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ORIGINAL ARTICLE

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Radial-growth and wood-anatomical changes in overaged *Quercus pyrenaica* coppice stands: functional responses in a new Mediterranean landscape

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Abstract Recent land-use changes in intensively managed forests such as Mediterranean coppice stands might profoundly alter their structure and function. We assessed how the abandonment of traditional management practices in coppice stands, which consisted of short cutting-cycles (10–15 years), has caused overaging (stems are usually much older than when they were coppiced) and altered their wood anatomy and hydraulic architecture. We studied the recent changes of wood anatomy, radial growth, and hydraulic architecture in two stands of *Quercus pyrenaica*, a transitional Mediterranean oak with ring-porous wood forming coppice stands in W–NW Spain. We selected a xeric and a mesic site because of their contrasting climates and disturbance histories. The xeric site experienced an intense defoliation after the severe 1993–1994 summer drought. The mesic site was thinned in late 1994. We studied the temporal variability in width, vessel number and diameter, and predicted the hydraulic conductivities (K_h) of earlywood and latewood. In the mesic site, we estimated the vulnerability to xylem cavitation of earlywood vessels. Overaging caused a steep decline in latewood production at a cambial age of 14 years., which was close to the customary cutting cycle of *Q. pyrenaica*. The diameter distribution of vessels was bimodal, and latewood vessels only accounted for 4% of the K_h. Overaging, acting as a predisposing factor in the decline episode, was observed at the xeric site, where most trees did not produce latewood in 1993–1995. At the mesic site, thinned trees formed wider tree-rings, more latewood and multiseriate tree-rings than overaged trees. The growth enhancement remained 8 years after thinning. Most of the hydraulic conductivity in earlywood was lost in a narrow range of potentials, between −2.5 and −3.5 MPa. We have shown how hydraulic conductivity and radial growth are closely related in *Q. pyrenaica* and how aging modulates this relationship.

Keywords Dendroecology · Hydraulic conductivity · Oak decline · Wood anatomy

Introduction

Most studies on the responses of forests to global change have focused on the effects of climatic change. However, additional components of global change such as changes in global biogeochemical cycles and land-use modifications can greatly affect forest dynamics (Vitousek 1994). In the forests of the western Mediterranean basin, intensive land-use changes have been common since the Neolithic (Blondel and Aronson 1999).

Typical examples of intensively exploited Mediterranean woodlands are coppice stands, which are characterized by secular traditional management techniques. Most Mediterranean coppice stands are dominated by *Quercus* forests located in mountainous areas. In the Mediterranean region, *Quercus* coppice stands were traditionally managed for fuel, wood and charcoal production (Barberó et al. 1990). A regular cutting cycle was followed for each oak species and this was recurrently applied in each stand. Thus, the coppicing system created and maintained an open woodland characterized by multistemmed clumps and usually intense stump sprouting (Giovannini et al. 1992). However, recent socioeconomical changes have led to the abandonment of traditional management in coppice stands. Currently, these woodlands form a new landscape characterized by the overaging of previously coppiced individuals due to undercutting, i.e. most individuals have much older stems today than when they were traditionally coppiced.

In Spain, traditional coppice management has declined rapidly since the 1960's, when the rural population and charcoal demand greatly decreased (Cañellas et al. 1994). Most Spanish coppice stands, which represent ca. 22% of

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the forest cover in the country, have surpassed the traditional rotation age and the age of their stems is greater than the maximum age imposed by the traditional cutting-cycle (Serrada et al. 1992). As a consequence, overaged coppice stands are characterized by a reduction in radial growth, canopy closure and the accumulation of biomass (Floret et al. 1989; Cañellas et al. 1996). These structural changes have also led to new management strategies such as the conversion from overaged coppice stands into high forests and open woodlands through selective thinning, a task which is not always successfully accomplished (Amorini et al. 1996).

In addition to these drastic land-use changes, several oak-decline episodes were described in the Iberian Peninsula during the 1980's and 1990's when several intense summer droughts occurred (Peñuelas et al. 2001; Corcuera et al. 2004a). The abiotic explanation was further supported by the detection of recent trends of climate warming and more frequent droughts in the western Mediterranean basin (IPCC 2001). Most affected stands in northeastern Spain were coppice stands but, to our knowledge, no study considered the relationship between the decline episodes and overaging of affected coppice stands.

