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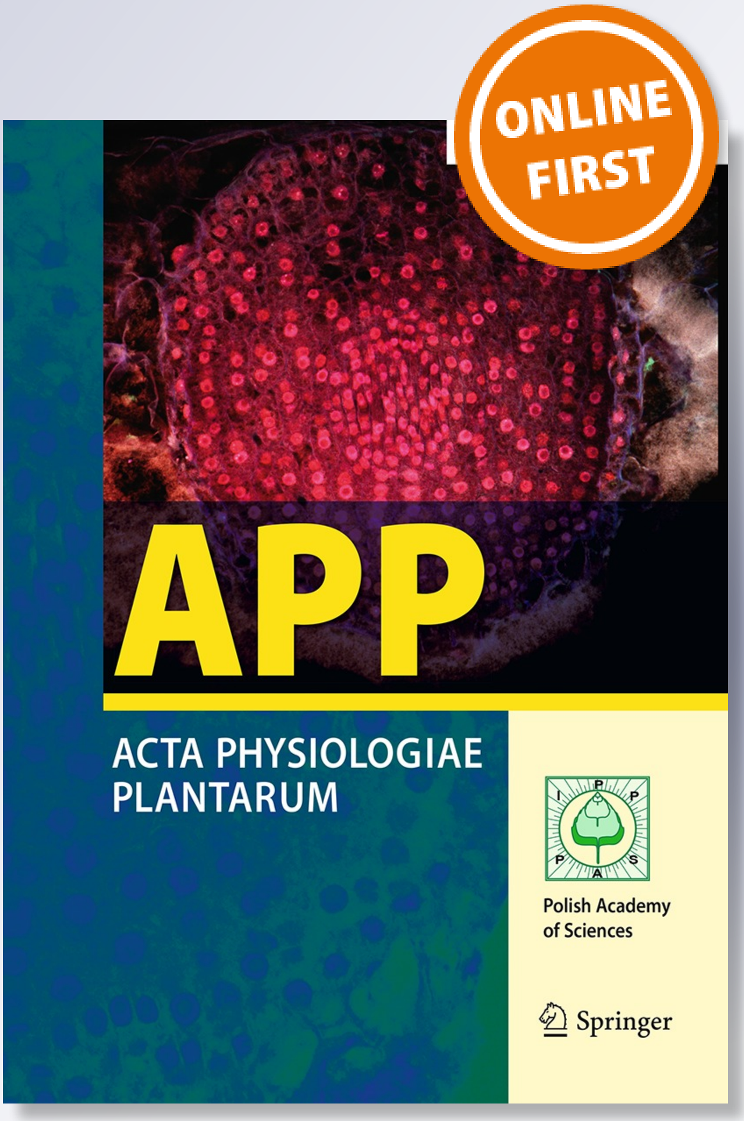

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ORIGINAL PAPER

Xylem cavitation affects the recovery of plant water status and consequently acorn production in a holm oak open woodland

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Abstract The hydraulic conductivity and gas exchange parameters of holm oak trees (*Quercus ilex* ssp. *ballota* (Desf.) Samp.) from an open woodland ecosystem in southwestern Spain were determined in young shoots ($\leq$1 year old) over the course of 3 years, at 6–7 week intervals. Acorn production (AP) was also determined. Specific hydraulic conductivity (K_s), leaf specific hydraulic conductivity (K_l), loss of hydraulic conductivity (PLC), and xylem water potential (Ψ) were assessed. In addition, histological cuttings of stem cross sections were examined to determine the density and diameter of xylem vessels. Acorn production was related to mid-summer K_s and PLC values, but not for other dates or to parameters associated with instantaneous gas exchange. Although AP may depend on several physiological and climatic variables, these results indicated a close non-linear relation between hydraulic conductivity during periods of summer water stress and AP. It was difficult to recover xylem conductivity after a rain event when the PLC of twigs exceeded a threshold of approximately 68 %, which therefore had a negative effect on the AP. However, if the PLC $\leq$ 55 %, then the hydraulic conductivity and Ψ could be quickly recovered after a rain event and the effect of water stress would have less importance. Because holm oak usually operates at the limits of safety for hydraulic conductivity, which are surpassed under severe water stress ($\Psi_{\text{predawn}} \leq -3.0$ MPa), a global change scenario leading to drier conditions in the Mediterranean basin will increase the negative effects of summer drought on AP, leading to negative consequences for the ecosystem dynamics. The right choice of drought-adapted ecotypes and silvicultural practices that increase soil water retention and reduce plant competition should be taken into account for forest management.

