +118% and +59%, and +93 and +71%, respectively. Growth recoveries are common to 9 stands in 1958 (+64%) and to 12 stands in 1977 (+62%). These rainy years are characterized by a very moderate

Table 4 Chronology statistics of tree-ring series. Means were calculated from the period 1949–1994 (except HET02, 1952–1994). $n = 30$ trees for each stand. *W (SD)* width (standard deviation). *IC* Series intercorrelation. *MS* Average mean sensitivity (unfiltered series). *AC* first-order autocorrelation (unfiltered series). *S/N* signal to noise ratio. *EPS* expressed population signal

Site code	Total ring (mm)						Earlywood (mm)						Latewood (mm)					
	W (SD)	IC	MS	AC	S/N	EPS	W (SD)	IC	MS	AC	S/N	EPS	W (SD)	IC	MS	AC	S/N	EPS
HET 02	3.80 (1.46)	0.529	0.203	0.665	33.7	0.971	3.38 (1.47)	0.553	0.241	0.651	37	0.974	0.43 (0.15)	0.199	0.295	0.229	7.5	0.882
HET 03	2.33 (0.98)	0.560	0.226	0.558	38.2	0.974	1.86 (0.88)	0.556	0.273	0.522	38	0.974	0.47 (0.20)	0.220	0.232	0.329	8.5	0.894
HET 04	2.02 (0.85)	0.592	0.203	0.652	43.5	0.978	1.76 (0.84)	0.591	0.235	0.646	43	0.977	0.26 (0.06)	0.092	0.198	0.217	3.0	0.752
HET 09	1.24 (0.54)	0.795	0.315	0.475	116.3	0.991	0.93 (0.11)	0.770	0.377	0.469	100	0.990	0.30 (0.11)	0.566	0.289	0.321	39.1	0.975
HET 14	2.27 (0.93)	0.616	0.287	0.533	48.1	0.980	1.89 (0.91)	0.598	0.340	0.524	45	0.978	0.37 (0.13)	0.251	0.263	0.234	10.1	0.910
HET 21	1.53 (0.72)	0.797	0.315	0.508	117.8	0.992	1.14 (0.61)	0.782	0.378	0.485	108	0.991	0.39 (0.16)	0.558	0.283	0.297	37.9	0.974
HET 29	1.91 (0.91)	0.462	0.310	0.607	25.8	0.963	1.57 (0.87)	0.475	0.372	0.591	27	0.964	0.34 (0.11)	0.326	0.270	0.347	14.5	0.936
HET 52	1.86 (0.75)	0.825	0.318	0.428	141.4	0.993	1.45 (0.68)	0.795	0.381	0.398	116	0.991	0.41 (0.16)	0.594	0.328	0.128	43.9	0.978
HET 54a	2.37 (1.06)	0.628	0.319	0.301	50.6	0.981	2.00 (1.00)	0.622	0.366	0.297	49	0.980	0.37 (0.15)	0.338	0.294	0.202	15.3	0.939
HET 54b	2.21 (0.96)	0.821	0.318	0.324	137.6	0.993	1.83 (0.88)	0.792	0.364	0.300	114	0.991	0.37 (0.18)	0.494	0.322	0.267	29.3	0.967
HET 55	2.85 (1.01)	0.623	0.221	0.613	49.6	0.980	2.36 (1.00)	0.609	0.262	0.605	47	0.979	0.49 (0.20)	0.334	0.277	0.250	15.0	0.938
HET 60	2.64 (1.00)	0.794	0.293	0.398	115.6	0.991	2.16 (1.00)	0.713	0.356	0.382	75	0.987	0.48 (0.17)	0.329	0.297	0.154	14.7	0.936
HET 64	2.94 (1.05)	0.574	0.199	0.620	40.4	0.976	2.39 (0.96)	0.567	0.240	0.596	39	0.975	0.55 (0.22)	0.245	0.274	0.292	9.7	0.907
HET 65	1.36 (0.68)	0.604	0.265	0.619	45.8	0.979	1.09 (0.62)	0.609	0.313	0.595	47	0.979	0.27 (0.11)	0.353	0.268	0.390	16.4	0.942
HET 88	2.51 (0.81)	0.677	0.205	0.537	62.9	0.984	2.08 (0.78)	0.716	0.253	0.500	76	0.987	0.43 (0.17)	0.307	0.279	0.133	13.3	0.930

Table 5. Number of pointer years for each ring component at each site (reference period: 1949–1994). Values in parentheses denote mean variation of ring width (%). *TR*, *EW*, *LW* total ring, earlywood and latewood. *N* number of pointer years for total tree-ring-width. *%PY* percent of pointer years for total ring for the period 1949–1994 (n=46 years)