Functional studies have dealt with the effects of thinning on tree water relations in oak stands (Bréda et al. 1995). However, only little work has considered the effects of overaging and climatic stress on wood anatomy and radial growth, despite the consequences of radial reduction on the functional responses of coppice stands. For instance, Corcuera et al. (2004b) studied radial-growth changes in *Quercus faginea* Lam., a transitional Mediterranean oak species with ring-porous wood. They found that most shoots did not produce latewood in overaged stems during years with intense summer drought. These changes in radial growth and wood anatomy imply functional adjustments because of the contrasting structure and function of earlywood and latewood in species with ring-porous wood.

In this study, we hypothesize that current overaging of coppice stands is a predisposing factor insufficiently investigated (Manion 1991; Manion and Lachance 1992) to explain oak decline in the Mediterranean region. Overaging might increase the sensitivity of coppice stands to climatic stress thus linking the effects of two components of global change on forests, i.e. land-use modifications and climatic change. Our idea also considers climatic disturbances (e.g. drought) as the main triggering factor initiating oak decline. As Führer (1998) suggested for oak forests in Central Europe, the combination of regional (climate) and local (overaging) factors may explain most variability in oak decline processes. Our main objective was the study of the effects of overaging on radial growth (wood anatomy, tree-ring width) and the consequences of growth reduction on hydraulic conductivity. We selected two sites showing contrasting management systems and climatic conditions but dominated by the same oak species.

Material and methods

Species

Oaks form several types of wood according to their anatomy, ranging from ring-porous to diffuse-porous wood. In this study, we focused on *Quercus pyrenaica* Willd. which forms ring-porous wood. The contrasting characteristics of earlywood (wide vessels, low density) and latewood (narrow vessels, high density) provide a good basis for understanding the functional consequences of radial-growth changes (Corcuera et al. 2004a, 2004b). *Q. pyrenaica* is a deciduous transitional Mediterranean oak with ring-porous wood, which is restricted to SW Europe (W–NW Spain, SW France) and isolated sites in N Morocco (Blanco et al. 1997). Its transitional character between Mediterranean and mesic oaks has been confirmed by ecophysiological studies (Corcuera et al. 2002). *Q. pyrenaica* is one of the main coppice species in central and western Spain, where it occupies ca. 650,000 ha (Jiménez Sancho et al. 1998). In the Iberian Peninsula, it is more abundant on gentle slopes and basal locations of mountainous areas, where soil-water reserves accumulate, and on acid soils (Ceballos and Ruiz de la Torre 1979). The traditional coppice cycle of this species was 10–15 years until the last half of the twentieth century, but current cycles are longer than 20 years due to the abandonment of traditional land-use management (Allué and San Miguel 1991; Cañellas et al. 1994).

Study sites

We studied two sites located in *Q. pyrenaica* coppice stands from two climatically contrasting areas in the Iberian System (NE Spain). The study sites were regarded as a mesic (hereafter ME site) and a xeric site (hereafter XE site). The main characteristics of both sites appear in Table 1. Structural variables were measured for all stems found within a 10 m × 10 m plot located in each stand. In the XE site, most *Q. pyrenaica* individuals showed defoliation in 1994 and 1995 after the severe 1993–1994 drought (Corcuera 2003). Climatic data were obtained from the Agramonte (1° 49′ W, 41° 49′ N, 1060 m asl.) and the Cubel-Casas Altas meteorological stations (1° 38′ W, 41° 06′ N, 1108 m asl) for the ME and the XE sites, respectively. The mean annual temperatures were 9.5°C (ME, range of mean monthly temperatures 1.6°C–17.8°C) and 11.3°C (XE, range m.m.t. 3.2°C–21.4°C). The total annual precipitation was higher at ME (794 mm) than at the XE site (449 mm), with maxima in spring and fall at both sites. The drought period (precipitation <2 temperature in the ombrothermic diagram) lasted for 1 month (August) and 2 months (July, August) at the ME and the XE sites, respectively. Phytoclimates correspond to a transitional nemoro-Mediterranean forest with continental influence

Table 1 Geographic, topographic and structural characteristics of the studied *Q. pyrenaica* stands in the Iberian System (NE Spain)

	ME	XE
Study area	Moncayo Sierra	Santa Cruz Sierra
Latitude (N)	41° 47′	41° 07′
Longitude (W)	1° 48′	1° 39′
Elevation (m asl)	900	1177
Slope (°)	15	5
Aspect	NE	SW
Bedrock type	quartzite	limestone
Density (stems·ha^{-1})	5375/2200	2800
Stems per individual	8±2/1±0	2±0
Basal area (m^2·ha^{-1})	34.2/20.2	25.3
Dbh (cm)	9.9±0.6/10.3±0.4	9.3±0.9
Height (m)	5.2±0.8/6.0±0.9	5.0±0.3
Age[a] (years)	40±2/41±3	35±2

The two values of structural variables for the mesic site correspond to the overaged and thinned coppice stands, respectively. Abbreviations are as follows: ME, mesic site; XE, xeric site; dbh, diameter at breast height (1.3 m). Mean values are given with standard errors

[a] Age of sampled stems estimated at 1.3 m

for the XE site, and a nemoro-Mediterranean deciduous forest for the ME site (Jiménez Sancho et al. 1998).

