

Leaf traits and tree rings suggest different water-use and carbon assimilation strategies by two co-occurring *Quercus* species in a Mediterranean mixed-forest stand in Tuscany, Italy

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Summary We compared the water-use characteristics of co-occurring mature *Quercus cerris* L. and *Quercus pubescens* Willd. trees growing in resource-limited (mainly water) hilly habitats in Tuscany, Italy. The species differed in their distribution along soil water gradients and in their access to, and use of, water, even though the study year was wetter than average, though with a summer drought. Compared with *Q. cerris*, *Q. pubescens* had greater access to soil water (less negative predawn water potentials) and a more conservative water-use strategy based on its relatively low stomatal conductance, high instantaneous water-use efficiency, less negative midday water potential and high soil-to-leaf hydraulic conductance. *Quercus cerris* had less conservative water-use characteristics than *Q. pubescens*, exhibiting relatively high stomatal conductance, low instantaneous water-use efficiency, more negative midday water potentials and low soil-to-leaf hydraulic conductance; however, *Q. cerris* had higher photosynthetic rates than *Q. pubescens*. Photosynthesis and stomatal conductance were positively correlated in both species. Although a strong correlation between ring widths and precipitation patterns was not found, some dry periods influenced ring-width growth. *Quercus pubescens* has always grown faster than *Q. cerris*, probably because of more efficient water use, although stand dynamics (driven by exogenous disturbance factors, including coppicing, browsing and competition) cannot be excluded. Ring-width variability, as well as tree-ring growth in dry years, which should be unaffected by stand dynamics, were higher in *Q. pubescens* than in *Q. cerris*. Moreover, *Q. pubescens* recovered completely after the drought in the seventies, even showing higher tree-ring growth than in the recent past, whereas *Q. cerris* showed a minor growth decline followed by a recovery to values comparable with those observed before the 1970s drought. Beginning in the early eighties, tree-ring growth decreased in both species, though *Q. pubescens* showed consis-

tently higher values than *Q. cerris*. These differences can be explained by differences in water-use efficiency. Despite differences between the species in water use and water status, the results are consistent with the interpretation that both are drought tolerant, but that *Q. pubescens* is at an advantage on xeric ridges because of its greater ability to access soil water and use it more conservatively compared with *Q. cerris*.

Keywords: Mediterranean forests, oak, photosynthesis, soil-to-leaf hydraulic conductance, water potential.

Introduction

Quercus species are adapted to a wide range of soil water conditions (Abrams 1990, Dickson and Tomlinson 1996). They usually avoid the development of severely negative tissue water potentials by deep rooting and stomatal control of gas exchange, and can tolerate more negative water potentials through osmotic adjustment and other morphological and physiological features (Rambal 1984, Stringer et al. 1989, Abrams 1990, Stone and Kalisz 1991, Bréda et al. 1993, Hamerlynck and Knapp 1996). Interspecific and ecotypic differences in water relations and gas exchange characteristics have been associated with occupation of sites differing in soil water availability (Wuenschel and Kozłowski 1971, Bahari et al. 1985, Abrams 1990, Kubiske and Abrams 1992, Hamerlynck and Knapp 1996). Variations among deciduous *Quercus* species in foliage characteristics, the result of differences among habitats and consequently in selection pressures, are important, particularly in Mediterranean-type ecosystems subjected to erratic environmental constraints (Damesin et al. 1997, Damesin et al. 1998). *Quercus cerris* L. is a northern Euro-Mediterranean and rather drought-tolerant species that co-dominates with *Q. pubescens* Willd. large areas of the Ital-

ian peninsula, from sea level to the mountain belt, being most frequent in inland hilly areas. Present rainfall barely meets potential evapotranspiration of Mediterranean forests, and expected climate change over the course of the 21st century is likely to increase the frequency of conditions causing plant water stress, thus creating uncertainty as to the future of Mediterranean oak forests (Houghton et al. 1990).