Keywords Plant hydraulic conductivity · Xylem conduits · Gas exchange · Water stress · Acorn production

Introduction

The holm oak (*Quercus ilex* ssp. *ballota*) is widely distributed across the Mediterranean basin, and together with the cork oak (*Quercus suber* L.), it is the most common species in agroforestry systems known as “dehesas” which are considered to be “wooded pasturelands”. Dehesa ecosystems have a high ecological value (Plieninger and Wilbrand 2001), and the study and analysis of these systems often involve the quantification of acorn production (AP). Acorns play a fundamental role in the regeneration of oaks and the diet of local wildlife (Perry and Thill 2003). In addition, AP in dehesas is economically important because it is the primary source of food for Iberian pigs (Junta de Andalucía 2008). Previous research on holm oaks supports the idea that not only carbon assimilation, but also ecophysiological factors such as water relations and silvicultural practices, can play an important role in AP at the whole-plant level (Alejano et al. 2008; Carevic et al. 2010; Pérez-Ramos et al. 2010).

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Drought is common in the Mediterranean climate during the summer, and its influence on water relations (water potential, osmotic adjustment, hydraulic conductivity, etc.), stomatal conductance, and gas exchange was previously evaluated in oak species (Tognetti et al. 1998; Savé et al. 1999; Hoff and Rambal 2003; Ogaya and Peñuelas 2003, 2007). However, the effects of these physiological variables on ecological traits, such as seed production, have scarcely been studied in *Quercus* species. Thus, this subject requires deeper understanding, especially during periods of water stress (Carevic et al. 2010).

The xylem is the primary pathway for water and mineral movement from the roots to the leaves of vascular plants. Gas exchange variables, such as leaf transpiration and stomatal conductance, have traditionally been considered the most important factors for xylem hydraulic flow (Sperry et al. 1988; McElrone et al. 2004). Plants can transport water under negative pressure according to the cohesion-tension theory, although this process may lead to a cavitation that disrupts water transportation, primarily during droughts or frosts (Tyree and Ewers 1991; Sparks et al. 2001), but to a lesser extent during the growing season, when there is no accompanying environmental stress (Magnani and Borghetti 1995). The relation between xylem status and climatic factors in the holm oak has been previously examined (Villar-Salvador et al. 1997; Tognetti et al. 1998), but there have been no studies of how seasonal changes influence the xylem status of this species and the threshold of xylem disruption that would cause an irreversible effect on the plant water status. Theoretically, long and wide xylem vessels would provide more efficient water flow, but they would also be more vulnerable to cavitation than short and narrow vessels (Zimmermann 1983; Lucas et al. 2013). Vulnerability to the water stress-induced cavitation of xylem conduits has been shown to result from many different factors, including the conduit diameter, the pore size of the pit membrane, the pit membrane flexibility and ion-mediated changes in the sap solute concentration (Tyree and Cochard 1996; Tognetti et al. 1998; Martínez-Vilalta et al. 2002; Jansen et al. 2011). Because the onset of vessel cavitation usually correlates with the point of stomatal closure, these parameters (i.e., xylem conductivity and stomatal conductance) can be used to evaluate species performance under drought conditions (Tognetti et al. 1998; Cruiziat et al. 2002). A diversity of responses among different plant species can be found under water stress (Oliveira et al. 1992; Lo Gullo et al. 2003a; Leal et al. 2007), and thus the association between the hydraulic system with stomatal control, carbon gain and water use warrants further study (Landsberg and Gower 1997; Lo Gullo et al. 2003b).

A better understanding of the strategies employed by different plants for drought tolerance would help in the development of comprehensive models for plant water requirements in the Mediterranean basin and other drought-prone regions, and it would be even more helpful during the climate change scenario that predicts drier conditions in the Mediterranean basin (IPCC 2013). Future scenarios for climate change in the study area predict an increase in the mean annual temperature of 2–3 °C for the 2011–2070 period (3–6 °C for 2071–2010) and a reduction in the annual precipitation of 5–15 % for the 2011–2070 period (20–40 % for 2071–2100), but with greater intensity during the summer months than in the fall or winter (AEMET 2009). Therefore, an additional increase in the drought intensity could influence several ecological and reproductive parameters in holm oak.

We hypothesized that the non-linear relations between some water relation parameters (such as the water potential or relative water content) and AP (Alejano et al. 2008; Carevic et al. 2010) might be primarily caused by the effect of overrunning a non-reversible limit such as xylem conductivity. Thus, the general aims of this study about a holm oak dehesa in southwestern Spain during three seasons of acorn production were as follows: (1) to evaluate seasonal variations in the hydraulic conductivity of twigs, the anatomical features of twig xylem vessels and gas exchange and (2) to analyze the influence of these variables on AP to establish criteria for improving forest management in a climate change scenario.

