

Leyre Corcuera · Jesús Julio Camarero ·  
Eustaquio Gil-Pelegrín

## Effects of a severe drought on *Quercus ilex* radial growth and xylem anatomy

Received: 22 November 2002 / Accepted: 25 June 2003 / Published online: 30 July 2003  
© Springer-Verlag 2003

**Abstract** We assessed the response of *Quercus ilex* subsp. *ballota* to the severe summer drought recorded in 1994 in NE Spain through the study of changes in radial growth and wood anatomy. We selected a coppice stand in the Iberian Peninsula, which is characterized by a Mediterranean climate under continental influence. We measured internode length, tree-ring width, mean and maximum vessel diameter, and vessel density for 1981–1997. The annual predicted hydraulic conductance ( $K_h$ ) was calculated following Hagen-Poiseuille's law. We compared the tree-ring width, vessel diameter and  $K_h$  of *Q. ilex* subsp. *ballota* and co-existing ring-porous oaks (*Q. faginea*, *Q. pyrenaica*) for a dry summer (1994) and a wet summer (1997). To evaluate the drought-resistance of xylem for *Q. ilex* subsp. *ballota* (dominant under continental conditions) and *Q. ilex* subsp. *ilex* (dominant in mild areas) we determined vulnerability curves. Dimensionless indices of internode length, tree-ring width, and vessel density were compared with climatic data (monthly total precipitation and mean temperature) using correlation analyses. Internode length, tree-ring width,  $K_h$ , and mean and maximum vessel diameter declined in 1994. According to vulnerability curves, *Q. ilex* subsp. *ballota* showed a greater drought resistance than *Q. ilex* subsp. *ilex*. During the year of growth, we found a positive influence of January and June–August precipitation on the internode length, tree-ring width, and vessel density. The response of *Q. ilex* subsp. *ballota* radial-growth to summer drought was comparable to that of *Q. faginea* latewood. Overall, growth and wood

anatomy of *Q. ilex* subsp. *ballota* showed a plastic response to drought.

**Keywords** Cavitation · Climate · Dendroecology · Vulnerability curve · Xylem

### Introduction

Climate affects both the morphological and functional features of the vegetation (Orshan 1989; Floret et al. 1990). For instance, summer dryness influences several growth features of plant species such as xylem anatomy and radial growth (Carlquist 1975; Fritts 1976; Villar-Salvador et al. 1997). Several studies have found changes in mean vessel diameter, especially in species with diffuse-porous wood, along climatic gradients of water availability (Baas et al. 1983; Baas and Schweingruber 1987; Zhang et al. 1992; Woodcock and Ignas 1994; Sass and Eckstein 1995). This is explained by the conflict between the increased conductive efficiency provided by wider vessels and interconduit pits and the increased risk of cavitation (Tyree and Sperry 1989; Tyree and Ewers 1991). Following Hagen-Poiseuille's law, the hydraulic conductivity of a cylindrical conduit is proportional to the vessel diameter raised to the fourth power (Tyree et al. 1994). However, it must be emphasized that the main limiting factor of maximum vessel diameter in temperate angiosperms is low temperature because of freezing-induced cavitation (Sperry and Sullivan 1992; Sperry et al. 1994).

Forest productivity in Mediterranean ecosystems is mainly limited by water stress (Di Castri 1981). Dry summers and a high interannual variability of precipitation, being both factors unfavorable for plant growth (Mitrakos 1980), characterize the Mediterranean climate (Font Tullot 1988). During the last 50 years, the area under Mediterranean influence in the Iberian Peninsula has experienced an increase in air temperature and evapotranspiration, a greater frequency of severe summer droughts, and a decrease in relative humidity (Piñol et al.

L. Corcuera · J. J. Camarero · E. Gil-Pelegrín (✉)  
Unidad de Recursos Forestales,  
Servicio de Investigación Agroalimentaria,  
Gobierno de Aragón, Apdo. 727, 50080 Saragossa, Spain  
e-mail: egilp@aragob.es  
Tel.: +34-976-716373  
Fax: +34-976-716353

J. J. Camarero  
Departament d'Ecologia, Facultat de Biologia,  
Universitat de Barcelona, Avda. Diagonal 645,  
08028 Barcelona, Spain

1998; IPCC 2001). An outstanding year, and a clear example of the interannual fluctuation of rainfall in the Mediterranean area, was 1994, when a severe summer drought affected most Mediterranean forests in the eastern half of the Iberian Peninsula (Lloret and Siscart 1995; Montoya Moreno 1995). The yellowing of the leaves in many woody plant species was followed by an intense defoliation in many species (Peñuelas et al. 2001). In the studied coppice stand, this decline was also observed in 1994, affecting both evergreen and deciduous *Quercus* species (Aït-Bachir 1998). This suggested that the 1994 summer drought and the previous 1993 winter drought were the causes of the decline observed (Tryon and True 1958; Becker and Lévy 1982; DeLatour 1983; Cramer 1984; Tainter et al. 1990). Indeed, the 1994 summer drought coincided with an intense defoliation in the trees studied. This behavior was observed in spite of the “drought-evader” role played by two of the main autoecological features of this species: (1) its diffuse-porous wood formed by narrow vessels with a risk of cavitation lower than wide earlywood vessels in ring-porous species, and (2) its evergreenness.

According to their geographic distribution and landscape dominance, the main *Quercus* species in the western Mediterranean area is *Quercus ilex* L. (holm oak). Approximately 60% of all *Q. ilex* forests are located in Spain (ca. 2,972,000 ha), and almost 44% of them are coppice stands (Ceballos and Ruiz de la Torre 1979; Rivas-Martínez and Sáenz 1991; Serrada et al. 1992). This is partially due to the ecological amplitude of *Q. ilex*, which can be found along a wide altitudinal range in Spain (0–2,000 m; 67% of the stands appear between 400 and 1,200 m), both on siliceous and calcareous bedrocks, and performing well under Mediterranean summer and winter droughts with a minimum summer rainfall of 100 mm (Rodà et al. 1999; Zavala et al. 2000).

According to botanical and phytogeographical studies, *Q. ilex* includes two subspecies morphologically different and distributed in distinct geographical areas (Sáenz de Rivas 1967; Lumaret et al. 2002). These are *Q. ilex* L. subsp. *ilex*—restricted to mild coastal areas from Greece to France—and *Q. ilex* L. subsp. *ballota* (Desf.) Samp.—dominant at continental sites in Spain and N. Africa (Tutin et al. 1993; Blanco et al. 1997). These subspecies showed an early genetic differentiation, probably in response to the contrasting climatic conditions of their distinct geographical areas (Lumaret et al. 2002). We noted that the vulnerability curves previously established for *Q. ilex* in Tyree and Cochard (1996) might correspond to these two different subspecies. To study the xylem vulnerability to embolism of each subspecies, we considered them separately to check for intraspecific differences in their resistance to water stress.

The main objective of this work was to study the growth response of *Q. ilex* subsp. *ballota* (hereafter *Q. ilex*) to the severe drought recorded in 1994. It is often expected that the response to a severe drought of a species with diffuse porous wood such as *Q. ilex* will

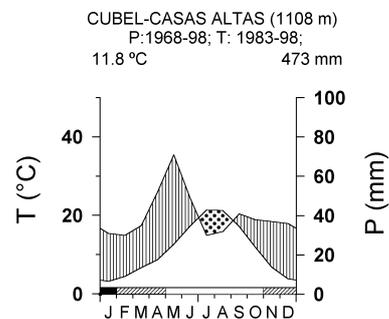
differ from that of the coexisting ring-porous oaks such as *Quercus faginea* Lam. or *Quercus pyrenaica* Willd. Thus, as a secondary objective we compared several growth and anatomical variables (tree-ring width, vessel diameter and predicted hydraulic conductance) of *Q. ilex* with co-occurring ring-porous oak species (*Q. faginea*, *Q. pyrenaica*), which also experienced defoliation in 1994.