Deciduous *Quercus* species growing in the Mediterranean climate of Tuscany, central Italy, are model systems for studying how gas exchange and water-use respond to environmental change and perturbations. In Tuscany, deciduous oak stands, in most cases coppice stands, are dominated by *Q. cerris* and *Q. pubescens* (Bernetti 2006). *Quercus cerris* is fast-growing and widely distributed, whereas *Q. pubescens* is present only on calcareous and clayey soils. These stands exist in areas that experience prolonged summer drought (Niccolai and Marchi 2006), after the soil profile has been filled by winter and spring rainfall. As soils dry over the summer, trees experience a wide diurnal range of temperatures, including extremely high temperatures and high vapor pressure deficits.

The present spread of silvicultural types, which includes managed and abandoned coppices and coppices converted into high forest, is generating concern about the future development of these oak woodlands. *Quercus* species at these latitudes are highly sensitive to environmental stresses (Corona 1989), therefore, evaluation of relationships between growth trends, climate changes and disturbance regimes (Cherubini et al. 1996, Motta et al. 1999) could be useful in understanding stand functioning and planning the management of these forests. Tree-rings provide an exact record of factors that determine growth dynamics.

In companion experiments, Tognetti et al. (2003) observed that the pattern of vertical leaf distribution in individual *Q. cerris* and *Q. pubescens* trees reflected crown architectural differences between species (cf. Čermák 1998). Branches of *Q. pubescens*, growing in a relatively open stand, had a basipetal growth pattern compared with *Q. cerris*, which showed an acropetal growth direction because of the higher stand density. The pattern of radial leaf area distribution also differed between species, with wider crowns in *Q. pubescens* than in *Q. cerris*. Čermák et al. (2007) further extended the analysis to the level of entire stands and found that peak foliage area occurred at a height of about 5 m in *Q. pubescens* (LAI = 2.8) and at about 11 m in *Q. cerris* (LAI = 4.7). Chiesi et al. (2002), who worked at the same site, concluded that stand growth could be simulated by running a model of forest ecosystem processes, which integrates stand-level and remote sensing data and may be implemented operationally on a regional scale. Nevertheless, descriptions of individual developmental stages and estimates of long-term growth at the stand level according to variations in ecological, climatic and silvicultural factors are lacking for these forest stands.

Based on observed differences in species distribution and apparent differences in adaptation to soil water availability (e.g., Valentini et al. 1995, Tognetti et al. 1999), we predicted that these *Quercus* species differ in ecophysiological charac-

teristics related to water status. In this study, we compared co-occurring mature *Q. cerris* and *Q. pubescens* to determine differences in gas exchange, intercellular CO₂ concentration, leaf water potential and instantaneous water-use efficiency. We hypothesized that: (1) the species differ in these characteristics where they co-occur; and (2) *Q. pubescens*, which dominates the most xeric sites, has a more conservative water-use strategy than *Q. cerris*, even under conditions of ample water availability. Tree-ring growth of coppice stands where *Q. pubescens* and *Q. cerris* are the most abundant species was analyzed by a dendroecological approach to compare the growth performance of these oaks under similar conditions. Our specific objectives were to: (1) describe past tree-ring growth (65–85 years) of *Q. pubescens* and *Q. cerris* and compare the growth rhythm of these species at the same location; and (2) evaluate the effects of severe droughts and of possible disturbance factors on the tree population.

Materials and methods

Site description

Ecophysiological measurements were conducted during the 2000 growing season, while stem core samples for the dendrochronological study were collected in 2002, in two experimental oak forest stands near Radicondoli, Tuscany, Italy (43°15' N, 11°05' E). These sites are on a slope (15–25%) at 420–430 m a.s.l., with a south-west exposure, and the climate is moderately dry sub-Mediterranean. Summers are typically hot and dry, whereas winters are cool and rainy. Miocene and Pleistocene deposits with a mixture of calcareous marl, sandstone and serpentine characterize the bedrock at both sites (Magazzini 1990). The soil is an inceptisol of medium depth (25 to 70 cm) with about 150 mm of available soil water capacity (Soil Taxonomy, USDA).