Site	%PY	Positive pointer years (growth recovery)			Negative pointer years (growth reduction)		
		TR	EW	LW	TR	EW	LW
HET02	17.4%	4 (53)	4 (71)	–	4 (-23)	4 (-27)	1 (-36)
HET03	19.6%	5 (43)	4 (63)	–	4 (-30)	4 (-35)	–
HET04	23.9%	5 (44)	4 (57)	–	6 (-23)	8 (-25)	–
HET09	32.6%	10 (70)	10 (94)	3 (70)	5 (-46)	6 (-46)	2 (-44)
HET14	30.4%	8 (55)	6 (77)	–	6 (-37)	7 (-39)	–
HET21	45.7%	13 (51)	12 (69)	2 (49)	8 (-36)	9 (-39)	4 (-31)
HET29	19.6%	5 (59)	4 (73)	1 (143)	4 (-37)	4 (-42)	1 (-42)
HET52	50.0%	12 (58)	13 (71)	5 (67)	11 (-34)	11 (-37)	5 (-35)
HET54a	41.3%	10 (64)	10 (81)	–	9 (-35)	9 (-38)	1 (-35)
HET54b	50.0%	14 (53)	16 (61)	4 (57)	9 (-35)	13 (-34)	4 (-31)
HET55	21.7%	6 (39)	7 (49)	1 (48)	4 (-30)	6 (-29)	–
HET60	45.7%	11 (59)	12 (77)	1 (61)	10 (-35)	12 (-37)	3 (-30)
HET64	19.6%	6 (36)	5 (47)	–	3 (-27)	5 (-27)	–
HET65	26.1%	7 (48)	7 (59)	–	5 (-33)	6 (-35)	1 (-34)
HET88	17.4%	4 (67)	5 (87)	1 (65)	4 (-28)	4 (-36)	2 (-31)

water stress (Fig. 4). Earlywood width is more sensitive to environmental factors showing between 8 and 29 pointer years. The more frequent pointer years are 1989 (12 sites, −25%), 1977 (13, +80%), 1976 (12, −46%), 1959 (10, −36%) and 1958 (9, +94%). At four sites, no pointer years are detectable for latewood-width. At the others sites, only 1–8 pointer years are detected in latewood ring-width. The negative pointer year 1976 appears at 5 sites.

Simple growth-climate correlations

The amount of variance in annual total ring indices accounted for by annual water stress indexes varies from 7.9% at site HET54b to 30.6% at site HET14 (Fig. 5). No significant correlation was observed at the highest elevation Pyrénées stands (HET65 and HET09). Correlations with annual number of days of water stress are less frequent and significant. The percentage of variance explained in earlywood chronologies varies from 8.1% to 30.8% This percent is slightly higher at ten sites and slightly lower at three sites. As previously observed for total ring indices, no significant correlation is observed at site HET65 and HET09. For latewood, only two stands present a significant correlation at the 95% level with annual water stress index (HET04, HET21).

Response functions analysis

The signs of the significant response function elements for total ring, earlywood and latewood are summarized in Table 6. Among the 24 climatic variables, a reduced group of 1–7 (2–4 in most cases) depending on sites, ring compartment, and climatic combinations explains a significant part of the variance in ring width. The dominant climatic factor controlling total tree-ring-widths at ten sites is soil water deficit in June and/or July (Table 6). The highest regression coefficients are observed in June and the percent of variance explained by the soil water deficit during this month ranges from 22.2% to 35.6% (mean value: 26.6%). Especially at sites HET21 and HET52, current

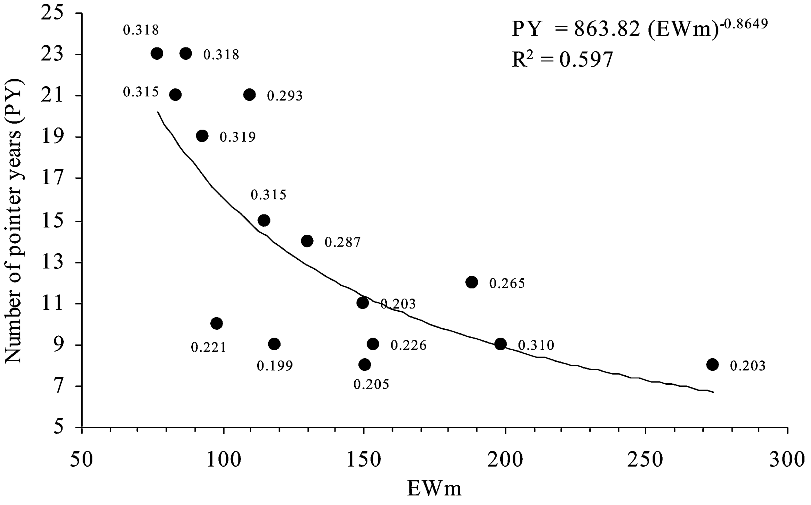


Fig. 3 Relationships between the number of pointer years (*PY*) for the total ring and the maximum extractable soil water (*EWm*, mm). For each point, mean sensitivity (MS) of ring-width series is given