Materials and methods

Experimental plots

This study was performed from June 2006 to January 2009 in a 2.9 ha plot located at Villanueva de los Castillejos (province of Huelva; UTM, zone 29: X, 645,220: Y, 4,154,000; 178 m.a.s.l.), in southwestern Spain. The primary activity of this farm is the breeding of Iberian pigs and sheep. The site has a Mediterranean climate, with dry, hot summers and wet winters. The average annual rainfall is 634 mm, the mean annual temperature is 18.6 °C, and the vegetation of the plot is dominated by holm oaks and *Cistus ladanifer* as the primary species at the understory. The average density of the trees was 69 trees ha^{-1} and their average size characteristics (mean ± SD) were 6.15 ± 1.68 m (height); they averaged 32.56 ± 10.79 cm (diameter) and 3.86 ± 1.36 m (crown radius). The plot was laid out and fenced during the autumn of 2005. The plot was split into three subplots, and each subplot was subjected to one soil treatment (plowing, plowing and sowing with *Lupinus luteus*, or untreated). Additional details about the study plot and soil treatments are presented in Carevic et al. (2010). Climatic data (Fig. 1) were

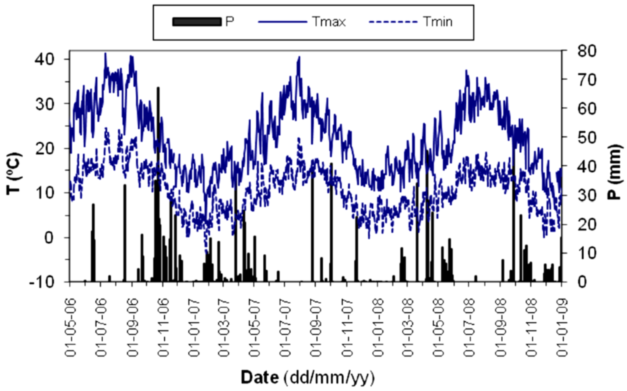

Fig. 1 Daily rainfall (mm) and daily minimum (T_{min}) and maximum (T_{max}) temperatures (°C) at the study site from May 2006 to January 2009. Absolute minimum temperature was −3.6 °C (January 2007) and absolute maximum temperature was 41.4 °C (July 2006)

obtained from a meteorological station near the study site (UTM, X: 654,836; Y: 4,157,771; 288 m.a.s.l.). Because of the small difference in altitude between the site and the climatic station, the temperature was corrected (0.65 °C/100 m), but not the precipitation. The AP was estimated by using a method described by Greenberg (2000) as shown in Carevic et al. (2010). Briefly, 18 trees were chosen at random, 9 of which were used to measure hydraulic and gas exchange parameters. Acorns were collected during three dissemination periods (2006–2007, 2007–2008, and 2008–2009) from October to January. The AP was expressed as the grams of acorns in dry weight (g_{dw}) per m^2 of the orthogonal projection of the crown on the ground.

Measuring water potential and hydraulic conductivity in the xylem

The water parameters for nine trees were chosen at random among the 18 trees selected for AP, and they were measured every 6–7 weeks over 3 years from June 2006 to December 2008. At each sampling date, the twigs were taken immediately after sunrise (two per tree, each of which was 15–20 cm in length) to measure the xylem hydraulic variables and xylem water potential (Ψ). The xylem water potential (Ψ) was measured by standard methodo logy in a pressure chamber (Model 1000, PMS Instruments, Corvallis, OR, USA). Hydraulic conductivity (K, kg_{H2O} m s^{-1} MPa^{-1}) and the percent loss of hydraulic conductivity (PLC, %) were determined as described by Sperry et al. (1988). Developed twigs with at least 4–5 full expanded leaves were used, and the stem segments were 4–12 months old, 3 cm long, and 2.1–2.8 mm in diameter. The specific hydraulic conductivity (K_s, kg_{H2O} m^{-1} MPa^{-1} s^{-1}) was expressed as the ratio of K to the cross section of the debarked stem segment, and the leaf specific hydraulic conductivity (K_l, kg m^{-1} MPa^{-1} s^{-1}) was expressed in terms of the leaf area above the cut segment.