The dominant species at the first stand was *Q. cerris* (84%), with an admixture of *Q. pubescens* (14%) and 1% of other deciduous woody species. There were also a few small (up to 0.5 m in height) shrubs, mainly *Juniperus communis* L. and *Erica arborea* L. At this site in the year 2002, dominant trees were about 46 years old. The stand had resprouted following cutting with the aim of conversion from coppice to high forest (1988). The second stand (3 km away) was composed mostly of *Q. pubescens* (60%) and *Q. cerris* (35%). Other deciduous tree species, which included *Prunus spinosa* L., *Sorbus aucuparia* L., *Pyrus pyraster* L., *Acer platanoides* L. and *Fraxinus ornus* L., were generally smaller (up to DBH of 12 cm). There were abundant understory species up to 4 m tall, including *Cornus sanguinea* L., *J. communis* L. and *Rubus caesius* L. At this site, mean age in the year 2002 was about 49 years with a wide range from about 20 years to over one hundred. The stand was coppiced in 1978 and artificially converted to high forest by releasing 500–700 saplings per hectare. More details about stand structure and location are provided by Chiesi et al. (2002) and Tognetti et al. (2003). *Quercus cerris* trees were substantially taller than *Q. pubescens* trees.

Environmental conditions

Meteorological data for the 2000 growing season were collected with a standard agrometeorological station placed near the experimental site and compared with 10-year mean data (1995–2005) measured at the meteorological station Pentolina, located at 450 m a.s.l. about 10 km from the study site (Figure 1). Daily reference evapotranspiration (ET_0) was calculated following the Hargreaves-Samani method (Allen et al. 1998). Soil water deficit (mm) was calculated as the difference between cumulative ET_0 and cumulative precipitation; we assumed that, by the beginning of January, soil water reserves had been replenished by autumn precipitation.

Within a plot of about 2000 m², soil samples were taken throughout summer 2000 at 10, 25 and 50 cm depths for determination of gravimetric soil water content. Soils were weighed wet, dried at 60 °C, and reweighed, with five replicates per depth. Volumetric soil water content was determined, taking into account apparent bulk density.

Water relations

Access to the canopy was provided by scaffolding erected to a height of 15 m beside each of three trees of each species. Ecophysiological measurements were taken under prevailing light and climatic conditions.

At intervals of approximately one month throughout the summer (from late June to early October 2000), leaf water potential (Ψ) was measured with a pressure chamber (PMS-100, PMS Instrument Co.) in mature, fully expanded mid-canopy leaves from three to six apical twigs per tree. Measurements were conducted from predawn to sunset on selected sunny days. The water potential of a leaf was measured within 3 min of excision at a crown height of 10 to 12 m. At the same time, diurnal courses of stomatal conductance to water vapor (g_s) were monitored on four to six fully illuminated apical leaves per tree with a steady-state diffusion porometer (LI-1600, Li-Cor, Lincoln, NE). The natural inclination and azimuth of leaves were maintained during measurements. For each mea-

surement, temperature inside the cuvette, leaf temperature, relative humidity and incoming photosynthetically active radiation (PAR) were recorded. Precautions were taken to avoid large differences between external environmental conditions and those inside the cuvette. Shading the cuvette between measurements minimized cuvette overheating. Leaf conductance was expressed in molar units to account for differences in temperature and atmospheric pressure with altitude. Boundary layer conductance inside the cuvette was assumed constant and large.

For comparative purposes, soil-to-leaf hydraulic conductance (K_{SL}) was calculated from cuvette transpiration measurements and mean Ψ , following the single point method and using predawn water potential (Ψ_{pd}) to approximate soil water potential (Thompson and Hinckley 1977, Pallardy et al. 1995): $K_{SL} = E_1/\Delta\Psi$; where $\Delta\Psi$ is the difference between Ψ_{pd} and Ψ_{md} (midday water potential) and E_1 is leaf transpiration (porometer) measured at the same time as Ψ_{md} .

Gas exchange

On the same sample trees, net photosynthesis (A), g_s , intercellular CO₂ concentration (C_i) and leaf transpiration (E) were measured with a portable photosynthesis system (Ciras-1, PP-system, Hitchin, Herts, U.K.) on several mature unshaded leaves (from late May to late September 2000) in incident radiation ranging from 1000 to 1500 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (above saturating PAR). For each individual on each sampling date, gas exchange measurements were made three times during the day, between 1000 and 1700 h. No consistent diurnal trends in A or g_s were evident in any species on any date, so the mean of 20–30 measurements on each tree per day was used in the analysis of subsequent time-of-season effects and correlations.