Dendroecology

We selected two close coppice stands at the ME site, one of them was overaged and the other had been thinned in November 1994. Sampling was performed between 2000 and 2002 to study whether the radial-growth increase remained 8 years after the thinning. We selected stems with similar diameters at h = 1.3 m from an area ca. 0.5 ha in each coppice stand. Dendrochronological sampling was carried out following standard methodology (Fritts 1976; Cook and Kairiukstis 1990). We took two cores per stem at 1.3 m height from 10–12 stems per stand. The cores were air-dried and polished using sandpaper of progressively finer grain. Then, they were cross-dated noting narrow tree rings (Yamaguchi 1991). Visual cross-dating was checked using the COFECHA software (Holmes 1983). Tree-ring width was measured to the nearest 0.01 mm using a LINTAB measurement device and associated TSAP software (Frank Rinn, Heidelberg, Germany). Finally, we also noted the frequency of shoots without latewood and the proportion of multiseriate tree-rings, i.e. those rings with more than one series of earlywood vessels. Usually, multiseriate tree-rings were biseriate.

Preparation of wood-anatomical samples

Sampling was done in January 1998 at the XE site. Ten branches were cut at mid crown from the S–SW side of 10 dominant multistemmed *Q. pyrenaica* individuals (one branch per individual) for the analyses of wood-anatomical variables. Despite the sample size being close to the minimum required in standard dendroecological studies (Fritts 1976), the exhaustive description of wood-anatomical variables made this an adequate sample size to be studied. The middle of the oldest internodal segment of each branch was transversally sectioned with a sliding microtome (Anglia Scientific AS200, UK). Sections with a thickness of 15–30 μm were stained with safranin and Fast Green, dehydrated by means of 96% ethanol, and permanently mounted on slides with Canada balsam. The cross-sections were studied microscopically (Olympus BH-2) with a photo-microadapter (Olympus OM-Mount) and a camera (Olympus OM101) for slide printing. The photos were digitized, calibrated, and visually cross-dated (Stokes and Smiley 1968). Finally, images were analysed on a Macintosh computer using the public domain NIH Image program (developed at the US National Institutes of Health and available at http://rsb.info.nih.gov/nih-image/).

Wood-anatomical variables

A sequence of 22 annual values was used (1976–97) because this was the period common to all trees selected for study. To describe the response of radial growth to overaging, the following variables were considered: tree-ring width (mean of two radii per ring located at right angles), and vessel number and diameter. Variables were measured separately for earlywood and latewood. The abrupt shift in vessel size across the ring allowed us to identify the two types of wood (earlywood and latewood). Vessel-related variables (diameter, number) were measured in a standard area formed by a rectangle with width 5 mm along the tangential axis. The conductive area was regarded as the total area occupied by the vessels. We obtained mean annual values for all the variables by averaging the values of different individuals.

Vessel diameter is the main anatomical variable determining hydraulic conductivity (Carlquist 1975). The hydraulic conductivity (K_h) of a cylindrical conduit increases with its radius (r) to the fourth power according to the Hagen–Poiseuille law (Zimmermann 1983). The predicted hydraulic conductivity (K_h; mm^4) was calculated as the sum of the fourth power radii of all the vessels from each section (Σr^4). Previous studies considered only the 10–25 widest conduits per section to estimate the predicted hydraulic conductivity (Villar-Salvador et al. 1997). In this study, for each tree-ring, we measured all the vessels whose tangential diameter was >10 μm within a rectangle with width 5 mm along the tangential axis cited above. The smallest and largest diameters were averaged for every vessel. We considered this comprehensive anatomical description to be necessary to estimate the hydraulic conductivity precisely.