## Materials and methods

### Study site

A coppice stand dominated by *Q. ilex* and *Q. faginea* was selected in the Sierra de Santa Cruz-Cubel, Saragossa, NE Spain (41°07'N, 1°39'W, 1,177 m a.s.l.). Precipitation and temperature data were obtained from the Cubel-Casas Altas station located 2 km from the stand (Fig. 1). To describe the temporal evolution of rainfall in the area during the twentieth century (1910–1999 data), we also used precipitation data from the nearby Daroca station (41°07'N, 1°25'W, 779 m). In the study area, the drought period in summer lasts ca. 2 months, from the end of June to early September. The estimated mean monthly evapotranspiration (ETP, mm day<sup>-1</sup>) at Daroca station for 1981–1989 (Faci González and Martínez Cob 1991) was also compared with the ring-width index. The maximum seasonal estimated ETP corresponds to the summer (141.2 mm). The years 1981, 1983, 1985 and 1994 showed very low annual precipitation (lower than the mean –1 SD for 1981–1997) at the Cubel-Casas Altas station. In fact, the lowest record of total annual precipitation during the last 50 years in the study area was 1994. In addition, this year was preceded by a short dry period (1992–1993).

The climate of the study area corresponds to a transition from Mediterranean to nemoro-Mediterranean forest with a tendency to sclerophylly and a clear continental influence (Allué Andrade 1990). This phytoclimate suggests that this landscape was previously dominated by coppice stands of *Q. faginea*, but *Q. ilex* is currently the most abundant tree due to selective logging. Remnant *Q. faginea* stands are found now within a *Q. ilex* matrix. Intense coppice management for fuel wood was carried out 40–50 years ago. The study site is located on very poor soils developed over Tertiary limestone outcrops. We assume that the thin soil and the high elevation of the study site make trees of both species very susceptible to climatic stress (high sensitivity; see Fritts 1976). For instance, Sass and Eckstein (1995) showed that precipitation



**Fig. 1** Climate in the study area according to the ombrothermogram of the nearby Cubel-Casas Altas meteorological station. The climate diagram describes the arid (precipitation < 2 temperature, dotted area) and humid seasons (precipitation > 2 temperature, area with vertical lines). The three thermic periods are: freeze month (January), i.e. mean minimum temperature  $\leq 0^\circ\text{C}$  (lower black block); months with probable freeze, i.e. absolute monthly minimum temperature  $\leq 0^\circ\text{C}$  (lower striped block); and freeze-free months, i.e. mean minimum temperature of the coldest month  $> 0^\circ\text{C}$ ; (lower white block)

deficiencies may have an immediate impact on the radial growth of *Fagus sylvatica* L. growing in soils with a low water-retaining capacity.

### Sampling procedure and sample preparation

To measure the radial-growth and xylem variables, ten branches ( $n=10$ ) at mid-height from the S-SW side of the crown were taken from ten dominant trees (one branch per tree) in January 1998. Although this sample size is close to the minimum required in standard dendroecological studies (Fritts 1976), the intensive description of wood-anatomical features made this the largest sample size that could be studied from a practical point of view. To study the relationship between the annual production of leaves along the main axis of sampled branches and the internode length, we counted the number of leaves and scars along the main axis of each branch for 1994–1999.

Fifteen additional branches were sampled in January 1997 to estimate the mean longitudinal growth (annual internode length). The branches showed a similar diameter and age. The mean age ( $\pm$ SD) was  $19 \pm 1$  years. The middle of the older internodal segment of each branch was transversally sectioned with a sliding microtome (Anglia Scientific AS200, UK). Sections with a thickness of 15–30  $\mu\text{m}$  were stained with safranin and fast green, dehydrated with 96% ethanol and permanently mounted on slides with Canada balsam. The stem cross-sections were studied under a microscope (Olympus BH-2) equipped with a photo-microadapter (Olympus OM-Mount) and a camera (Olympus OM101) for slide printing. All the samples were visually cross-dated (Stokes and Smiley 1968).

### Wood-anatomical variables

A sequence of 17 annual values was studied (1982–1997), as this was the common period including the maximum sample size of the trees ( $n=10$ ). We considered the 1982–1996 interval for internode length because the 1997 internode was not formed in January 1997. In addition, the age-dependent variability of the vessel diameter found for other oak species stabilized approximately at a cambial age of 10 years (Huber 1993). All mean annual values were based on a minimum sample size of ten branches. To describe the growth response to climate variability, the following variables were considered: internode length, tree-ring width (mean of two radii per ring), mean and maximum vessel diameter, vessel density (number of vessels per transverse xylem area), and conductive area (absolute,  $\text{mm}^2$ ; or relative, percentage transverse section occupied by vessels in a tree-ring). Abrupt shifts in the vessel size across the ring allowed us to identify consecutive annual rings. First, we obtained the mean annual values of tree-ring width averaging the individual values of different branches. Second, as the tree-ring width followed a biological growth-trend due to the aging and the increase in stem perimeter we converted the mean raw ring-width data into indexed values for each sample to maximize their climatic signal (Fritts 1976). This was done fitting simple linear functions, retaining the residuals of these fits as indexed values and averaging them to obtain a mean indexed series. This was carried out using ARSTAN (Cook and Holmes 1992). The standardized series of indices were assumed to be constant with respect to the mean and variance. Generally, the temporal autocorrelation of the tree-ring width is low in xeric sites, and it is difficult to estimate with short series such as ours (Fritts 1976). Therefore, we did not perform any autoregressive modeling.

The main wood-anatomical variable related with the hydraulic conductance is the vessel diameter (Carlquist 1975). In this study, the predicted hydraulic conductance ( $K_h$ ;  $\text{mm}^4$ ) was calculated, according to Hagen-Poiseuille's law, as the sum of the fourth power diameters of all the vessels in each section (Zimmermann 1983; Tyree et al. 1994). Previous works have considered only the 10–25 widest conduits per section as a good approximation to estimate the predicted hydraulic conductance (Woodcock 1989; Villar-Salvador et al. 1997). However, we measured for each tree-ring section all

the vessels whose tangential diameter was greater than 10  $\mu\text{m}$  within an area of ca. 5 mm in width. We considered this intensive anatomical description as necessary to estimate correctly the theoretical hydraulic conductance. The long and short diameters were averaged for non-circular vessels. We used the hydraulically weighted mean diameter for each ring of every branch ( $n>10$  vessels) calculated as  $2(\sum r^5/\sum r^4)$ , where  $r$  is the radius of a conduit (Sperry et al. 1994; Cavender-Bares and Holbrook 2001). Then, we computed a grand mean for the ten branches considering each annual tree-ring ( $n>200$  vessels). We compared the tree-ring width, vessel diameter and  $K_h$  of *Q. ilex* with the values measured in branches of a similar size and age from co-occurring individuals of *Q. faginea* and *Q. pyrenaica*. In the case of the oaks with ring-porous wood, we considered earlywood and latewood separately and followed the same methodological procedures.

To describe the interannual variability of the measured variables, we used the mean sensitivity, a classical dendrochronological parameter which ranges from 0 to 2 (Douglass 1936). This is calculated as the average mean sensitivity of a series ( $ms_x$ ):

$$ms_x = [1/(n-1)] \sum |2(x_{t+1} - x_t)/(x_{t+1} + x_t)| \quad (1)$$

where  $n$  is the number of data, and  $x_{t+1}$  and  $x_t$  are the consecutive annual values of the measured variable.

### Vulnerability to xylem cavitation

To quantify the xylem vulnerability to embolism we built vulnerability curves for each *Q. ilex* subspecies. We collected seeds from provenance zones characteristic of each subspecies. Seedlings were grown under controlled environmental conditions as described by Corcuera et al. (2002). We used shoots from 1-year-old seedlings because several authors had reported that vulnerability curves based on oak seedlings are similar to curves based on branches of similar age and size (Tyree et al. 1992; Simonin et al. 1994). We used the air injection method to establish the vulnerability curves (Cochard et al. 1992; Jarbeau et al. 1995).