Gas exchange was monitored at three different positions in the canopy profile, following a gradient of decreasing irradiance from the upper, through intermediate, to the lower canopy (corresponding to about 9, 6, 3 m for *Q. pubescens* and 11, 8, 5 m for *Q. cerris*). For each canopy level, 7–10 leaves on every tree were measured per day.

Dendroecological analysis

In early 2003, 10 dominant trees of each species were sampled for dendroecological analyses. Trees of *Q. cerris* and *Q. pubescens* were cored at a height of 1 m. To avoid reaction (tension) wood, two wood cores were taken at 180° to each other with a 0.5-cm diameter increment borer. Cores were seasoned in a fresh-air dry store and sanded a few months later. Ring widths were measured to the nearest 0.01 mm with LINTAB-measurement equipment coupled to a stereomicroscope (60× magnification, Leica, Germany) and Time Series Analysis Programme (TSAP) software (Frank Rinn, Heidelberg, Germany). Because of the likely presence of false rings, commonly found in trees of the Mediterranean region (Cherubini et al. 2003), and the possibility of missing rings, care was taken to ensure that each measured ring width was assigned the correct calendar date (see Tognetti et al. 2000). Raw

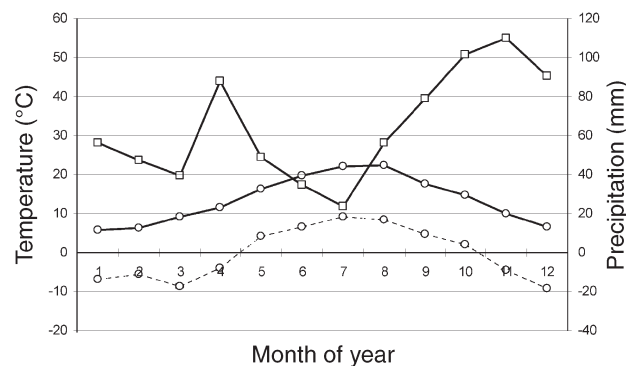


Figure 1. Ten-year mean monthly meteorological data (mean temperature (○, solid line), minimum temperature (○, dashed line) and precipitation (□, solid line)) collected at Pentolina (ARSIA, Regione Toscana), about 10 km from the study site over the period 1995–2005. The mean annual temperature was 13.5 °C, and the total annual precipitation was 776.4 mm.

ring widths of the single curves of each dated tree were plotted, cross-dated visually and then cross-dated statistically by (1) the percent agreement in the signs of the first-differences of two time series (the *Gleichläufigkeit*) and (2) Student's *t*-test, which determines the degree of correlation between the curves. Locally missing or discontinuous rings were identified by cross-dating (1) the duplicate tree-ring curves from a single tree and (2) the chronologies of different trees. Standard methods were used to build an averaged series (Fritts 1976).

Ring width was converted to tree basal area increment (BAI) according to the standard formula: $BAI = \pi(R_n^2 - R_{n-1}^2)$; where R is the radius of the tree and n is the year of tree ring formation. To examine the mean growth trend of the canopy trees at each site, BAI for each year was averaged over all individuals at each site. Tree-ring data are usually standardized to remove age trends and maximize the common climatic signal between trees (Cook et al. 1990); although, standardization methods remove long-term growth trends as well as age trends. Because our interest was in long-term growth trends, we worked with mean non-standardized BAI values across all trees at each site in each year. These provide interpretable yearly values of growth rather than a standardized index and display growth trends clearly, though at the expense of the loss of detailed information on growth responses to climate.

Mean sensitivity, an indicator of the responsiveness of trees to environmental factors such as climate, was analyzed for all averaged chronologies and for each tree within a specific chronology. Mean sensitivity was calculated as the absolute value of the difference in BAI between adjacent rings divided by the mean of the two BAI values, and was therefore defined as a measure of the percentage by which overall ring width varies from year to year (Fritts 1976). The influence of climate on tree-ring width at the site was assessed based on meteorological data recorded by the Servizio Idrologico Regionale (Pisa, Tuscany, Italy). Annual precipitation was calculated for the period 1921–2003.