Xylem vessel measurements

All stem segments were preserved in FAA solution (formaldehyde 10 %, acetic acid 5 %, and ethanol 35 %). The segments were then washed with distilled water, dehydrated, and embedded in parafilm to facilitate cuts with a rotary microtome that was held in a cassette clamp (MicroTec, cut 4060, Germany). Cross sections (10 µm thick) were used to measure the density and diameter of xylem vessels. Thirty-one xylem vessels from each xylem cross section were randomly selected to measure the vessel diameter; the vessels included in eight randomly distributed squares of 0.25 mm^2 each were counted to determine the vessel density (7–16 vessels per square). For vessels with non-circular cross sections, the smallest and the largest diameters were measured and the average value was recorded. Measurements of the tested vessels were obtained throughout the whole xylem cross section (after excluding the pith and the cambium-phloem areas). Because the stem segments were very young (<1 year old) and thin (<3 mm diameter), and because they were collected over the entire year, early and late wood could have been present depending on the measurement date. Analysis Five software (Soft Imaging System, Japan) was used for making the measurements. The magnification was ×40 for vessel density and ×200 for vessel diameters.

Gas exchange

Leaf gas exchange was also measured with a portable analysis system (LCi, ADC, UK) in the same trees that were used to measure the stem hydraulics and AP. All measurements were taken mid-morning, at 2–3 h after sunrise, and healthy green fully expanded leaves were selected. The following variables were estimated: stomatal conductance (gs; mol_{H2O} m^{-2} s^{-1}), transpiration rate (E; $mmol_{H2O}$ m^{-2} s^{-1}), and net photosynthetic rate (A; μmol_{CO2} m^{-2} s^{-1}), all of which were expressed in terms of leaf area. The water use efficiency (WUE) and intrinsic water use efficiency (WUE_i) were estimated as A/E and A/gs, respectively.

Data analysis

Differences in the physiological and anatomical parameters (hydraulic conductivity, gas exchange, and vessel characteristics) were analyzed separately by repeated analyses of variance, with soil treatment as the between-subject primary effect and the date as the within-subject factor. Two comparisons were made of the normality of the data and

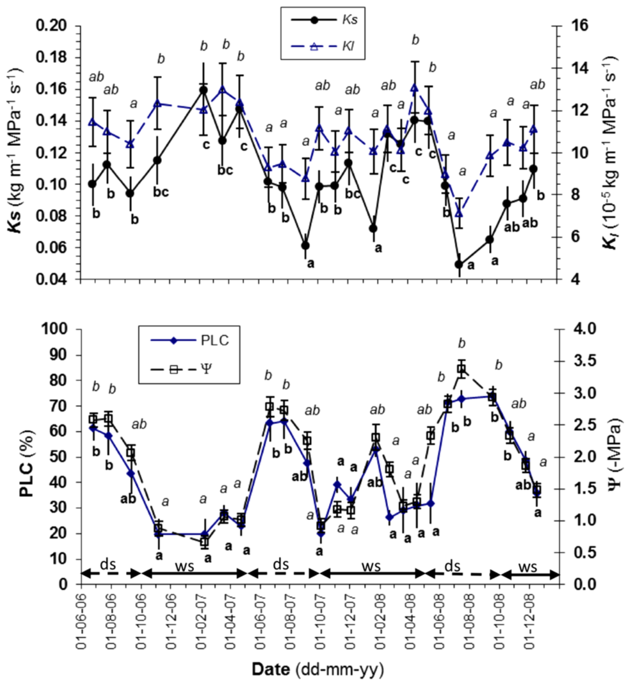

Fig. 2 Seasonal patterns of: (*above*) specific hydraulic conductivity (K_s) and leaf specific hydraulic conductivity (K_l). (*below*) xylem embolisms expressed in percentage of loss of hydraulic conductivity (PLC, %) and xylem water potential measured just after daybreak (Ψ, MPa) ($\mathrm{PLC} = 21.284\ \Psi + 3.406$, $r^2 = 0.85$, $p < 0.001$). Values with different letters denote significant differences ($p < 0.05$) between dates (in *italics* for K_l and Ψ, in **bold** type for K_s and PLC). *ds* and *ws* indicate dry season and wet season, respectively