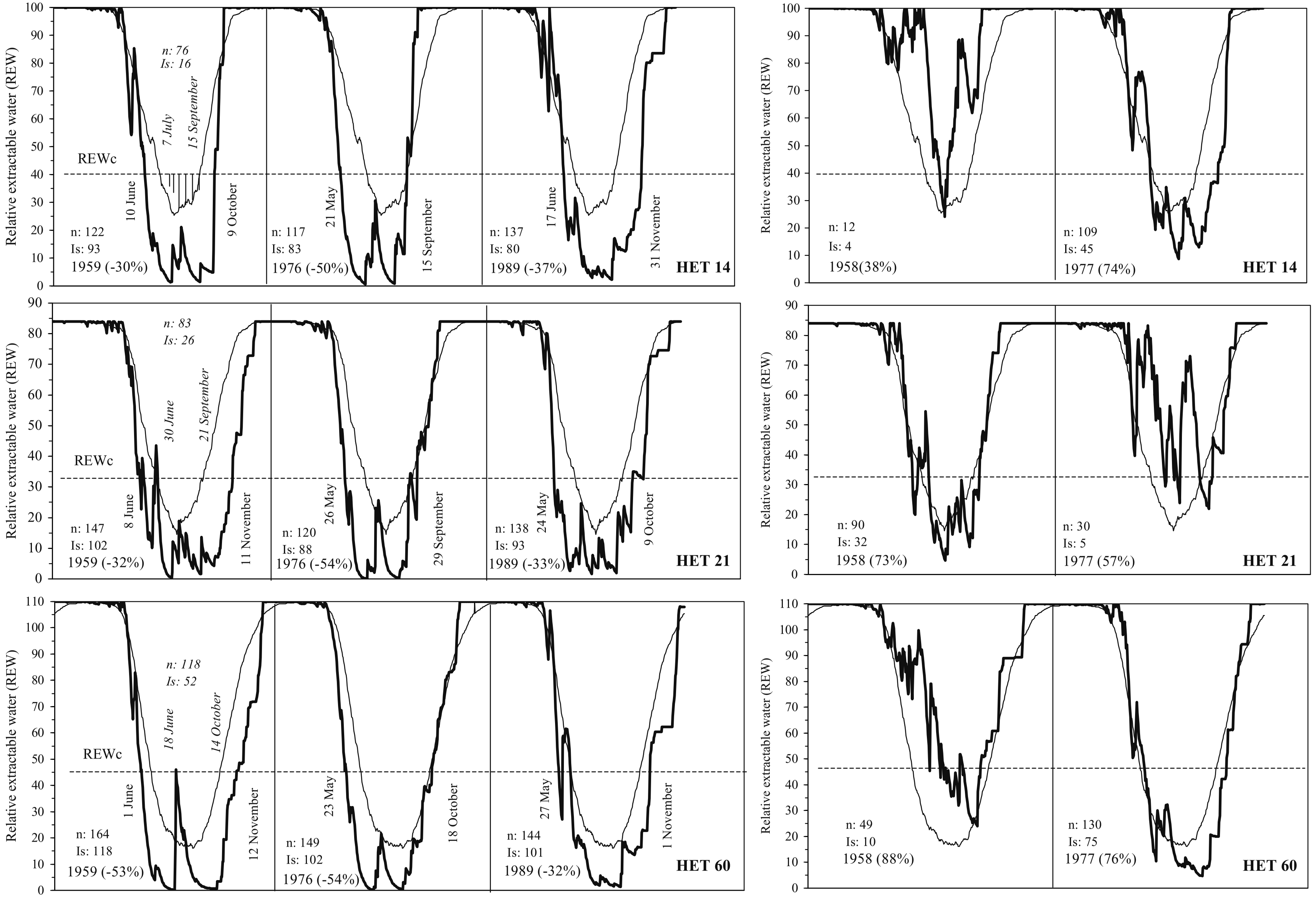


Fig. 4 Time-course of relative extractable water in the soil (REW, *thick line*) simulated with the daily water balance model during the 3 negative pointer years 1959, 1976 and 1989 and the 2 positive years 1958 and 1977 for the stands HET 14 (EWm=100 mm), HET 21 (84 mm) and HET 60 (110 mm) (see Fig. 1 for the geographical location of each stand). The *thin line* represents the average annual time-course of the relative extractable water in the soil for the period 1961–1990. For each year, the *values in brackets* correspond to the relative growth reduction or increase for the total tree-ring-width. Water stress is assumed to occur when REW drops below 40% of EWm (critical REW, REWc). The *dotted line* represents the threshold of REWc for each stand. The dates illustrate the onset and the end of the water stress. *n* number of days of water stress. *Is*: water stress index (example of dashed area in the first curve). Mean values for the period 1961–1990 are presented in bold and italic