Statistical analysis

Ecophysiological characteristics measured on sampling dates were analyzed by multivariate repeated measures analysis of variance (MANOVA) on untransformed data to test for seasonal trends and differences among species. Analysis of covariance (ANCOVA) was performed to test for equality of correlation coefficients. Tree-ring width and climate relationships were evaluated by regression analysis. For correlation analyses, total annual precipitation, and precipitation of the periods January–April (current year), May and August (current year) and December (previous year)–January (current year) were calculated, according to previous studies of the same species at a site located about 20 km from our site (Cherubini et al. 2003).

Results

Site characteristics

Compared with long-term trends, precipitation in 2000 was

near average in the spring, below average in winter and summer, and consistently higher than average in autumn; air temperature was above average during winter, spring and autumn, but similar to the average in summer (Figure 2). On a yearly basis, 2000 was warmer and wetter than the 10-year mean (mean annual temperature 14.5 °C and total annual precipitation 818 mm). The seasonal courses of ET_0 and VPD were typical for this sub-humid Mediterranean environment (Figure 2). Scant precipitation during summer months did not balance the high seasonal evapotranspiration. Soil water deficit developed in April, increased during the summer, reaching maximum values by the end of September, decreasing gradually thereafter (Figure 2).

Soil water content during the growing season did not differ among the 10, 25 and 50 cm depths ($P > 0.05$, not shown). At both stands, soil water content decreased gradually from late spring (ranging around $20.9 \pm 2.6\%$ by volume) to midsummer (ranging around $13.6 \pm 1.2\%$ by volume), and then increased in early fall. At the *Q. pubescens* site, recovery of soil water content was complete (about $21.7 \pm 1.5\%$ by volume), whereas at the *Q. cerris* site, soil water content did not reach pre-summer values (about $14.9 \pm 1.5\%$ by volume; $P < 0.05$).

Leaf traits

Daily courses of g_s and Ψ in June (onset of summer), July and August (drought period) and October (recovery phase) are shown in Figure 3. The diurnal course of g_s as a function of Ψ at different times during the season showed clear differences between species. In both *Q. cerris* and *Q. pubescens*, g_s patterns roughly followed changes in VPD during the day (Figure 3). In June, g_s of *Q. pubescens* was high early in the morning and decreased gradually during the day. Midday depression of g_s , as a result of high evaporative demand combined with water deficit (low Ψ) was observed in *Q. pubescens*, whereas g_s of *Q. cerris* changed little throughout the day and was comparable with the maximum g_s values of *Q. pubescens*. In July and August, g_s of *Q. pubescens* gradually declined, as Ψ dropped to low values, and stomata closed almost completely during the afternoon. For *Q. cerris*, g_s was typified by the existence of a rather stable diurnal pattern in July, whereas in August, when soil dryness was at a maximum, it showed a similar diurnal pattern to that of *Q. pubescens*. After the rain in October, g_s of both species increased, with differences between species (higher values in *Q. cerris* than in *Q. pubescens*) clearly apparent by midmorning. Diurnal time courses of Ψ showed a progressive decrease in predawn and midday values in both species with increasing seasonal drought, though the decreases were more consistent for Ψ_{pd} than for Ψ_{md} ($\Delta\Psi$ from about 2.5 to 1.8 MPa); seasonal means and maxima for $\Delta\Psi$ being 2.11 and 2.65 MPa for *Q. cerris* and 2.12 and 2.45 MPa for *Q. pubescens*, respectively. Both Ψ_{pd} and Ψ_{md} were significantly lower, whereas daily maximum g_s (g_{smax}) and the corresponding E_l (E_{lmax} , not shown) were higher in *Q. cerris* than in *Q. pubescens* (Table 1). There was a significant species effect and time effect for K_{SL} (Table 1, Figure 4). Throughout the season, *Q. cerris* had higher K_{SL} values than *Q. pubescens*.