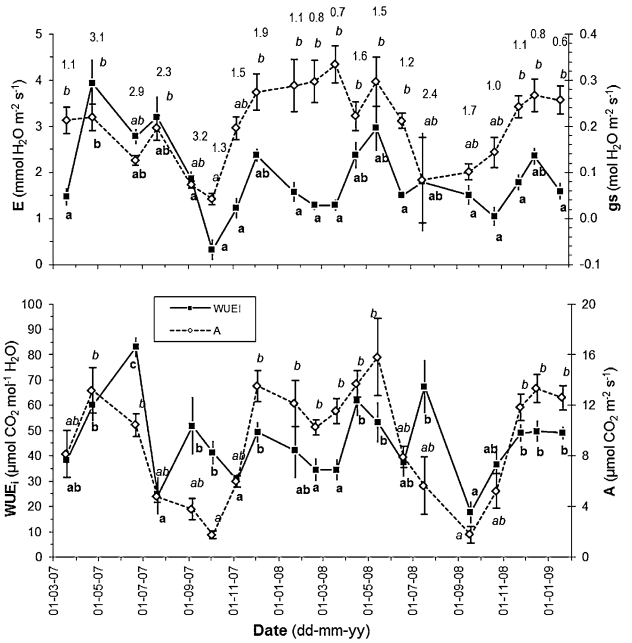

Fig. 3 Seasonal patterns (mean ± standard error) of: (*above*) transpiration rate (E, *black squares*) and stomatal conductance (gs, *open rhombus*). Numbers at the top indicate the vapor pressure deficit (VPD, kPa) just at the moment when the gas exchange measurements were taken.(*below*) net photosynthetic rate (*A*) and intrinsic water use efficiency ($\mathrm{WUE_i}$). Values with different letters indicate significant differences ($p < 0.05$) between dates (in italics for gs and A, in bold type for E and $\mathrm{WUE_i}$)

the equality of variances, indicating that data transformation was not necessary. The Bonferroni test was used to assess differences at different dates. The stem segment diameter was included as a covariate in the statistical analysis. Relations between the physiological and anatomical parameters and the AP were assessed by regression analysis and Pearson correlation procedures. All statistical analyses were performed with SPSS (Version 17.0, SPSS, Chicago, USA).

Results

Climate variables

The climatic data showed that the summers of 2006 and 2007 had rainfall of more than 50 mm, but the summer of 2008 (which was characterized as a drought) had less than 5 mm of rain (12 % of the average summer precipitation). Additionally, there was a rainfall shortage in December 07 and January-08 (<4 mm of rain, 5 % of average precipitation during this period). The annual AP average (±SE) was $194.5 \pm 47.7\ \mathrm{g_{dw}\ m^{-2}}$ (2006), $176.6 \pm 34.3\ \mathrm{g_{dw}\ m^{-2}}$ (2007), and $98.3 \pm 15.0\ \mathrm{g_{dw}\ m^{-2}}$ (2008). There were no significant differences among soil treatments ($p > 0.05$) in the AP and whole-plant physiological parameters. However, there were significant differences at different dates for the latter (Figs. 2 and 3).

Hydraulic conductivity

In analyzing the hydraulic conductivity, seasonal changes in the K_s and K_l exhibited similar trends over the three-year study period (Fig. 2). The maximum actual values of K_s and K_l occurred at the end of winter and spring. As the seasonal water stress increased, both K_s and K_l parameters decreased, and they reached their minimum values in mid-summer. There were significant changes in K_s and K_l over time ($p < 0.001$, $F = 6.56$; and $p < 0.001$, $F = 4.25$, respectively), and there was a significant positive correlation between K_s and K_l ($K_s = 0.016\ K_l = -0.061$; and $r = 0.799$; $p < 0.001$). The PLC also exhibited a significant change over time ($p < 0.001$, $F = 4.72$), from 20–30 % in the autumn–winter to 60–80 % in the summer, except for autumn of 2008, when the PLC evolved from 60 to 35 % after a summer with Ψ values below −3.0 MPa (Fig. 2). Tyloses were not observed during the analysis. The seasonal pattern of PLC values correlated with the tree