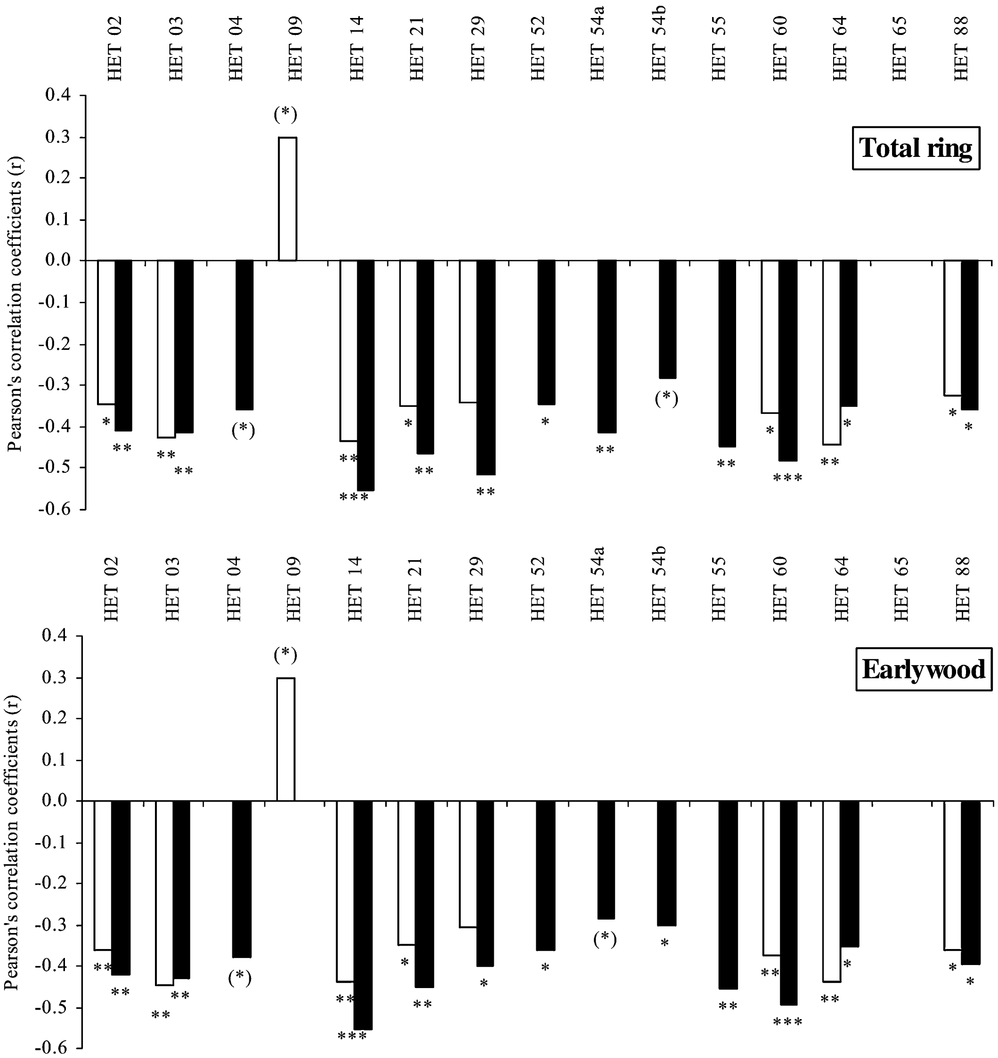


Fig. 5 Simple correlations *r* between growth indexes (total ring and earlywood) and annual number of days of water stress (*white bars*) and annual water stress indexes (*black bars*) for each stand. The number of asterisks indicates significance at the 90% (*), 95% *, 99% **, 99.9% *** levels. Only significant correlations are presented

water deficit in summer and prior water deficit in June and Autumn (September and/or October) negatively influence total annual radial growth. Soil water deficits for the others months and weather conditions during the previous season accounted for substantially less variance in radial growth indices. The effect of temperature on total tree-ring widths is less frequent and significant. Winter and summer temperatures entered in five and three models with positive and negative regression coefficients, respectively. For the response functions established taking into account as predictors the (Def-T_{min}) combination, the amount of variance in annual radial increment accounted for by climatic variables varies from 16% at site HET64 to 56.4% at site HET21. For the (Def-T_{max}) combination, the explained variance ranges from 18.5% (HET02) to 57% (HET21) (Fig. 6). For HET04, no monthly climatic data appear to be significantly correlated with total tree-ring widths for the studied period (1968–1994).

The response functions obtained for earlywood series are quite similar to the results obtained for total ring, and the percentage of variance explained in earlywood chronologies is often higher (Table 6). For the (Def-T_{min}) and (Def-T_{max}) combinations, it ranges from 16.2% (HET64) to 57.6% (HET21) and 26.2% (HET64) to 57.8% (HET21), respectively. The mean value is 39.4%. As previously observed for total ring, earlywood widths are strongly and negatively influenced by soil water deficit in June and July (11 sites), the other months and the temperatures playing a secondary role.