Vulnerability of the earlywood to cavitation

The use of positive pressures to quantify the vulnerability of the xylem to cavitation is based on the estimate of the percent loss in hydraulic conductivity (PLC) at different induced pressures or water potentials (Ψ) (Cochard et al. 1992). We estimated the loss in conductivity based on the percentage of cavitated earlywood vessels at different pressures. We used the air injection method (Sperry and Pockman 1993) to induce cavitation in earlywood vessels of overaged branches taken from the ME site. The low number of latewood vessels in overaging branches did not allow the performance of the vulnerability curves for these conduits. Branches of similar age (9 years) were sampled from the lower crown in August, and they were recut under water. We built a 5-way manifold with diameters similar to those of shoots (8–10 mm) to perfuse gas at different pressures into the cut side-branches for 60 min. A nitrogen gas cylinder supplied the following pressures: 0.1, 2.5, 3.0, 3.5, and 4.0 MPa. Five shoots per pressure were perfused. The first pressure was considered as a reference value to avoid estimation errors due to artifacts in the method (Sperry and Pockman 1993). Each manifold was comprised of by a pressure-tight collar and a compressible gasket to inject air. After pressurization, branches were transported inside plastic black bags with humid air to a nearby laboratory, property of the Forest Services. Six-year-old segments were cut under distilled water to avoid the incoming flux of air or solids (Tyree et al. 1993). The PLC was estimated for five branches from five different trees. To detect which earlywood conduits were cavitated, branches used to build cavitation curves were perfused under low pressure (0.5 m) during 12 h with a previously filtered (0.22-µm mesh) and degassed aqueous safranin solution (0.5%) (Lo Gullo and Salleo 1991). We did not express the initial conductivity as a percentage of the maximum obtained after removal of emboli in order to prevent the de-embolization in vessels of previous years (Sperry 1986). The subsequent preparation of wood samples was similar to wood-anatomical samples taken at the XE site. Xylem photographs of the most recent tree-ring were taken for the different potentials using an epifluorescence microscope. This technique allows the detection of very

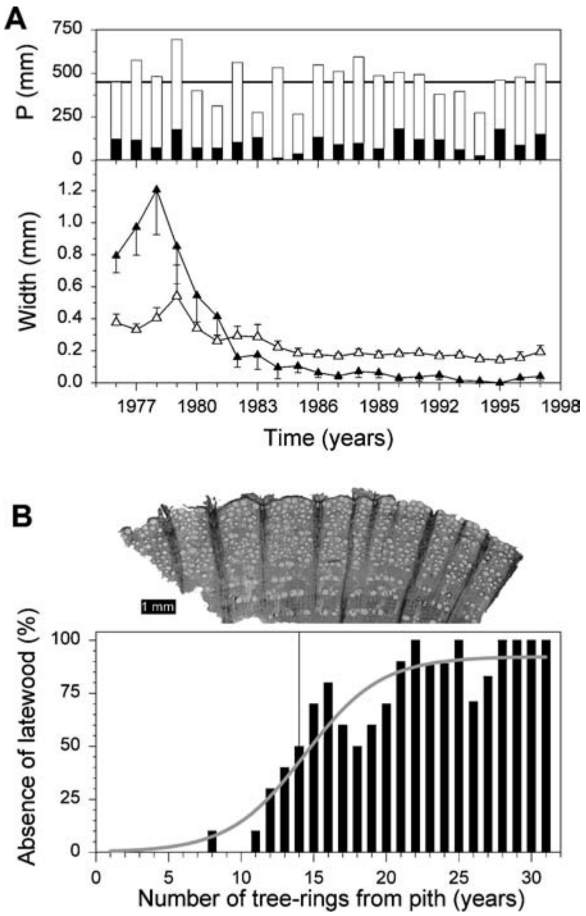

Fig. 1 **A** Temporal variability of earlywood (empty triangles) and latewood (filled triangles) width of *Q. pyrenaica* at the xeric site as compared with annual (bars) and summer (black section) precipitation in the study area (the horizontal line is the mean annual precipitation for the 1976–1997 period). Note the low production of latewood during the 1993–1995 period after the summer droughts in 1993–1994. The error bars are standard errors, and they are presented in one direction for visual clarity. **B** Frequency (f) of shoots at this site without latewood as a function of cambial age (a). The fitted logistic function ($f = 92.28 / (1 + e^{(-(a-14.39)/2.62)})$; $r^2 = 0.93$, $p < 0.001$) indicates that 50% of shoots did not form latewood starting from the age of fourteen (vertical line). The photograph illustrates how overaging caused the formation of tree-rings without latewood