Following Pammeter and Vander Willigen (1998), the vulnerability curve was fitted by least squares regression using this sigmoidal function:

$$PLC = 100 / \left( 1 + e^{a(\Psi - b)} \right) \quad (2)$$

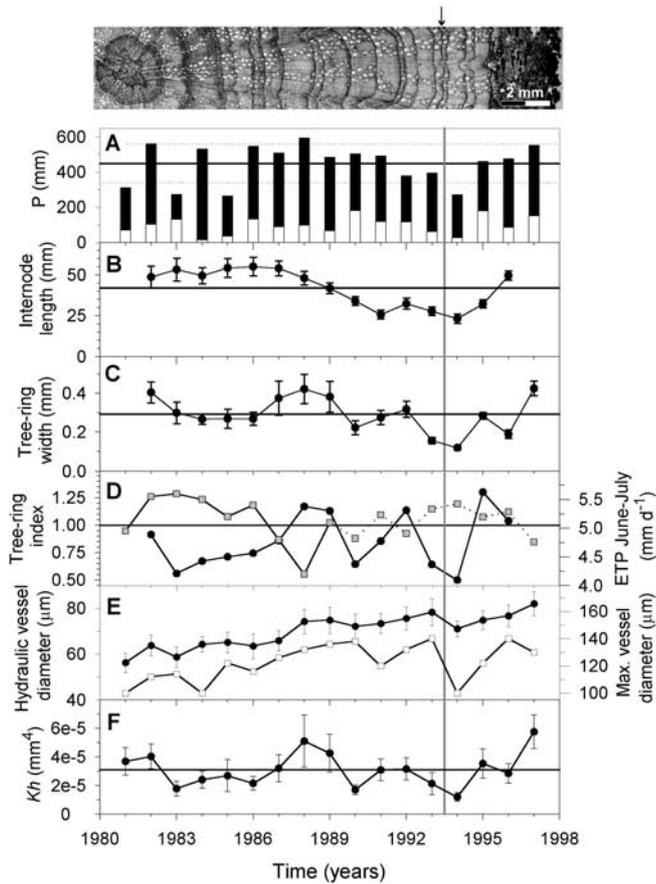
where PLC is the percentage loss of conductivity,  $a$  is a constant describing the range of potentials over which conductivity decreases,  $\Psi$  is the water potential (MPa), and  $b$  is the water potential corresponding to a 50% loss of conductivity.

### Climate-growth relationships

The influence of climate (monthly precipitation and mean temperature) on the growth (internode length, tree-ring width, and vessel diameter) was analyzed by means of Spearman's rank correlation coefficient ( $r_s$ ; Sokal and Rohlf 1995). The raw data of internode length, vessel diameter and vessel density were converted into standardized indices using a similar procedure as the previously described for the tree-ring width. Temporal trends of several variables were also assessed using Kendall's tau ( $\tau$ ) coefficient. We performed correlation analyses between the indexed growth variables and the climatic monthly data from April of the year previous to growth ( $t-1$ ) up to October of the year of growth ( $t$ ). Seasonal climatic data were also used. Statistical analyses were performed using SPSS 6.1.2 (SPSS, Chicago, USA).

## Results

The severe 1994 summer drought affected the leaf and internode growth in *Q. ilex* until 1995 (Fig. 2A–C). The



**Fig. 2A–F** *Quercus ilex* growth and precipitation variability during 1981–1997. The photography shows a typical transverse section of a branch (the arrow indicates the 1994 tree-ring). Comparison of **A** total annual (black bars) and summer (white bars) precipitation at the Cubel-Casas Altas station (the thick and dotted lines are the mean and  $\pm$  1SD, respectively) with **B** longitudinal (internode length) and **C** radial (tree-ring width) growth. The negative effect of summer drought on radial growth is indicated by the inverse relationship **D** between the June–July evapotranspiration (ETP) and the ring-width index. The dotted line of ETP for 1990–1997 indicates that these values were estimated using June–July precipitation data from the Daroca station. In addition, both the hydraulically weighted mean diameter (filled circle) and the maximum (empty box) vessel diameter reached low values in years with intense summer drought, e.g. 1994 (**E**; note the different scales). The temporal evolution of the total predicted hydraulic conductance ( $K_h$ , **F**) paralleled that of the ring-width index (**D**). In all cases the horizontal line is the mean for the data shown and the vertical line marks the beginning of the 1994 year. The error bars are standard errors

**Table 1** Descriptive statistics of the growth and the wood-anatomical variables for the 1982–1997 mean series ( $n=10$  trees). The 1982–1996 period was considered for internode length. [ $\tau$  (%), relative frequency (in percentage) of individual series showing a significant ( $P \leq 0.05$ )

Variables	Mean $\pm$ SD	Minimum (year)	Maximum (year)	$\tau$ (%)	AR1	$ms_x$
INTI (mm)	42.81 $\pm$ 11.20	23.26 (94)	55.13 (86)	29	0.21	0.14
TRw (mm)	0.33 $\pm$ 0.13	0.12 (94)	0.43 (97)	30	0.41	0.31
V_D ( $\mu$ m)	53.39 $\pm$ 5.95	42.96 (81)	62.97 (97)	80	0.56	0.06
V_d ( $mm^{-2}$ )	39 $\pm$ 15	25 (97)	77 (81)	70	0.22	0.11
C ( $mm^2$ ) <sup>a</sup>	2.44 $\pm$ 0.67	1.31 (83)	3.81 (96)	60	0.23	0.22
CA (%)	8.48 $\pm$ 0.87	6.93 (92)	10.02 (81)	10	0.03	0.09

<sup>a</sup>  $mm^4 \times mm^{-2}$ . Mean, minimum and maximum values must be multiplied by  $10^{-5}$

annual number of leaves along the main axis of sampled branches was related to the internode length. We found a significant relationship ( $r=0.79$ ,  $P<0.0001$ ,  $n=346$ , data for the 1994–99 period) using a power fit (No. of leaves =  $2.11 \times$  internode length<sup>0.47</sup>).

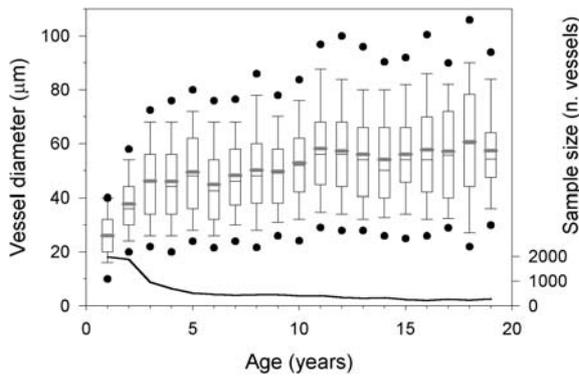
The internode length and the tree-ring width of *Q. ilex* branches declined from 1993 to 1994 (Fig. 2B, C), following a decrease in the annual and summer precipitation (Fig. 2A). In 1994 the tree-ring width reached its lowest mean value since 1982 (Table 1). The ring-width index and the June–July ETP were significantly and inversely related ( $r=-0.50$ ,  $P=0.03$ ) for the period 1982–1997 (Fig. 2D). This explained why the periods characterized by low annual precipitation and/or dry summers (1983–1984, 1993–1994) coincided with the formation of narrow tree-rings characterized by low values of mean and maximum vessel diameter (Fig. 2E), and a low total predicted hydraulic conductance (Fig. 2F). The curves of the total predicted hydraulic conductance and the ring-width index showed similar trends ( $r=0.83$ ,  $P<0.01$ ) and reached minimum values in 1994.