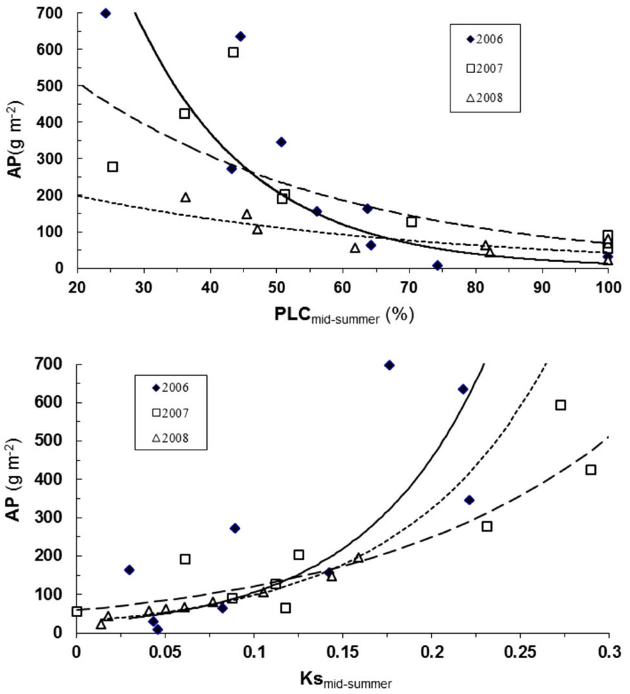

Fig. 4 Relationships between: (*above*) percent of loss of hydraulic conductivity (PLC, %) measured in mid-summer (July) and acorn production (AP). Each year is shown by the average value per tree ($n = 9$); 2006 ($AP = 3523.1\ e^{-0.056PLC}$, $r^2 = 0.66$, $p < 0.001$, *continuous line*), 2007 ($AP = 840.9\ e^{-0.025PLC}$, $r^2 = 0.81$, $p < 0.0001$, *dashed line*), 2008 ($AP = 290.8\ e^{-0.019PLC}$, $r^2 = 0.56$, $p < 0.001$, *dotted line*). (*below*) Specific hydraulic conductivity measured on July (K_s, kg m^{-1} MPa^{-1} s^{-1}) and acorn production (AP). Each year is shown by the average value per tree ($n = 9$); 2006 ($AP = 24.523\ e^{14.615K_s}$, $r^2 = 0.55$, $p < 0.010$, *continuous line*), 2007 ($AP = 59.395\ e^{7.177K_s}$, $r^2 = 0.74$, $p < 0.001$, *dashed line*), 2008 ($AP = 26.673\ e^{11.958K_s}$, $r^2 = 0.91$, $p < 0.0001$, *dotted line*)

water potential ($PLC = -21.284\ \Psi + 3.406$, $r = -0.924$, $p < 0.001$). The drought period during the winter of 2007–2008 also increased the PLC and decreased the Ψ and K_s (Fig. 2). For all the measurements as a whole, there were also significant positive relations between Ψ and K_s ($r = 0.656$, $p < 0.05$) and Ψ and K_l ($r = 0.724$, $p < 0.001$), and they were negative between PLC and K_s ($r = -0.722$, $p < 0.05$) and PLC and K_l ($r = -0.727$, $p < 0.05$). Additionally, the maximum values of K, K_s and K_l exhibited no significant changes over time or among soil treatments ($p > 0.05$).

There was a significant and negative relation between AP and the PLC [2006 ($AP = 3523.1\ e^{-0.056PLC}$, $r^2 = 0.66$, and $p < 0.001$), 2007 ($AP = 840.9\ e^{-0.025PLC}$, $r^2 = 0.80$, and $p < 0.0001$), and 2008 ($AP = 290.8\ e^{-0.019PLC}$, $r^2 = 0.56$, and $p < 0.001$)], and a significant positive relation between AP and the actual K_s [2006 ($AP = 24.523\ e^{14.615K_s}$, $r^2 = 0.55$, and $p < 0.010$), 2007 ($AP = 59.395\ e^{7.177K_s}$, $r^2 = 0.74$, and $p < 0.001$), and 2008 ($AP = 26.673\ e^{11.958x}$, $r^2 = 0.91$, and $p < 0.0001$)] (Fig. 4) based on the measurements from mid-summer during the 3 years of the study, but not for other measurement dates.

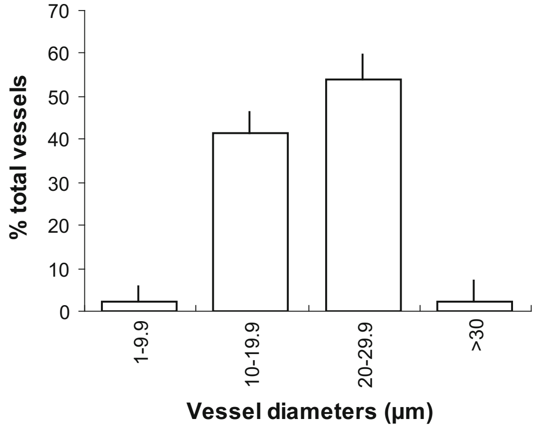

Fig. 5 Distribution of the frequencies of the vessels diameters of the 4–12 months old twigs of holm Oak