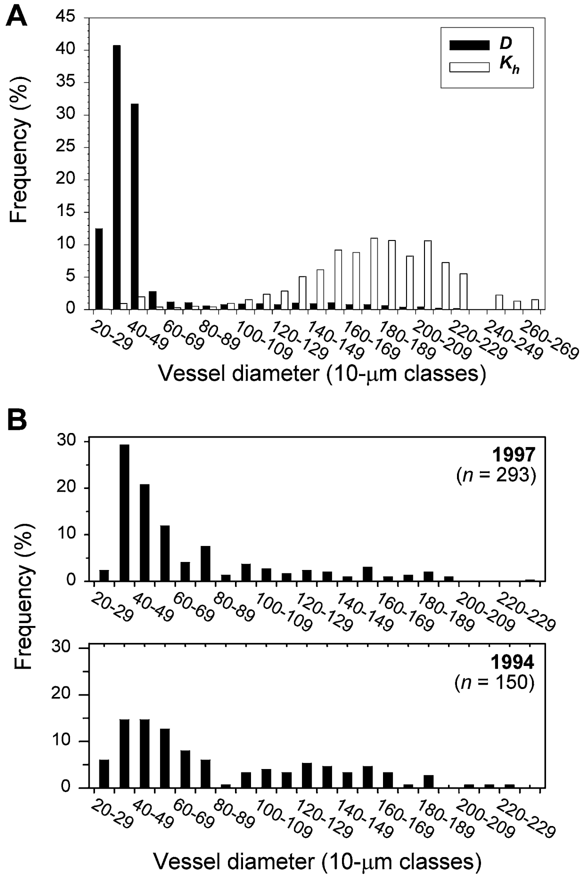

Fig. 2 **A** Relative frequency of *Q. pyrenaica* vessels (1976–97 period) according to their diameter (D, 10-µm classes), and their relative contribution to the total predicted hydraulic conductivity (K_h) at the xeric site. **B** Comparison of the relative distribution of vessels based on their diameter between 2 years contrasting in their summer precipitation: 1997-wet, 1994-dry

low levels of safranin in hardly-stained vessels, and the existence of functional vessels, which appear as bright areas, to be demonstrated. The images were analyzed using the public domain NIH Image program mentioned above (see *Preparation of wood-anatomical samples*). The loss in conductivity was estimated at each of the applied pressures as the percentage of unstained (cavitated) vessels to total vessels.

Results

In the xeric site, summer precipitation during 1993–1994 was very low and coincided with an almost complete absence of latewood (Fig. 1A). Most trees (90–100%) had not produced latewood from 1993 up to 1996. No latewood was observed in 1995, when most trees showed defoliation after the severe 1993–94 summer droughts. However, during previous periods, such as 1984–85, with intense summer drought in the study area, only 40–60% of trees did not form latewood. The dissimilarity in latewood production between these two summer droughts was due to the difference in cambial age. In specimens having a cambial age of approximately 14 years, i.e. those tree-rings formed after 1989, there was a steep decrease in latewood production (Fig. 1B). We noted a decrease in latewood width since 1982 but the width of earlywood remained nearly constant, reaching values close to 0.17 mm.

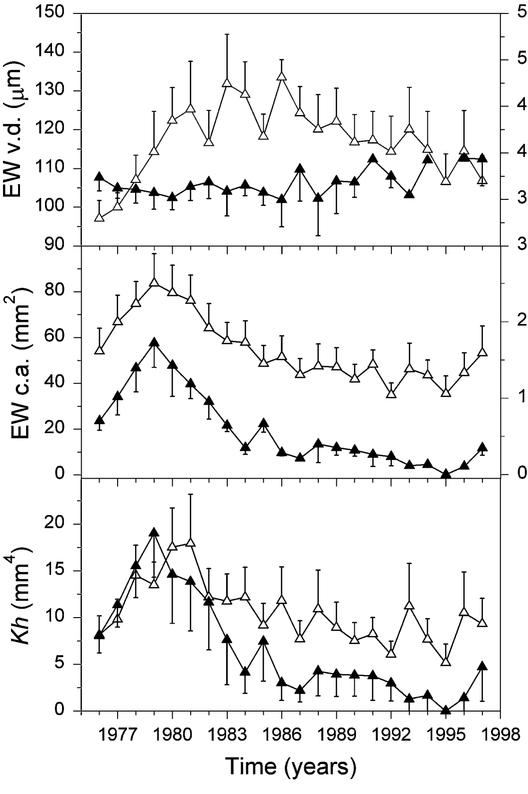

Fig. 3 Temporal variability of vessel diameter (v.d.), conductive area (c.a.) and predicted hydraulic conductivity (K_h) for earlywood (mm^4 10^{-2}) and latewood (mm^4 10^{-4}) in *Q. pyrenaica* at the xeric site. Symbols as in Fig. 1. No latewood was formed in 1995

The distribution of vessel diameters was bimodal, i.e. typical of a ring-porous wood (Fig. 2A). Most vessels (90%) showed diameters <80 μm and only accounted for 4% of the total predicted hydraulic conductivity. On the contrary, earlywood vessels were 10% of all conduits but accounted for 96% of the conductivity. This pattern changed slightly in years of contrasting climatic conditions, specifically summer precipitation. The proportion of narrow vessels increased in years with wet summers (e.g. 1997), whereas the proportion of wide vessels increased in years with summer drought (e.g. 1994) when latewood production was low.