The effect of summer water deficit in latewood formation is less significant according to the number and the values of the corresponding regression coefficients (Table 6). For this ring compartment, temperature in late summer often plays an important role in determining latewood variability. The temperature signal is mostly related to minimum values, and high temperatures in August and/or September favour wide latewood widths at eight sites. For two sites, July temperature positively influences latewoood ring-widths too. The negative effect of water deficit in late summer is only significant at three sites (HET14, HET21, HET29). The percentage of variance explained in latewood chronologies ranges from 8.8% to 67.4% (mean value: 30.5%). No significant correlations with climatic data are observed at site HET64.

Table 6 Summary of the significant response function elements for total tree-ring (*TR*), earlywood (*EW*) and latewood (*LW*). The first line corresponds to the (Def-T_{min}) response functions. The second line corresponds to the (Def-T_{max}) response function (except for HET54a and HET54b with only (Def-T_{mean}) response functions.) + expresses a direct relation whereas − indicates an inverse relation. Each code indicates that the corresponding regression coefficient attains 90% (1), 95% (2), 99% (3) 99.9% (4) of probability, respectively. The percent of variance related to climate based on indices chronology is given by the r^2 coefficient ($P<0.05$) (see text for details)

–		Indexes of drought												Temperature												r^2
		year n						year n − 1						N1	D1	J	F	M	A	M	Ju	Jul	A	S	O	
		M	Ju	Jul	A	S	O	M	J	J	A	S	O													
HET 02	TR											1		2												17.0%
1949–94														1					2							18.5%
	EW											1		2												26.3%
														1					2	-1						27.5%
	LW								−2	−4	−1				3						2		3			45.3%
										−2					3			−1	−2							30.8%
HET 03	TR			−3									−1						1							42.0%
1950–94				−3			−2						−1		4											43.8%
	EW			−3			−1						−1													42.4%
				−2			−2						−2		4								1			44.4%
	LW			−1						−1		−2											2	3		47.2%
				−2						−1					2											11.1%
HET 04	TR																									ns
1968–94																										ns
	EW																									ns
																										ns
	LW			2																		1	1			39.7%
				1					2				−1						−2			2	1			48.6%
HET 09	TR										−2									2						21.6%
1956–94											−2								−2	1						28.3%
	EW		−1								−2				1					2						38.7%
			−1								−2								−2	1						39.3%
	LW																			1					−2	19.4%
											−1								−2			2				38.6%
HET 14	TR		−2	−2															1	1						42.2%
1952–94			−2	−2																						33.5%
	EW		−2	−2															1	1						42.3%
			−2	−2																						33.7%
	LW				−2	−1												2								13.8%
					−1	−1																				15.2%
HET 21	TR		−4	−3					−2				−2													56.4%
1956–94			−4	−2					−2				−2													57.0%
	EW		−4	−3					−2				−2													57.6%
			−4	−2					−1				−2													57.8%
	LW		−3		−3				−1			−2	−1						−2				2			67.4%
			−2		−2			−1	−1			−1							−1							46.6%
HET 29	TR					−1																				20.4%
1965–94						−1																				20.4%
	EW																									ns
																										ns
	LW			1		−3																1				25.7%
						−2	−1			−1												2				37.2%
HET 52	TR	−1	−4	−2					−2			−1	−2													52.4%
1956–94			−3	−1					−2			−2	−1													50.1%
	EW	−1	−3	−3					−2				−1								−1					56.7%
			−3	−2					−2				−1								−1					56.1%
	LW		−3							−2									−2							29.8%
			−1							−3																18.1%

Table 6 Continued

–		Indexes of drought												Temperature												r^2
		year n						year n − 1						N1	D1	J	F	M	A	M	Ju	Jul	A	S	O	
		M	Ju	Jul	A	S	O	M	J	J	A	S	O													
HET 54a*	TR		−2	−2								3														24.3%
1950–94	EW		−1								−2															22.3%
	LW																							2		9.2%
HET 54b*	TR		−3																							24.5%
1950–94	EW		−3	−1																						29.3%
	LW																							1		8.8%
HET 55	TR		−2														2					−1				32.3%
1962–94			−2													1					−1					37.6%
	EW		−2														2					−1				34.5%
			−2																		−2	−1				34.2%
	LW														1								4			38.8%
			−1												3			−1								17.4%
HET 60	TR	−1	−3							1	3				1							−1				45.0%
1949–94		−2	−3														2					−1				44.2%
	EW	−1	−3							2	3				1					1		−2				50.7%
		−2	−3								2						1					−1				49.5%
	LW	−2	−1																	−2						18.2%
		−2	−1	1								1								−2						26.1%
HET 64	TR			−1														−2								15.8%
1955–94				−1															2							27.5%
	EW			−1														−2								16.2%
				−1															2							26.2%
	LW																									ns
																										ns
HET 65	TR					2								2							−2		2	−1		35.1%
1956–94						1				−2						1					−1					36.1%
	EW					2								2	1						−2		1	−1		44.2%
						1				−1						1					−1					37.2%
	LW			−2																			3			19.1%
																										ns
HET 88	TR		−1		−1		1																			33.8%
1956–94			−2															−1								26.2%
	EW		−2		−1		2																			41.2%
			−2		−1													−1								36.5%
	LW			2										−2					2							47.9%
														−1								2	1			28.1%