Among the growth variables studied, the highest mean sensitivity corresponded to the tree-ring width, whereas most of the vessel-diameter series showed significant temporal trends (Table 1). The total conductance per unit area was positively and significantly related to the tree-ring width and vessel diameter (Table 2). There were also positive relationships between the internode length and total conductance or tree-ring width but they were not significant. In contrast, the relative conductive area only showed a direct relationship with the vessel diameter. The

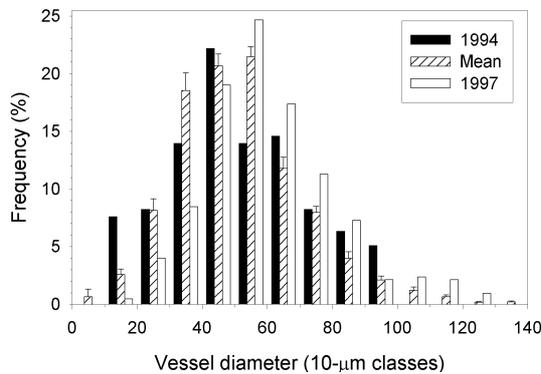
**Table 2** Correlation values ( $r_s$ , Spearman's coefficient) between the growth and wood-anatomical variables of *Q. ilex* for 1982–1996 considering the average series ( $n=10$  trees). The correlations were performed using standardized indices of tree-ring width, internode length, vessel diameter and vessel density. The abbreviations are the same as in Table 1. Significance levels: \*:  $0.01 < P \leq 0.05$ ; \*\*:  $P \leq 0.01$

Variables	INTI	TRw	V_D	V_d	C	CA
INTI	–					
TRw	0.26	–				
V_D	–0.37	0.39	–			
V_d	0.24	–0.47	–0.66*	–		
C	0.31	0.87**	0.52*	–0.30	–	
CA	0.13	0.03	0.42	0.23	0.44	–

time trend based on Kendall's tau ( $\tau$ ) coefficient, AR, mean temporal autocorrelation,  $ms_x$ , mean sensitivity, INTI internode length, TRw tree-ring width, V\_D vessel diameter, V\_d vessel density, C total conductance per unit area, CA relative conductive area]



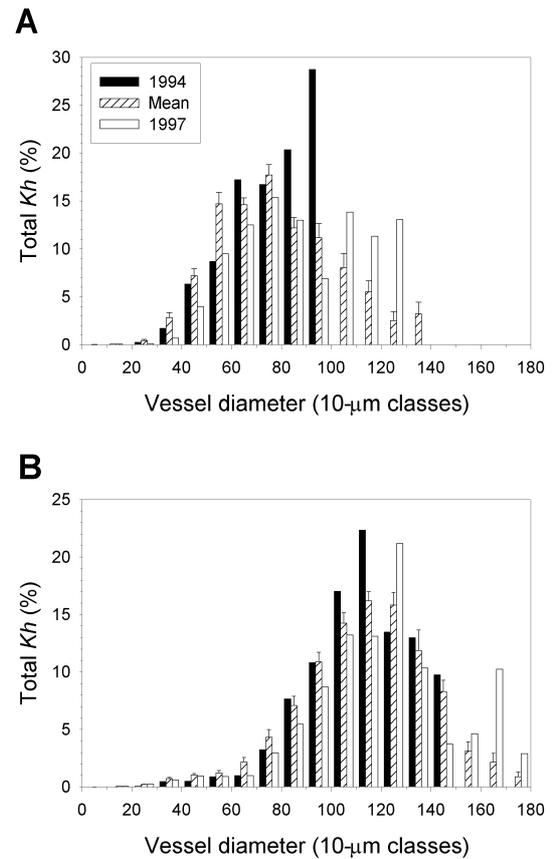
**Fig. 3** Changes in the mean vessel diameter of *Q. ilex* according to the cambial age of the tree-ring. The box plots indicate for each age: the median (*horizontal central line*), the mean (*thick horizontal central line*), the 25% and the 75% percentiles (*box limits*), the 5% and the 95% percentiles (*error bars*), and the outliers (*black dots*). The *line* represents the sample size (number of vessels)



**Fig. 4** Relative frequency (percentage) of the vessels according to their diameter (10- $\mu\text{m}$  classes) for *Q. ilex*. We compared the mean frequency distribution for 1981–1997 with those of two contrasting years in terms of total annual precipitation (see Fig. 2): 1994 (dry year) and 1997 (wet year). The *error bars* are standard errors

vessel diameter and vessel density showed a significant inverse relationship.

The mean vessel diameter stabilized when the branches reached an age of ca. 10 years showing an evident age-related trend (Fig. 3). The vessel diameters distribution showed a unimodal pattern (Fig. 4). The vessels formed from 1981 to 1997 ( $n=7,193$ ) had a mean diameter ( $\pm 1\text{SD}$ ) of  $51\pm 19\ \mu\text{m}$  (mode =  $40\ \mu\text{m}$ ). There were more narrow vessels (diameter 30–70  $\mu\text{m}$ ) and less wide vessels (diameter  $>100\ \mu\text{m}$ ) in a year with a dry summer (1994) than in one (1997) with a wet summer (Fig. 4). This explains why most of the total predicted hydraulic conductance for 1994 was provided by intermediate vessels (80–100  $\mu\text{m}$ ) in *Q. ilex* (diffuse-porous wood) and by wider conduits (100–120  $\mu\text{m}$ ) in the co-occurring *Q. faginea* (ring-porous wood; Fig. 5). In contrast, in a wet year (1997) the wide vessels contributed mostly to the predicted hydraulic conductance in both species. During an average year for precipitation, the importance of the

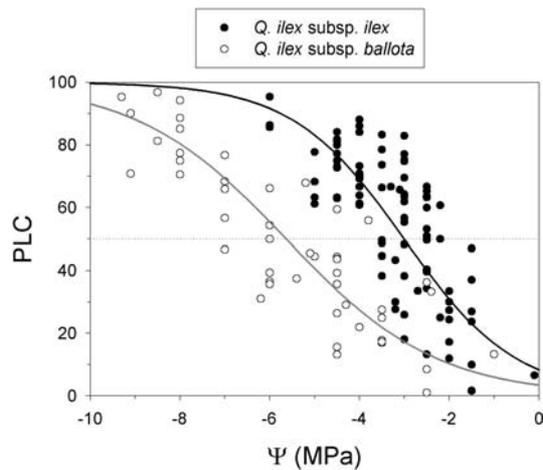


**Fig. 5** Relative contribution (percentage) to the total predicted hydraulic conductance ( $K_h$ ) according to the diameter of vessels (10- $\mu\text{m}$  classes) for *Q. ilex* (A diffuse-porous wood) and *Q. faginea* (B ring-porous wood). The data correspond to vessels measured from rings for 1981–1997. The rest of symbols are the same as in Fig. 4

narrow vessels was comparatively greater for the diffuse-porous than for the ring-porous species.

Both *Q. ilex* subspecies showed different xylem vulnerability to cavitation. The 50% loss of hydraulic conductivity ( $b$ ) was reached on average at a xylem pressure potential of  $-3.0\ \text{MPa}$  and  $-5.6\ \text{MPa}$  for *Q. ilex* subsp. *ilex* and *Q. ilex* subsp. *ballota*, respectively (Fig. 6). This suggests a greater drought resistance of *Q. ilex* subsp. *ballota* in comparison with *Q. ilex* subsp. *ilex*, which is in agreement with the dominance of the former subspecies in inland arid sites under continental influence, such as the study site.

The internode length was positively related with January ( $t$ ) and August ( $t$ ) precipitation and October ( $t-1$ ,  $t$ ) mean temperature, and negatively related with August ( $t$ ) temperature (Fig. 7). The only significant relationship between the climate and the radial growth was obtained for July ( $t$ ) precipitation and June–July ( $t$ ) temperature (Fig. 7). The precipitation and mean temperature only showed clear reverse influences for June–July ( $t$ ) and summer, indicating the negative impact on the radial growth of an increased ETP during these months (Fig. 2). January ( $t$ ) and April ( $t$ ) precipitation were also



**Fig. 6** Vulnerability curves of *Q. ilex* subsp. *ilex* and *Q. ilex* subsp. *ballota*. Each point corresponds to a seedling. Note the contrasting values of water potential corresponding to 50% loss of conductivity (dotted line) for each subspecies. Both fits [*Q. ilex* subsp. *ilex*,  $PLC=100 / (1+e^{0.80(\Psi+3.00)})$ ,  $R^2=0.55$ ; *Q. ilex* subsp. *ballota*,  $PLC=100 / [1+e^{0.59(\Psi+5.63)}]$ ,  $R^2=0.69$ ] were highly significant ( $P \leq 0.001$ )

positively related to the tree-ring width (Fig. 7), and this relationship was significant for the vessel density (Fig. 7). Overall, precipitation and temperature showed reverse influences on the growth in the summer (*t*) months, specifically in August (*t*) for the internode length, and in June–July (*t*) for the tree-ring width and vessel density.