The earlywood mean vessel diameter ranged from 106 to 130 μm during the period 1982–1995 with a mean (±SE) diameter of 111.60±1.25 μm (Fig. 3). Mean earlywood vessel diameters decreased in 1985 and 1995 after severe summer droughts during the previous years. During the same period, the mean latewood vessel diameter was 36.71±1.25 μm with a range of 35–39 μm. Conductive area and hydraulic conductivity followed similar trends, specially in the case of latewood. Earlywood conductivity also declined in 1985 and 1995. On average, hydraulic conductivity was 2–3 orders of magnitude higher in earlywood than in latewood.

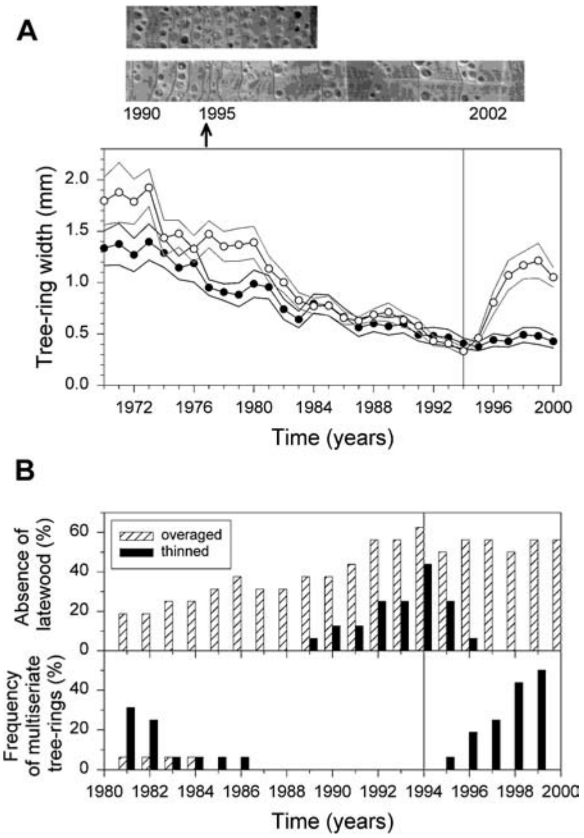

Fig. 4 Effects of thinning on radial growth **(A)** and wood anatomy **(B)** of *Q. pyrenaica* at the mesic site. **A** Temporal changes in tree-ring width for overaged (filled circles) and thinned (empty circles) after a thinning done at the end of 1994 (vertical line). Two illustrative cores sampled in late 2002 are displayed above (the arrow indicates the thinning year). The envelopes correspond to standard errors. **B** Temporal variability in the production of latewood and multiseriate tree-rings in overaged and thinned individuals