Spatial analysis

The result of clustering of (Def-$T_{\min}$) response functions for total ring is presented in the form of a dendrogram in the Fig. 7. The four levels of classification mostly reflect the site characteristics. Selected stands growing on the driest soils (HET21–HET52) respond individualistically. Mesic soils form groups of comparable sensitivity to environmental factors, whereas high elevation sites (HET04, HET09, HET65) and/or humid stands (HET02, HET29) are separated. The ordination of the beech populations on the basis of response functions (Def-$T_{\max}$) or with earlywood gives the same results. For latewood, the cluster analysis does not show any very clear grouping of either site characteristics or sampling area.

Discussion

Chronology statistics as indicators of climate forcing

The values in Table 4 give evidence for a high statistical quality of site chronologies obtained. Tree ring series of beech have high values of MS, EPS and S/N ratio which demonstrates that the ring width of beech is a very sensitive parameter reflecting clearly the signal of exogenous influences. This is in agreement with previous studies which showed high suitability of beech tree rings for dendroclimatological analyses (Dittmar et al. 2003). Our results indicate that stands HET21, HET52, HET54a, HET54b and HET09 might be regarded as most environmental stressed, which coincides well with local conditions given in

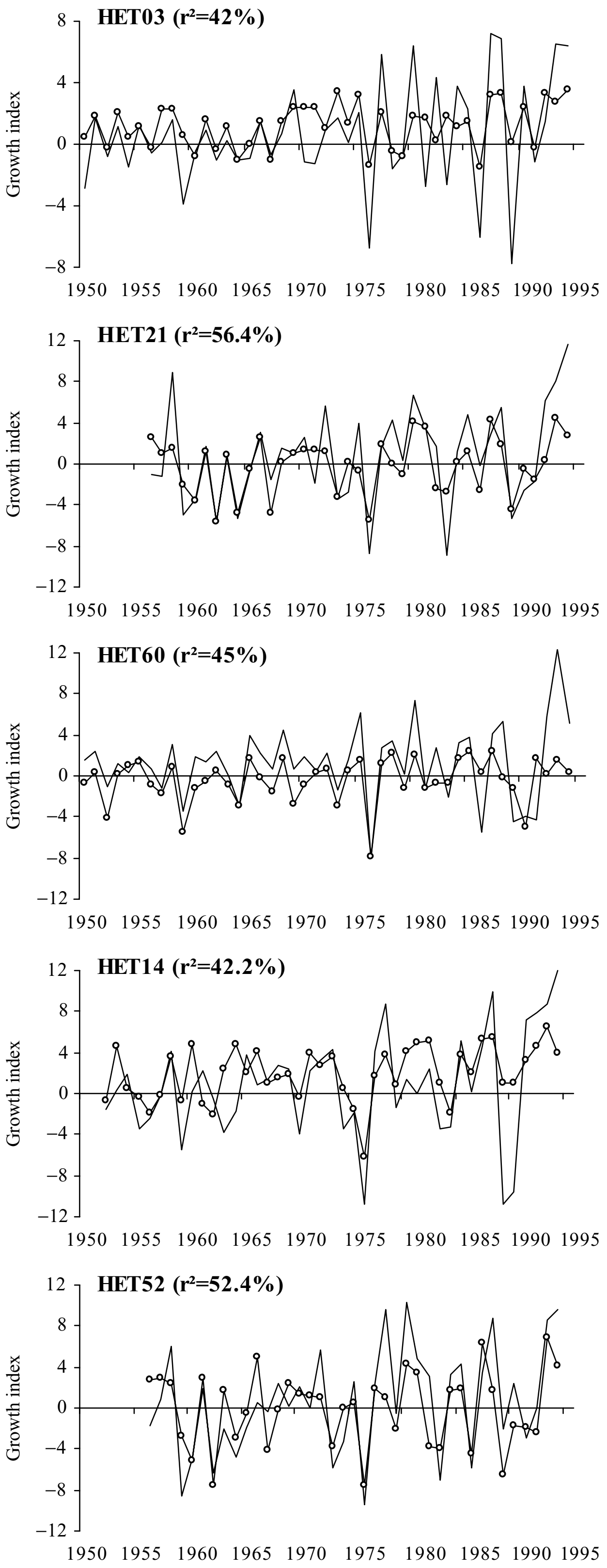


Fig. 6 Inter-annual variations of standardized total radial growth index (*thin line*) compared to predicted growth index by climatic models (*open symbols*) for five beech stands. Predicted growth index was calculated from the (Def-T_{min}) response functions. The percent of variance related to climate based on indices chronology is given by the r^2 coefficient ($P<0.05$) (see text and Table 6 for details)

Tables 1 and 2 (dry sites at low or high altitude). At each site, EPS and S/N ratio values also indicate that a strong climatic force acts on tree growth (Table 4). Both parameters, which express the strength of the common signal among trees, appear very well linked with site characteristics too. The three driest sites (HET52, HET21, HET54b), and the dry high elevation stand (HET09) present the highest values of both EPS and S/N ratio. In contrast, the most humid stands (HET02 and HET26) present lower values. Thus, high MS and S/N values and low influence of the prior year on ring-width exist on dry sites, whereas high first-order autocorrelations could be detected at sites showing minor S/N-ratios (wet sites). Similar observations can be done for the earlywood and for latewood. Moreover, the highest values of MS, EPS and S/N ratio suggest that earlywood is more sensitive to climate variations than latewood.