Gas exchange parameters

With respect to the gas exchange variables, all studied parameters exhibited significant changes over time (gs: $p < 0.010$, $F = 5.72$; A: $p < 0.001$, $F = 14.77$; E: $p < 0.001$, $F = 22.68$; WUE: $p < 0.010$, $F = 7.71$; WUE_i: and $p < 0.050$, $F = 3.419$) (Fig. 3). In addition, gs was significantly related to Ψ ($gs = 0.059\ \Psi + 0.327$; $n = 18$, $r = 0.564$, and $p = 0.015$) and PLC ($gs = -0.0029\ PLC + 0.3451$; $n = 18$, $r = 0.658$, and $p = 0.005$); and A was significantly associated with gs ($A = 38.83\ gs + 1.378$; $n = 20$, $r^2 = 0.619$, and $p < 0.001$) and the actual K_s ($A = 83.21\ K_s + 0.64$; $n = 18$, $r^2 = 0.21$, and $p = 0.043$). In addition, seasonal measurements of E were significantly associated with the vapor pressure deficit ($E = 0.6282\ VPD + 0.9085$; $n = 20$, $r^2 = 0.37$, and $p = 0.005$), and with VPD and gs ($E = 0.987\ VPD + 6.952\ gs - 1.073$; $n = 20$; and $r^2 = 0.75$; $p < 0.001$). AP was not related to any instantaneous gas exchange parameter.

Xylem features

The distribution of vessel diameters is shown in Fig. 5. More than 90 % of twig vessels had diameters of 10–30 µm. There were no significant differences over time ($p = 0.887$ and $F = 0.79$; $p = 0.670$ and $F = 0.69$, respectively). Vessels had the smallest diameters in July 2006 (15.24 ± 1.79 µm) and the largest diameters in July 2008 (26.48 ± 0.58 µm), but they were not significantly different. Only the vessel density, which increased in early autumn of 2006, was significantly different over time

($p < 0.001$; $F = 8.36$). The lowest vessel density occurred in June and July 2006 (35.00 ± 1.83 and 37.67 ± 1.45 vessels/mm^2, respectively). Thereafter, the vessel density increased significantly during September 2006 and remained at approximately 55 vessels/mm^2 until the autumn of 2008. The greatest vessel density occurred in September 2008 (55.83 ± 1.64 vessels/mm^2).

Discussion

The well-known increase in xylem cavitation during the summer in *Quercus* species (Martínez-Vilalta et al. 2002; Lo Gullo et al. 2003b; Aranda et al. 2005) is reinforced in this study by the influence of this physiological parameter (e.g., PLC) during water stress periods, especially summer periods, on acorn production. We evaluated the effect of hydraulic variables during the three years on AP, and we found that when the PLC at mid-summer was less than 55 %, the AP did not depend on xylem conductivity and could depend on other physiological and climatic variables. However, when the PLC was more than 55 %, there was a significant limitation in AP. This finding indicates that there must be a threshold of water stress at which the recovery of sap flow is seriously impeded, affecting AP. Our results indicated that AP depended on K_s during periods of summer drought. These physiological characteristics (PLC, K_s), together with other water relation parameters and the amount of leaves in the canopy, are strongly related to the ability of plants to supply water to foliage and fruits and achieve optimal productivity (Siscart et al. 1999; Camarero et al. 2010). Thus, under moderate water stress ($\Psi_{\text{at dawn}} > -2.5$ MPa; PLC < 55 %), the Ψ and PLC recovery in this study was satisfactory after a rain event, and PLC was not a limitation for Ψ and AP, but the loss of hydraulic conductivity under more severe water stress during the summer ($\Psi_{\text{at dawn}} < -3.0$ MPa; PLC > 68 %) together with stomatal closure and the probable loss of cell turgor (Tognetti et al. 1996, 1998; Villar-Salvador et al. 2004; Carevic et al. 2010) seriously limited AP in this study. Under these circumstances, the immature seeds will abort during the summer (Pérez-Ramos et al. 2010) before the new growth in the autumn begins to return to xylem normality.

Our study also detected low K_s values in January 2008 that were similar to the values recorded during the summer; this trend may be explained by the lack of rainfall during the winter of 2008, which led to an increase in the PLC to 50 % or more (Lo Gullo and Salleo 1993; Tognetti et al. 1998). Our data also indicate an association between PLC and Ψ, with a PLC of 50 % at approximately −2.2 MPa, and hydraulic conductivity was adversely affected during periods of low Ψ. The recovery of xylem conductivity after a summer drought is usually far from being complete in response to autumn rainfall, so the embolized xylem that is not completely refilled will remain as residual damage after the stress was relieved, and the recovery of xylem function after early autumn rainfall could occur through the construction of new xylem tissue (Tyree and Cochard 1996; Tognetti et al. 1998). In fact, the recovery rate of xylem conductivity during the autumn of 2008 was lower and slower than it was during the two previous years. Lo Gullo and Salleo (1993) established that the larger PLC in *Q. ilex* ssp. *ilex* was caused by xylem water potentials below −3.1 MPa that were much less reversible than those caused by more moderate water stress ($\Psi \geq -2.7$ MPa), which was very close to our results.