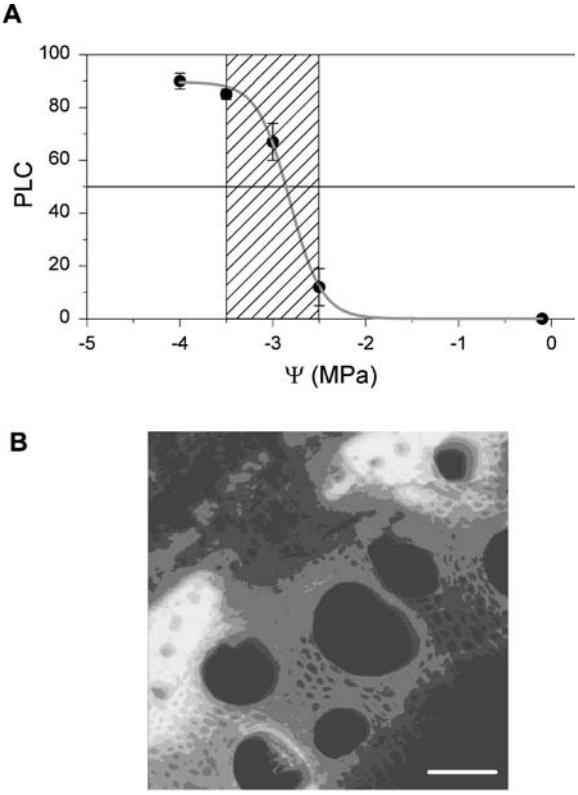

Fig. 5 Vulnerability to cavitation of earlywood vessels in *Q. pyrenaica* at the mesic site. **A** Vulnerability curve showing the percent lost in conductivity (PLC) for several negative pressures (Ψ). The fitted logistic function ($f = 89.59/(1 + e^{-(\psi+2.82)/-0.17})$); $r^2 = 0.99$, $p < 0.005$). The hatched area represents the sharp loss in conductivity (ca. 75%) between −2.5 and −3.5 MPa. **B** Photograph of the most recently formed tree-ring based on epifluorescence microscopy showing how at a pressure $\Psi = -3.5$ MPa, functional conduits are mostly latewood vessels (*white areas*), whereas earlywood vessels are cavitated (*dark areas*). Bar scale is 100 μm

At the mesic site, thinning enhanced radial growth and the production of latewood, which coincided with a greater frequency of multiseriate tree-rings (Fig. 4). The absence of latewood and the frequency of uniseriate tree rings was much greater among overaged trees than thinned trees even before the thinning, which suggests that the latter occupied better sites (e.g. higher soil–water availability) than the former. The increase in radial growth remained 8 years after thinning. Earlywood vessels lost half of their hydraulic conductivity at a potential $\Psi = -2.9$ MPa (Fig. 5A.). At potentials lower than −3.5 MPa, most earlywood vessels (88%) had cavitated and the only functional conduits were latewood vessels. (Fig. 5B). During the summer water potentials of −3.0 MPa were recorded at the ME site.

Discussion

We have described how structural changes in radial growth and wood anatomy, i.e. overaging in Mediterranean coppice stands, have profound consequences on the hydraulic function of oaks with ring-porous wood such as *Q. pyrenaica*. In this species the presence of tree rings exclusively constituted by earlywood, increased exponentially with cambial age. Nonetheless, this absence of latewood started at a much earlier age than in high oak forests (Führer 1998), and this trend was not reversible in unmanaged stands. Moreover, overaged stems mainly produced uniseriate tree rings. These seem to be two intrinsic characteristics of overaged coppice stands dominated by oaks with ring-porous wood. Our results imply two functional consequences for these stands: (*i*) a stagnation of radial growth causing a slight increment of the stem perimeter, and (*ii*) a high vulnerability to cavitation and climatic stress due to the lack of latewood vessels, less vulnerable to embolism than earlywood vessels (Lo Gullo et al. 1991).

The earlywood width in overaged *Q. pyrenaica* individuals was slightly greater than the mean diameter of earlywood vessels, which indicated that these trees formed mostly uniseriate tree-rings. In oak species with ring-porous wood, most hydraulic conductivity relies on the wide earlywood vessels. Hence, conductivity will be directly related to the number and diameter of earlywood vessels. In the case of overaged trees, the hydraulic conductivity will be mainly influenced by the number of earlywood vessels whose mean diameter does not change greatly. In overaged *Q. pyrenaica*, earlywood vessels were closely arranged around the perimeter of the previous tree-ring. In this case, the number of earlywood vessels formed in overaged trees will be positively related to latewood width of the previous tree-ring, which determines tree-ring width and the perimeter increase (Woodcock 1989; Corcuera et al. 2004b). To summarise, the hydraulic conductivity of the growth year will be influenced by the latewood width of the previous year in the case of uniseriate tree-rings, which is the usual in overaged trees. Therefore, those overaged trees which did not produce latewood, will not greatly increase their tree-ring width and stem perimeter, and will not augment the number of earlywood vessels the next spring.

Overaged trees might be more susceptible to stress factors such as summer drought than non-overaged trees. The reduction in the number of earlywood vessels involves a decrease in theoretical hydraulic conductivity, and a lower ability to conduct water, to assimilate carbon, and to grow. The reduction in growth of *Q. pyrenaica* due to overaging was previously described by Allué and San Miguel (1991). This drop in biomass production might explain the decline episodes observed at the xeric study site after the severe summer droughts in 1993–1994. At this site, radial growth was at a minimum between 1993 and 1995, and no latewood was formed in 1995. Similar responses were observed in other oak species with ring-porous wood (Woodcock 1989; Corcuera et al. 2004b). In 1994, most trees showed defoliation in the upper crown and some shoots died, a possible reaction to reduce photosynthetic area and decrease transpiration (Mencuccini and Grace 1995). The sharp reduction in leaf area was only observed in the xeric site, which suggests the interaction between overaging and water stress in this decline episode (Führer 1998). Other factors such as shallow or rocky soils with low water retention might also act as additional predisposing factors (Thomas and Hartmann 1996).