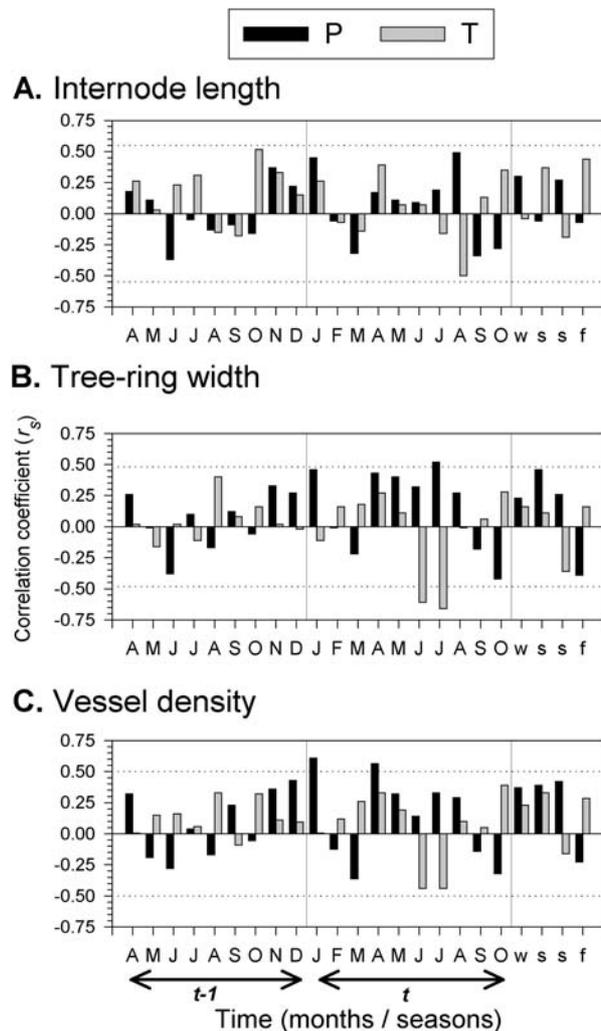
On average, *Q. ilex* showed intermediate vessel diameter and total predicted hydraulic conductance values within those of the wide earlywood vessels and the narrow latewood vessels of the coexisting deciduous oaks with ring-porous wood (*Q. faginea*, *Q. pyrenaica*; Fig. 8). We have only found significant differences ( $P \leq 0.05$ ) in the tree-ring width, vessel diameter and total predicted hydraulic conductance for the latewood of *Q. faginea* and *Q. ilex* when comparing data from a dry (1994) and a wet (1997) year.

## Discussion

### Xylem anatomy and vulnerability to cavitation

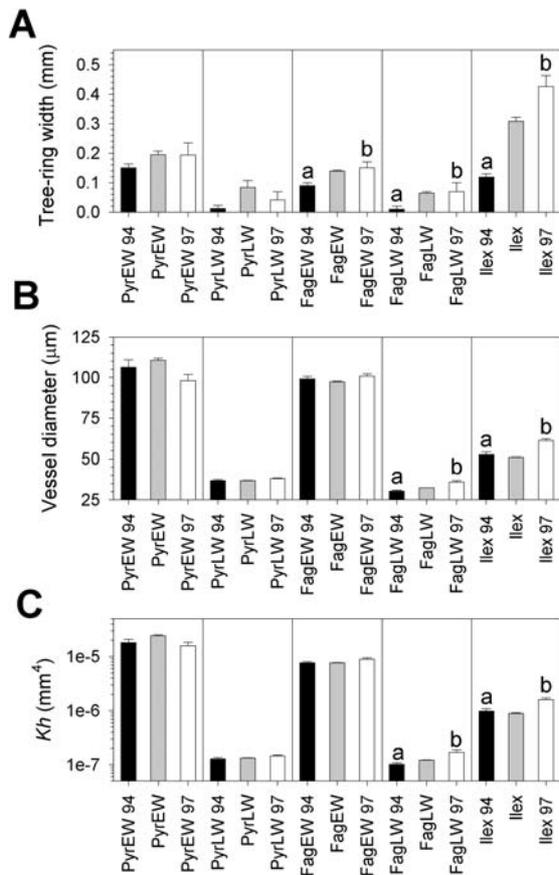
The unimodal distribution of the *Q. ilex* vessels corresponded to a typical diffuse-porous wood (Carlquist 1975). Thus, the hydraulic conductance and resistance against freezing-induced cavitation are not spatially segregated in different types of vessels like in species with ring-porous wood. Low minimum temperatures, like those experienced in the stand under continental influence studied (Fig. 1), may cause freezing-induced cavitation in *Q. ilex* vessels (Lo Gullo and Salleo 1993). Indeed, the higher vulnerability of *Q. ilex* xylem to freeze than to drought stress determinates its northern limit of distribution (Nardini et al. 1998, 2000).

A trade-off is expectable between hydraulic efficiency and freezing tolerance of xylem because vessel diameter



**Fig. 7** Climate-growth relationships of *Q. ilex* based on the correlation between the monthly meteorological data (total precipitation *black bars*, mean temperature *gray bars*) and the standardized indices of: the internode length (A), the tree-ring width (B), and the vessel density (C). Growth and climate were compared from April of the year previous to growth (*t*-1) up to October of the year of growth (*t*). The last four bars to the right represent the seasonal climatic values (winter *JFM*; spring *AMJ*; summer *JAS*; and fall *OND*). The dotted horizontal lines are significance thresholds for  $P \leq 0.05$

is directly related to the reduction in stem hydraulic conductivity by freezing-induced cavitation (Tyree et al. 1994, Davis et al. 1999, Feild and Brodrigg 2001). Even so, the trade-off between vessel diameter and freezing-induced cavitation may be unclear due to the narrow range of vessel sizes found in phylogenetically related oaks (Cavender-Bares and Holbrook 2001). On the other hand, interspecific comparisons suggest that drought-induced cavitation is mainly affected by interconduit pit diameter (Hacke and Sperry 2001, Martínez-Vilalta et al. 2002). In fact, a direct relationship between resistance to drought-induced cavitation and xylem construction costs (wood density) has been found (Hacke et al. 2001). In this study, the vessel diameter of *Q. ilex* changed in response



**Fig. 8** Comparison of the mean width (A), vessel diameter (B) and predicted hydraulic conductance ( $K_h$ ) (C) of the *Quercus* species (*Q. pyrenaica* Pyr, *Q. faginea* Fag, *Q. ilex* Ilex) growing in the study area for two contrasting years in terms of total annual precipitation (1994 dry year–, and 1997 wet year; Fig. 2), and the mean value for 1981–97 (gray bars). The data for oaks with ring-porous wood are represented separately for the earlywood (EW) and the latewood (LW). The different letters above the bars correspond to significant ( $P \leq 0.05$ ) differences between the 1994 and 1997 mean according to the Mann-Whitney test. The error bars are standard errors

to the intensity of summer drought (Fig. 2). The mean vessel diameter decreased in 1994 because most vessels showed small-intermediate diameters (Figs. 3, 4). Thus, most of the total predicted hydraulic conductance of *Q. ilex* in 1994 depended on relatively narrow conduits (Fig. 5), which provide a low hydraulic conductance (Cochard and Tyree 1990).

Several studies on freeze and drought-induced xylem embolism have suggested that *Q. ilex* was a drought-tolerant species (Lo Gullo and Salleo 1993; Tognetti et al. 1998). However, *Q. ilex* also has features usually found in drought-evader species, such as deep roots (Oppenheimer 1957), a great phenotypic plasticity of its leaves (Gratani 1996; Castro-Díez et al. 1997; Bussotti et al. 2002), a rapid stomatal response to soil drying (Eckardt et al. 1975, Tretiach 1993; Gulías et al. 2002), and mesophyll parenchyma cells with relatively rigid walls that allow a great hydric potential drop in response to minimal water

losses (Salleo and Lo Gullo 1990; Corcuera et al. 2002). We have confirmed the greater resistance to drought of *Q. ilex* subsp. *ballota* in comparison with *Q. ilex* subsp. *ilex*, which agrees with their phylogeographic distribution (Lumaret et al. 2002). However, the great phenotypic plasticity of *Q. ilex* might also explain its high adaptive value in the environmentally unpredictable Mediterranean communities (Valladares et al. 2002).