When measuring xylem cavitation by generating vulnerability curves in holm oak, Martínez-Vilalta et al. (2002) showed a PLC of approximately 50 % at −2.0 MPa and a PLC of 75 % at −4.0 MPa; Lo Gullo and Salleo (1993) and Tognetti et al. (1996, 1998) recorded PLC values in a range from 50 to 70 % with a predawn water potential of approximately −3.0 to −4.3 MPa. Nevertheless, other authors (Tyree and Cochard 1996; Corcuera et al. 2004; Cochard et al. 2005) found PLC values of approximately 50 % at lower Ψ values (−4.1 to −5.5 MPa). Therefore, it is difficult to contrast the results of different studies with each other because we should account for the measurement technique used, the age and size of the stem segment and the subspecies (*Q. ilex* ssp. *ilex* or *Q. ilex* ssp. *ballota*). Moreover, we did not generate vulnerability curves, but we measured the Ψ and the PLC on several dates during the study period.

Oaks appear to be able to vary their hydraulic structure depending on annual and seasonal variations in climatic conditions (Tognetti et al. 1999; Limousin et al. 2010; Andivia et al. 2012; Abrantes et al. 2013). Previous research has demonstrated a close relation between the hydraulic efficiency of the xylem (K_s), the amount and size of xylem conduits and the pit pore size (Tyree and Ewers 1991; Martínez-Vilalta et al. 2002). The increased number of vessels from the summer to the autumn of 2006 could be associated with the construction of new xylem tissue through a stem diameter increase in these trees (Corcuera et al. 2004; Martín et al. 2009), and the foliage increase in response to the severe drought the previous year (2005), when annual rainfall was only 340 mm, i.e., 52 % of the average annual precipitation (Alejano et al. 2008), plus the dry May 2006. In fact, the lowest values of K_l occurred during September 2006, and this finding was most likely associated with leaf expansion.

There are typically significant annual variations in the AP of many *Quercus* species (Cañellas et al. 2007; Pérez-Ramos et al. 2010). These variations may be caused by changes in the availability of environmental resources (Siscart et al. 1999; Rodríguez-Estévez et al. 2007), primarily water availability (Pérez-Ramos et al. 2010), the activity of predators (Koenig et al. 1994), or the development of the canopy cover (Camarero et al. 2010). Although our study only lasted 3 years, we noted that significant annual changes in AP coincided with differences in rainfall and, subsequently, plant water potential and xylem conductivity. Recent studies (Alejano et al. 2008, 2011; Carevic et al. 2010) have shown a positive non-linear relation between the water relations of *Q. ilex* ssp. *ballota* in mid- and late-summer and AP. Environmental conditions during January 2008, when rainfall was negligible, might also have caused low AP values during 2008. A previous study of *Q. ilex* (García-Mozo et al. 2007) found that these two factors were associated with low AP. Therefore, it will be interesting to make a future in-depth study of the relations between climate conditions, silvicultural practices and plant ecophysiological variables to establish criteria for forest management. These criteria should account for the current and future climate (Landsberg and Gower 1997; Pérez-Ramos et al. 2010; IPCC 2013), the choice of appropriate ecotype (Andivia et al. 2012) and the application of silvicultural practices such as mulching, tillage, etc. that favor infiltration and water retention in the soil (i.e., soil water availability for trees) and reduce competition for water resources among plants (Moreno et al. 2007; Alejano et al. 2008; Moreno and Cubera 2008). Similarly, the future climate scenarios in southwestern Spain will be characterized by decreased precipitation and increased mean temperatures, which could negatively influence acorn production in open woodlands because of drought-induced xylem cavitation. This result should be used now to take necessary measures to alleviate the reduced productivity of oak species.

In conclusion, our research demonstrated that *Q. ilex* ssp. *ballota* must maintain security thresholds of hydraulic conductivity during periods when there is a high risk of cavitation. The close relation between hydraulic parameters and AP indicates the significance of mid-summer hydraulic parameters on the recovery of the plant water potential and consequently on the acorn production of holm oak in dehesa ecosystems.

Author contribution In the present research Dr. Felipe Carevic conducted the physiological analysis and supervised the work, Dr. Manuel Fernández planned the stage of xylem features, Dr. Reyes Alejano performed the measures of acorn production while Dr Javier Vazquez-Pique provided overall guidance in statistical analysis. All authors discussed the results and implications on the manuscript at all stages.

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