The development of wide earlywood vessels allows ring-porous species to transport water during the early growing season, but at the expense of an increased risk of embolism (Sperry et al. 1994; Tyree et al. 1994). Contrastingly, narrow latewood vessels remain functional for a few years and may act as safe conductive elements if earlywood vessels are cavitated. However, as in other species with ring-porous wood (Ellmore and Ewers 1986), latewood of *Q. pyrenaica* accounted for only 4% of the total hydraulic conductivity in the most recently formed tree-ring. Earlywood made up the remaining 96%. Those tree-rings formed only by earlywood will show a much lower hydraulic conductivity than tree-rings formed by both earlywood and latewood if there is a reduction in the number and diameter of earlywood vessels as occurred during 1995 in the xeric site. We found that, at potentials lower than −3.5 MPa, most earlywood vessels had cavitated and the only functional conduits were latewood vessels. This potential is easily achieved by transitional oak species in Mediterranean sites such as the studied stands (results not presented), which underlines the high vulnerability to cavitation of *Q. pyrenaica* earlywood. Moreover, the narrow threshold of cavitation of earlywood vessels (75% of them cavitated between −2.5 and −3.5 MPa) does not allow a progressive adjustment between conductive area and transpiration leaf area. This might lead to a rapid crown defoliation such as that observed at the xeric site after severe summer droughts. The sharp threshold of earlywood cavitation might be caused by a narrow distribution of pit sizes in earlywood vessels (Jarbeau et al. 1995).

Thinning at the mesic *Q. pyrenaica* site caused a double increase in radial growth, especially in latewood width, which coincided with a slight enhancement of longitudinal growth (personal observation). Thinning in *Quercus petraea* (Matt.) Liebl. stands also promoted radial growth through an increase in the availability of soil water due to a decrease in both interception and transpiration (Bréda et al. 1995). The positive effects of thinning on radial growth usually last until 10–12 years after thinning, with growth rates falling afterwards as the canopy closes (Cañellas et al. 2004). Our data show that the radial-growth enhancement in the mesic site was at a maximum 5 years after thinning. We also noted that thinned trees formed more latewood and multiseriate tree-rings than overaged trees. These changes imply a much higher hydraulic conductivity in thinned than in overaged trees, which might explain the enhancement of radial growth.

Overaging acted as a predisposing factor in the decline episode observed at the xeric site. There, previous summer-drought episodes did not always cause defoliation because the production of latewood also depended on cambial age. The frequency of shoots without latewood steeply increased for cambial ages >14 years, which was within the range (10–15 years) of the traditional cutting cycle of *Q. pyrenaica* coppices. The traditional management of these stands promoted latewood formation thus avoiding the negative consequences of overaging. Management procedures in Mediterranean coppice stands dominated by ring-porous oak species should apply specific cutting cycles similar to those formerly used at least in xeric sites developed on poor soils. These practices would improve radial growth, and enhance latewood formation, at least temporarily. The thinning and the subsequent vigour improvement might enhance the resistance of overaged coppice stands against the expected increase of severe summer droughts in S Europe (IPCC 2001).

Current silvicultural practices consider conversion from coppice to high forest as the best alternative to recover abandoned *Q. pyrenaica* coppice stands. However, Cañellas et al. (2004) advised against this practice in xeric sites or in stands located on very poor soils (e.g. the studied xeric site), which should be kept as coppice stands because of their low productivity as compared with other mesic stands. The positive radial-growth response to thinning in the studied mesic site supports the development of suitable silvicultural treatments on similar sites without climatic and edaphic constrains to promote their conversion to high forests.

Nowadays, formerly coppiced oak stands constitute a new landscape dominated by overaged multistemmed individuals growing on centennial stumps. The observed age-dependent growth stagnation might be caused by a negative net balance between photosynthesis and respiration in overaged individuals. The traditional cutting of all stems enhanced the translocation of underground reserves to the aboveground fraction. Currently, overaged individuals might show a great biomass decompensation between the subterranean and aerial parts. The growth stagnation and the absence of dense latewood should be taken into account in estimating the carbon sink strength of overaged coppice stands. A greater vulnerability to climatic stress might enhance the mortality rate of the stems and reduce the ability of these coppice stands to retain large carbon stocks as subterranean biomass.

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