Climate limitations on tree growth

The calculation of response functions provides readily accessible information about the dominant mode of linear response between tree-ring and climate variables over many years. A disadvantage, however, is that response functions and 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. The combination of these different procedures gives the most comprehensive dendroclimatological information.

Our study confirms that this water balance model, based on a physiological approach of the water stress, is relevant to explain the inter-annual variations of beech tree-ring widths under a wide range of ecological conditions. This water balance model involves a process model that includes threshold effects (i.e., the soil water deficit threshold of 0.4 leading to stomatal closure), integrates the daily variations of air vapour pressure deficits, which play a major role in beech water loss regulation, simulates climate effects on tree transpiration, which is the major cause of soil depletion during phenologically defined periods of the growing season. Thus, by integrating the different daily climatic parameters which can modulate water relations in beech, this approach provides great insight into causal biological relationships. For the studied stands, the percentage of variance accounted for by climatic models increases between 4% to 21% (mean: 12%) when monthly water stress indices are taken into account instead of monthly precipitation and temperatures (data not shown).

Spatial differences in the strength of beech growth-climate correlations among the 15 study sites are consistent with differences in site characteristics. Thus, the soil storage capacity plays a major role in modulating mean climate-tree growth relationships. Similarities in growth response to climatic variations can be found between stands showing corresponding site characteristics, especially soil water availability. Selected stands growing on mesic soils form groups of comparable sensitivity to

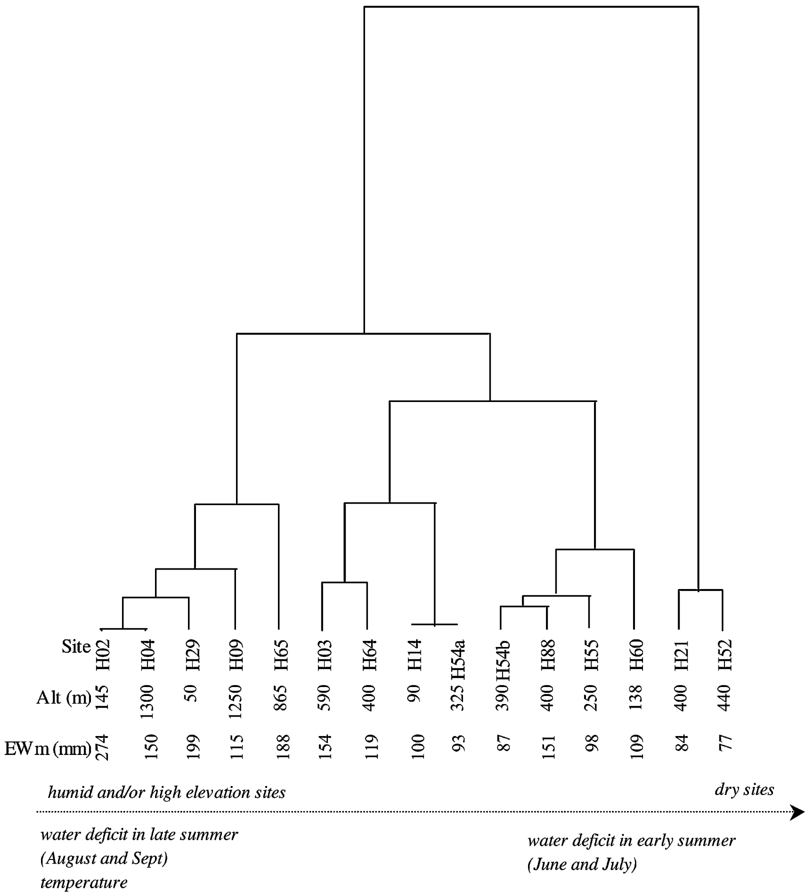


Fig. 7 Group average dendrogram of total tree-ring-indices using Euclidean distances based on response functions (Def-$T_{\min}$) (type of hierarchy algorithm used: Ward's method). *Alt* Altitude (m). *EWm*: Maximum extractable soil water (mm)

environmental factors, whereas dry sites, high elevation sites and/or wet soils are separated. Analysis of pointer years also indicates that the susceptibility of radial beech growth to extreme climatic events mainly depends on soil water characteristics. The frequency of pointer years decreases with increasing soil water capacity.