#### Responses of *Q. ilex* growth to drought

In spite of the evidenced plasticity of the vessel diameter in response to increasing aridity, most *Q. ilex* trees lost their leaves in response to the 1994 summer drought and they recovered by 1996 (Ait-Bachir 1998). The drought was not severe and long enough to cause high rates of tree mortality, which indeed were reported for *Pinus* spp. in NE Spain (Martínez-Vilalta and Piñol 2002). During 1994, the great reduction in the tree-ring width, internode length, leaf production and hydraulic conductance and the abundant leaf shedding in response to an increased ETP probably led to a decrease in the leaf area/sapwood area ratio (Mencuccini and Grace 1995). The droughts of winter 1993 and summer 1994 were the most probable climatic causes of this response because co-occurring oak species such as *Q. faginea* showed a similar growth reduction. *Q. faginea* responded to dry 1993–1994 winter with a decrease in the internode length, tree-ring width, and predicted hydraulic conductance (Corcuera 2003). The similar sensitivity to climate variability of *Q. ilex* wood and *Q. faginea* latewood agrees with the presence of both species in sites more xeric than those dominated by *Q. pyrenaica* (Blanco et al. 1997).

A direct influence of August rainfall on longitudinal growth of *Q. ilex* was observed (Fig. 7), which implies a greater leaf production during wet summers as internode length and leaf number were directly related. In spite of the reduction in the internode length and leaf production in 1994, which might be viewed as a first adjustment (Poole and Miller 1975), there was an intense defoliation (second adjustment). The decrease in leaf production and the consequent reduction in transpiration probably led to an adequate water balance (Tyree and Sperry 1989). These adjustments allow *Q. ilex* to withstand the negative effects of the interannual variability of precipitation, typically observed in Mediterranean areas (Di Castri 1981).

#### Sensitivity of *Q. ilex* growth to climate variability

The good synchronization between the cores from different trees, and the coincidence of narrow tree-rings with dry-summer years confirm that the cross-dated *Q. ilex* samples formed annual rings in the study area. This may be explained by the marked seasonality of the study site due to its high elevation and continental influence (Fig. 1). Villar-Salvador et al. (1997) noted the sensitivity

of *Q. ilex* radial growth to the rainfall variability. In the study site, *Q. ilex* radial growth was positively affected by winter (January) and summer (July) precipitation during the year of growth (Fig. 7), which are responses to the climatically contrasting limiting factors characteristic of Mediterranean areas under continental influence (Mitrakos 1980). The main climatic factor limiting the radial growth of *Q. ilex* is the water availability in summer (Zhang and Romane 1991; Cartan-Son et al. 1992; Mayor et al. 1994; Enjalbal et al. 1996; Nabais et al. 1998–1999), which is related to the increased ETP rate in Mediterranean summers (Fig. 2). Silvicultural studies have supported this claim as the thinning of holm oak stands cause a positive effect on girth increment due to the reduced competition for water and nutrients (Ducrey and Toth 1992; Mayor and Rodà 1993; Cutini and Mascia 1996). The winter drought coincides with low temperatures that reduce the production of photosynthates for spring growth (Corcuera 2003). High precipitation in January might also reduce the impact of summer droughts through a higher water storage in the soil (Nabais et al. 1998–1999).

We cannot ignore the negative effects of cold winters in the study area which has a clear continental influence (Fig. 1). In the Cubel-Casas Altas station, 1992 was the year with the coldest January (lowest mean minimum temperature) since 1969. This could have predisposed *Q. ilex* xylem to the negative effects of the dry summer in 1994 because of previous freezing-induced cavitation. Several authors have shown that *Q. ilex* is sensitive to cold and drought stress (Terradas and Savé 1992; Lo Gullo and Salleo 1993; Nardini et al. 2000). If temperatures reach values from  $-5^{\circ}\text{C}$  to  $-11^{\circ}\text{C}$  freeze-induced embolism is irreversible (Lo Gullo and Salleo 1993). In addition, very low water potentials have been observed in *Q. ilex* during winter, which might be due to a decrease of water uptake (Terradas and Savé 1992). In conclusion, *Q. ilex* must cope with the spring conductivity loss due to freezing-induced cavitation in winter through alternative mechanisms of freeze tolerance (replacement of cavitated vessels, root pressure in spring and refilling of the xylem). Future studies should evaluate the cumulative effects of low winter temperatures and summer drought on *Q. ilex* growth.

The sensitivity to climate of *Q. ilex* may be related with its Arcto-Tertiary origin (Pignatti 1978; Axelrod 1983; Palamarev 1989; Zhou et al. 1995). Several facts confirm this subtropical origin under conditions with a less marked seasonal drought (Manos et al. 2001): a great sensitivity to droughts (this study), a pronounced phenological and cambial activity in spring-summer (Lipshitz and Lev-Yadun 1986; Gratani 1996; Castro-Díez and Montserrat-Martí 1998), and ancestral reproductive-biological features (Herrera 1992).

## Conclusions

The *Q. ilex* individuals studied showed a plastic response to the 1994 summer drought mediated by: (1) a great sensitivity of growth and wood-anatomical variables, and (2) a fast recovery of growth. There was a reduction in the radial and longitudinal growth and probably widespread xylem embolism. In spite of the deep roots usually developed by *Q. ilex*, this species was not able to use deep water layers and reduced its ETP through enhanced leaf dropping and reduced leaf production. The remarkable loss of leaves in 1994 is especially important for *Q. ilex*, which can reach high photosynthetic rates in September (Tretiach and Rondi 1994). This also can explain the reduced longitudinal growth in 1995 in spite of the wet 1994 fall, which might indicate certain growth inertia.

The *Q. ilex* individuals studied survived the severe 1994 drought because a given threshold of ecophysiological resistance was not exceeded and mortality was low. If the frequency and duration of the severe summer droughts increased, as several climate assessments and models suggest (Piervitali et al. 1997; Osborne et al. 2000; IPCC 2001), there could be progressive substitution of *Q. ilex* with species more resistant to summer droughts. However, this process would happen within a very fragmented landscape.

**Acknowledgements** This work was supported by IFD97–0911-C03–01 project (Subpr. 1) and a INIA grant to L.C. We thank M.A. Pascual Navarro (SIA-DGA), G. Montserrat Martí and C. Pérez Rontomé (IPE-CSIC) for their kind help with the vulnerability curves and the microtome. We thank N.M. Holbrook and two anonymous reviewers for their valuable comments.

## References

- Ait-Bachir S (1998) Utilisation des images-satellite Landsat-TM pour l'étude diachronique du syndrome de déperissement des chênaies de la région de Cubel (Aragón). Master Thesis. IAMZ, Saragossa
- Allué Andrade JL (1990) Atlas fitoclimático de España: taxonomías. MAPA-INIA, Madrid
- Axelrod DI (1983) Biogeography of oaks in the Arcto-Tertiary province. *Ann Mo Bot Gard* 70: 629–657
- Baas P, Schweingruber FH (1987) Ecological trends in the wood anatomy of trees, shrubs and climbers from Europe. *IAWA Bull* 8:245–274
- Baas P, Werker E, Fahn A (1983) Some ecological trends in vessel characters. *IAWA Bull* 4:141–159
- Becker M, Lévy G (1982) Le déperissement du chêne en forêt de Tronçais. Les causes écologiques. *Ann Sci For* 39:439–444
- Blanco E, Casado MA, Costa M, Escribano R, García M, Génova M, Gómez A, Gómez F, Moreno JC, Morla C, Regato P, Sáinz H (1997) Los bosques ibéricos: una interpretación geobotánica. Planeta, Madrid
- Bussotti F, Bettini D, Grossoni P, Mansuino S, Nibbi R, Soda C, Tani C (2002) Structural and functional traits of *Quercus ilex* in response to water availability. *Environ Exp Bot* 47:11–23
- Carlquist S (1975) Ecological strategies of xylem evolution. University of California Press, Los Angeles
- Cartan-Son M, Floret C, Galan MJ, Grandjanny M, Le Floc'h E, Maistre M, Perret P, Romane F (1992) Factors affecting radial growth of *Quercus ilex* L. in a coppice stand in southern France. *Vegetatio* 99–100:61–68

- Castro-Díez P, Montserrat-Martí G (1998) Phenological pattern of fifteen Mediterranean phanerophytes from *Quercus ilex* communities of NE-Spain. *Plant Ecol* 139:103–112
- Castro-Díez P, Villar-Salvador P, Pérez-Rontomé C, Maestro-Martínez M, Montserrat-Martí G (1997) Leaf morphology and leaf chemical composition in three *Quercus* (Fagaceae) species along a rainfall gradient in NE Spain. *Trees* 11:127–134
- Cavender-Bares J, Holbrook NM (2001) Hydraulic properties and freezing-induced cavitation in sympatric evergreen and deciduous oaks with contrasting habitats. *Plant Cell Environ* 24:1243–1256
- Ceballos L, Ruiz de la Torre J (1979) Árboles y arbustos de la España peninsular. ETSIM, Madrid
- Cochard H, Tyree MT (1990) Xylem dysfunction in *Quercus*: vessel sizes, tyloses, cavitation and seasonal changes in embolism. *Tree Physiol* 6:393–407
- Cochard H, Cruziat P, Tyree MT (1992) Use of positive pressures to establish vulnerability curves. *Plant Physiol* 100:205–209
- Cook ER, Holmes RL (1992) Guide for computer program ARSTAN, Dendrochronology Program Library. Laboratory of Tree-Ring Research, University of Arizona, Tucson
- Corcuera L (2003) Respuesta al clima de distintas especies del género *Quercus*: Estructura y funcionamiento comparado. PhD thesis, University of Lleida, Spain
- Corcuera L, Camarero JJ, Gil-Pelegrín E (2002) Functional groups in *Quercus* species derived from the analysis of pressure-volume curves. *Trees* 16:465–472
- Cramer HH (1984) On the predisposition to disorders of Middle European forests. *Pflanzenschutz-Nachr* 2:97–207
- Cutini A, Mascia V (1996) Silvicultural treatment of holm oak (*Quercus ilex* L.) coppices in Southern Sardinia: effects of thinning on water potential, transpiration and stomatal conductance. *Ann Ist Sper Selv* 27:47–53
- Davis SD, Sperry JS, Hacke UG (1999) The relationship between xylem conduit diameter and cavitation caused by freezing. *Am J Bot* 86:1367–1372
- Delatour C (1983) Le dépérissement des chênes en Europe. *Rev For Fr* 35:265–282
- Di Castri F (1981) Mediterranean-type shrublands of the world. In: Di Castri F, Goodall DW, Specht RL (eds), *Mediterranean-type shrublands*. Elsevier, Amsterdam, pp 1–52
- Douglass AE (1936) Climatic cycles and tree growth, vol III. A study of cycles. Publication 289. Carnegie Institute of Washington, Washington
- Ducrey M, Toth J (1992) Effect of cleaning and thinning on height growth and girth increment in holm oak coppices (*Quercus ilex* L.). *Vegetatio* 99–100:365–376
- Eckardt FE, Heim G, Methy M, Sauvezon R (1975) Interception de l'énergie rayonnante, échanges gazeux et croissance dans un forêt méditerranéenne à feuillage persistant (*Quercetum ilicis*). *Photosynthetica* 9:145–156
- Enjalbal I, Grandjanny M, Maistre M, Perret P, Romane F, Shater Z (1996) The holm oak (*Quercus ilex* L.) radial growth facing the rainfall unpredictability. An example in Southern France. *Ann Ist Sper Selv* 27:31–37
- Faci González JM, Martínez Cob A (1991) Cálculo de la evapotranspiración de referencia en Aragón. DGA, Saragossa
- Feild TS, Brodribb T (2001) Stem water transport and freeze-thaw xylem embolism in conifers and angiosperms in a Tasmanian treeline heath. *Oecologia* 127:314–320
- Floret C, Galán MJ, Lefloc'h E, Orshan E, Romane F (1990) Growth forms and phenomorphology traits along an environmental gradient: tools for studying vegetation? *J Veg Sci* 1:71–80
- Font Tullot I (1988) Historia del clima de España. Cambios climáticos y sus causas. INM, Madrid
- Fritts HC (1976) Tree rings and climate. Academic Press, London
- Gratani L (1996) Leaf and shoot growth dynamics of *Quercus ilex* L. *Acta Oecol* 17:17–27
- Gulías J, Flexas J, Abadía A, Medrano H (2002) Photosynthetic response to water deficit in six Mediterranean sclerophyll species: possible factors explaining the declining distribution of *Rhamnus ludovici-salvatoris*, an endemic Balearic species. *Tree Physiol* 22:687–697
- Hacke UG, Sperry JS (2001) Functional and ecological xylem anatomy. *Perspect Plant Ecol Evol Syst* 4:97–115
- Hacke UG, Sperry JS, Pockman WT, Davis SD, McCulloh KA (2001) Trends in wood density and structure are linked to prevention of xylem implosion by negative pressure. *Oecologia* 126:457–461
- Herrera CM (1992) Historical effects and sorting processes as explanations for contemporary ecological patterns: Character syndromes in Mediterranean woody plants. *Am Nat* 140:421–446
- Huber F (1993) Déterminisme de la surface des vaisseaux du bois des chênes indigènes (*Quercus robur* L., *Quercus petraea* Liebl.). Effet individuel, effet de l'appareil foliaire, des conditions climatiques et de l'âge de l'arbre. *Ann Sci For* 50:509–524
- IPCC (2001) Climate change 2001: the scientific basis. Cambridge University Press, Cambridge
- Jarbeau JA, Ewers FW, Davis SD (1995) The mechanism of water-stress-induced embolism in two species of chaparral shrubs. *Plant Cell Environ* 18:189–196
- Liphshitz N, Lev-Yadun S (1986) Cambial activity of evergreen and seasonal dimorphics around the Mediterranean. *IAWA Bull* 7:145–153
- Lloret F, Siscart D (1995) Los efectos demográficos de la sequía en poblaciones de encina. *CSECF* 2:77–81
- Lo Gullo MA, Salleo S (1993) Different vulnerabilities of *Quercus ilex* to freeze- and summer drought-induced xylem embolism: an ecological interpretation. *Plant Cell Environ* 16:511–519
- Lumaret R, Mir C, Michaud H, Raynal V (2002) Phytogeographical variation of chloroplast DNA in holm oak (*Quercus ilex* L.). *Mol Ecol* 11:2327–2336
- Manos PS, Zhou ZK, Cannon CH (2001) Systematics of Fagaceae: phylogenetic tests of reproductive trait evolution. *Int J Plant Sci* 162:1361–1379
- Martínez-Vilalta J, Piñol J (2002) Drought-induced mortality and hydraulic architecture in pine populations of the NE Iberian Peninsula. *For Ecol Manage* 161:247–256
- Martínez-Vilalta J, Prat E, Oliveras I, Piñol J (2002) Hydraulic properties of roots and stems of nine woody species from a holm oak forest in NE Spain. *Oecologia* 133:19–29
- Mayor X, Rodà F (1993) Growth response of holm oak (*Quercus ilex* L.) to commercial thinning in the Montseny mountains (NE Spain). *Ann Sci For* 50:247–256
- Mayor X, Belmonte R, Rodrigo A, Rodà F, Piñol J (1994) Crecimiento diametral de la encina (*Quercus ilex* L.) en un año de abundante precipitación estival: efecto de la irrigación previa y de la fertilización. *Orsis* 9:13–23
- Mencuccini M, Grace J (1995) Climate influences the leaf area/sapwood area ratio in Scots pine. *Tree Physiol* 15:1–10
- Mitrakos KA (1980) A theory for Mediterranean plant life. *Acta Oecol* 1:245–252
- Montoya Moreno R (1995) Red de seguimiento de daños en los montes. Daños originados por la sequía en 1994. *CSECF* 2:83–97
- Nabais C, Freitas H, Hagemeyer J (1998–1999) Tree-rings to climate relationships of *Quercus ilex* L. in NE-Portugal. *Dendrochronologia* 16–17:37–44
- Nardini A, Ghirardelli L, Salleo S (1998) Vulnerability to freeze stress of seedlings of *Quercus ilex* L.: an ecological interpretation. *Ann Sci For* 55:553–565
- Nardini A, Salleo S, Lo Gullo MA, Pitt F (2000) Different responses to drought and freeze stress of *Quercus ilex* L. growing along a latitudinal gradient. *Plant Ecol* 148:139–147
- Oppenheimer HR (1957) Further observations on roots penetrating into rocks and their structure. *Bull Res Counc Isr* 6D:18–31
- Orshan G (1989) Plant pheno-morphological studies in Mediterranean type ecosystems. Kluwer, Dordrecht
- Osborne CP, Mitchell PL, Sheehy JE, Woodward FI (2000) Modelling the recent historical impacts of atmospheric CO<sub>2</sub> and