Both pointer years and response functions clearly showed that soil water deficit (especially in June and/or July) is the primary growth-limiting factor in the selected stands. The three most frequent negative pointer years (1959, 1989 and 1976) result from a particularly intense and durable soil water deficit, whereas positive years (1977 and 1958) mainly coincide with wet conditions. Few pointer years observed in the beech stands are in agreement with observations from the 30 oak stands of the RENECOFOR network. For example, the wet year 1958 and the dry years 1976 and 1989 have been observed in 70%, 76% and 60% of the oak stands, respectively (Lebourgeois 1997). These 3 years seem to be very important throughout Europe for oak and beech forests because they have also been observed in different French areas (Becker et al. 1994; Badeau 1995; Lebourgeois et al. 2004), and in a wide range of taxa in England (Bridge et al. 1996).

Among the 24 initial regressors, response functions indicate that the number of significant predictor variables mainly ranges between two and four (Table 6). The percentage of climatic variance accounted for by total ring-width chronologies averages 34.1% and soil water deficit in June alone explains a large part of the radial growth variability (mean value: 26.6%). Our results are in agreement with previous studies of beech stands sampled under different climatic and environmental conditions in Belgium (Penninckx et al. 1999), in Denmark (Holmsgaard 1962), in Germany (Eckstein et al. 1984), in Spain (Gutiérrez 1988; Rozas 2001), throughout Italy (Biondi 1993; Piutti and Cescatti 1997) and in central Europe (Dittmar et al. 2003). For this last study, the climatic models explain between 13 and 69% of the radial growth (mean value: 29.6%). Recent ecophysiological studies have highlighted the incidence of June climate on the beech seasonal growth pattern. Beech trees present a rapid increase of radial increment from mid-May to July as soon as leaf expansion begins and CO_2 assimilation. At the end of June between 30 and 70% of annual growth is achieved and the radial growth stops between the end of August and mid-September (Lebaube et al. 2000; Schmitt et al. 2000; Barbaroux and Bréda 2002; Bouriaud et al. 2003). On a superficial soil offering a low extractable water amount, transpiration and photosynthesis are quickly limited by early summer soil water deficit (rapid stomatal closure), which prevents trees from dividing and enlarging cells (Aranda et al. 2000; Granier et al. 2000; Raftoyannis and Radoglou 2002). In their study of carbon isotope fractionation in beech tree rings, Dupouey et al. (1993) and Saurer et al. (1997) showed that interannual variations of $\delta^{13}C$ were closely linked to ring width variations and to water stress index in summer. High water deficits lead to an increase of $\delta^{13}C$ values which corresponds to a decrease in transpiration rate and CO_2 supply, and thus to a narrow ring. With a dry summer the stomata are closed more often than in a wet summer, which corresponds to a decrease in CO_2 supply. Thus, the radial increment is quickly stopped or strongly limited as soon as soil water deficit occurs.

The small vessels in beeches are not very sensitive to winter embolism, and so spring reactivation of growth is less dependent on stored carbon (Lemoine et al. 1999). For this diffuse-porous species, a small part of the previous year's earlywood vessels are embolized by frost events each winter; therefore, the production of new earlywood before leaf expansion is unnecessary for spring recovery of hydraulic conductivity. This pattern could partially explain the low effect of winter temperature on annual growth, but also the positive correlation between growth and winter temperature observed at five sites (decreasing winter embolism with increasing winter temperature). A warm winter may also influence the breaking of dormancy and the resumption of physiological activity in the tree, and thus increase the duration of the current growing season.

Response functions obtained from earlywood width are usually more significant than those obtained from total ring series, which is coherent with the highest mean sensitivity observed in earlywood. However, inter-annual variations of both ring parameters are very similar and contain the same climatic signal. The behavior of the latewood series is different. High temperature (mainly minimum temperature) at the end of the growing season (August and/or September) often positively influence latewood width, whereas water deficits in early or late summer play a secondary role. The effect of high temperatures on cell wall thickening has already been described as positive for coniferous trees, while activating enzymes, increasing the ability of membranes to transport substances (Antonova and Stasova 1997), and decreasing duration of tracheid development in the secondary thickening zone (Antonova and Stasova 1993). Thus, the maturation phase of wood elements, involving secondary cell wall synthesis and lignification, appears less sensitive to tree water status than the growth phase (Barbaroux and Bréda 2002). During the late growing season, radial increment is almost stopped (Schmitt et al. 2000; Bouriaud et al. 2003), and some assimilates may be oriented towards secondary cell wall building that may continue for several weeks (2–3 weeks for beech) past the cell growth stop, or even more for latewood cells (Gindl et al. 2000).

In conclusion, beech appears particularly sensitive to drought at the beginning of the growing season. The geographic situation and the characteristics of the sampled stands (mature stands with high values of LAI) makes the recurrence of summer drought relatively likely. Changes in frequency and/or intensity of years of drought, as predicted as possible consequences of a climate change (Lebourgeois et al. 2001) may shift the competition ratio of beech and others species more or less abruptly in favour of less sensitive tree species (oaks for example).

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