- climate change on Mediterranean vegetation. *Global Change Biol* 6:445–458
- Palamarev E (1989) Paleobotanical evidences of the Tertiary history and origin of the Mediterranean sclerophyll dendroflora. *Plant Syst Evol* 162:93–107
- Pammenter NW, Vander Willigen C (1998) A mathematical and statistical analysis of the curves illustrating vulnerability of xylem to cavitation. *Tree Physiol* 18:589–593
- Peñuelas J, Lloret F, Montoya R (2001) Severe drought effects on Mediterranean woody flora. *For Sci* 47:214–218
- Piervitali E, Colacino M, Conte M (1997) Signals of climatic change in the Central-Western Mediterranean Basin. *Theor Appl Climatol* 58:211–219
- Pignatti S (1978) Evolutionary trends in Mediterranean flora and vegetation. *Vegetatio* 37:175–185
- Piñol J, Terradas J, Lloret F (1998) Climate warming, wildfire hazard, and wildfire occurrence in coastal eastern Spain. *Clim Change* 38:345–357
- Poole DK, Miller PC (1975) Water relations of selected species of chaparral and coastal sage communities. *Ecology* 56:1118–1128
- Rivas-Martínez S, Sáenz C (1991) Enumeración de los *Quercus* de la Península Ibérica. *Rivasgodaya* 6:101–110
- Rodà F, Retana J, Gracia CA, Bellot J (1999) Ecology of Mediterranean evergreen oak forests. Springer, Berlin Heidelberg New York
- Sáenz de Rivas C (1967) Estudios sobre *Quercus ilex* L. y *Quercus rotundifolia* Lamk. *Ana Inst Bot Cavanilles* 2:243–262
- Salleo S, Lo Gullo MA (1990) Sclerophylly and plant water relations in three Mediterranean *Quercus* species. *Ann Bot* 65:259–270
- Sass U, Eckstein D (1995) The variability of vessel size in beech (*Fagus sylvatica* L.) and its ecophysiological interpretation. *Trees* 9:247–252
- Serrada R, Allué M, San Miguel A (1992) The coppice system in Spain. Current situation, state of art and major areas to be investigated. *Ann Ist Sper Selv* 23:266–275
- Simonin G, Cocharad H, Delatour C, Granier A, Dreyer E (1994) Vulnerability of young oak seedlings (*Quercus robur* L.) to embolism: responses to drought and to an inoculation with *Ophiostoma quercu* (Georgevitch) Nannf. *Ann Sci For* 51:493–504
- Sokal RR, Rohlf FJ (1995) Biometry: the principles and practice of statistics in biological research. Freeman, New York
- Sperry JS, Sullivan JE (1992) Xylem embolism in response to freeze-thaw cycles and water stress in ring porous, diffuse porous and conifer species. *Plant Physiol* 100:605–613
- Sperry JS, Nichols KL, Sullivan JE, Eastlack SE (1994) Xylem embolism in ring-porous, diffuse-porous and coniferous trees in northern Utah and interior Alaska. *Ecology* 75:1736–1752
- Stokes MA, Smiley TL (1968) An introduction to tree-ring dating. University of Chicago Press, Chicago
- Tainter FH, Retzlaff WA, Starkey DA, Oak SW (1990) Decline of radial growth in red oaks is associated with short-term changes in climate. *Eur J For Pathol* 20:95–105
- Terradas J, Savé R (1992) The influence of summer and winter stress and water relationships on the distribution of *Quercus ilex* L. *Vegetatio* 99–100:137–145
- Tognetti R, Longobucco A, Raschi A (1998) Vulnerability of xylem to embolism in relation to plant hydraulic resistance in *Quercus pubescens* and *Quercus ilex* co-occurring in a Mediterranean coppice stand in central Italy. *New Phytol* 139:437–447
- Tretiach M (1993) Photosynthesis and transpiration of evergreen Mediterranean and deciduous trees in an ecotone during a growing season. *Acta Oecol* 14:341–360
- Tretiach M, Rondi A (1994) Variazione stagionale dell'attività fotosintetica e maturazione fogliare in sei arboree nella costiera Triestina (NE Italia). *Stud Trent Sci Nat* 69:1–16
- Tryon EH, True RP (1958). Recent reductions in annual radial increments in dying scarlet oaks related to rainfall deficiencies. *For Sci* 4:219–230
- Tutin TG, Heywood VH, Burges NA, Moore DM, Valentine DH, Walters SM, Webb DA (1993) *Flora Europaea*, vol. 1. Cambridge University Press, London
- Tyree MT, Cocharad H (1996) Summer and winter embolism in oak: impact on water relations. *Ann Sci For* 53:173–180
- Tyree MT, Ewers FW (1991) The hydraulic architecture of trees and other woody plants. *New Phytol* 119:345–360
- Tyree MT, Sperry JS (1989) Vulnerability of xylem to cavitation and embolism. *Annu Rev Plant Physiol* 40:19–38
- Tyree MT, Alexander JL, Machado JL (1992) Loss of hydraulic conductivity due to water stress in intact juveniles of *Quercus rubra* and *Populus deltoides*. *Tree Physiol* 10:411–415
- Tyree MT, Davis SD, Cocharad H (1994) Biophysical perspectives of xylem evolution: is there a tradeoff of hydraulic efficiency for vulnerability to dysfunction? *IAWA J* 15:335–360
- Valladares F, Balaguer L, Martínez-Ferri E, Pérez-Corona E, Manrique E (2002) Plasticity, instability and canalization: is the phenotypic variation in seedlings of sclerophyll oaks consistent with the environmental unpredictability of Mediterranean ecosystems? *New Phytol* 156:457–467
- Villar-Salvador P, Castro Díez P, Pérez Rontomé C, Montserrat Martí G (1997) Stem xylem features in three *Quercus* (Fagaceae) species along a climatic gradient in NE Spain. *Trees* 12:90–96
- Woodcock DW (1989) Climate sensitivity of wood-anatomical features in a ring-porous oak (*Quercus macrocarpa*). *Can J For Res* 19:639–644
- Woodcock DW, Ignas CM (1994) Prevalence of wood characters in Eastern North America: what characters are most promising for interpreting climates from fossil wood? *Am J Bot* 81:1243–1251
- Zavala MA, Espelta JM, Lloret F (2000) Constraints and trade-offs in Mediterranean plant communities: The case of holm oak-Aleppo pine forests. *Bot Rev* 66:119–149
- Zhang SH, Romane F (1991) Variations de la croissance radiale de *Quercus ilex* L. en fonction du climat. *Ann Sci For* 48:225–234
- Zhang SY, Baas P, Zandee M (1992) Wood structure of the Rosaceae in relation to ecology, habit and phenology. *IAWA J* 13:307–349
- Zhou Z, Wilkinson H, Zheng-Yi W (1995) Taxonomical and evolutionary implications of the leaf anatomy and architecture of *Quercus* L. subgenus *Quercus* from China. *Cathaya* 7:1–34
- Zimmermann MH (1983) Xylem structure and the ascent of sap. Springer, Berlin Heidelberg New York