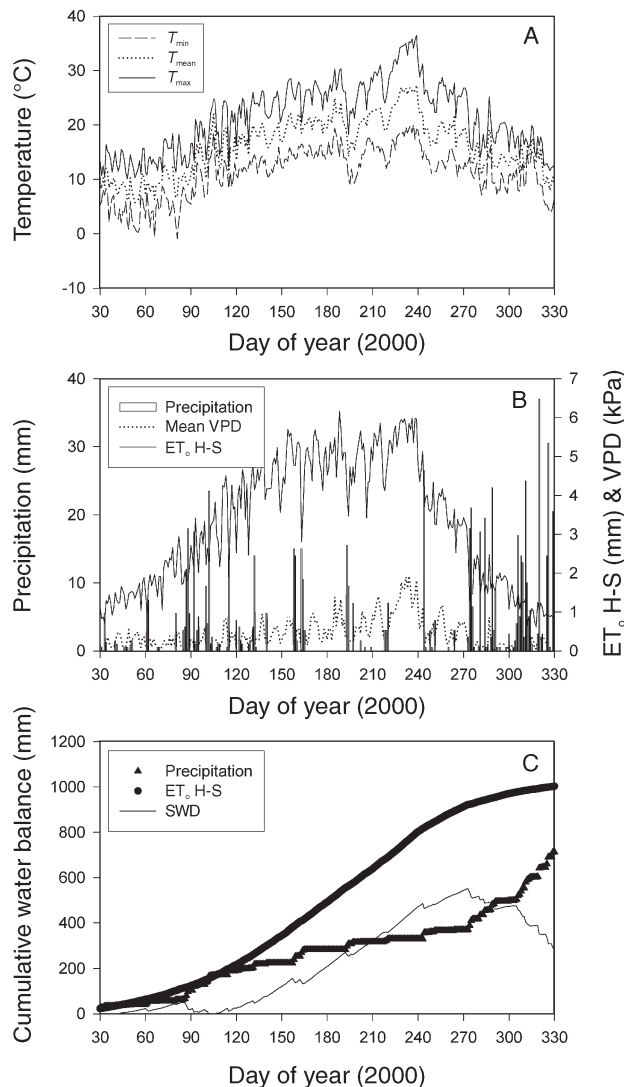


Figure 2. Seasonal patterns of: (A) daily minimum (T_{min}), mean (T_{mean}) and maximum (T_{max}) temperature; (B) total precipitation, daily reference evapotranspiration (Hargreaves-Samani; ET_o H-S) and mean daily vapor pressure deficit (VPD), as recorded by a meteorological station during 2000; and (C) cumulative water balance, including precipitation, ET_o H-S and soil water deficit (SWD).

There was a significant species effect on A , although A declined abruptly in both *Q. cerris* and *Q. pubescens* in midsummer (Table 1, Figure 5). *Quercus cerris* had higher A than *Q. pubescens* throughout the study, and this difference was particularly evident after the midsummer decline and late in the season. Species-related differences were less clear, though significant, for g_s and E (Table 1, Figure 5), which also showed a seasonal decline with a midsummer drop. Species did not differ significantly in C_i or C_i/C_a (intercellular-to-ambient CO_2 concentration ratio, not shown), with values declining throughout the season (Table 1, Figure 5). Species \times time interactions were significant for all gas exchange parameters.

The three canopy positions showed consistently different irradiances throughout the season ($P < 0.0001$) with PAR aver-

aging 1525 ± 80 , 1014 ± 194 and $686 \pm 209 \mu mol m^{-2} s^{-1}$ for *Q. cerris*, and 1602 ± 65 , 1122 ± 200 and $647 \pm 156 \mu mol m^{-2} s^{-1}$ for *Q. pubescens*, respectively for the upper, middle and lower canopy. Gas exchange parameters varied with canopy height (Table 2), following the seasonal variation in PAR (Figure 6). Although g_s was generally higher in upper-canopy positions than in middle- and lower-canopy positions, with little difference between species, A showed a more gradual change with canopy height and species-related variation was clear (Table 2, Figure 6); C_i and E differed significantly with canopy position, species and time of measurements (data not shown).

There were generally significant positive relationships between Ψ_{pd} and g_{smax} , Ψ_{pd} and Ψ_{md} , and g_{smax} and K_{SL} , whereas the correlation between Ψ_{md} and K_{SL} was weak. There were significant positive correlations between A and g_{wv} for each species on each date and across dates, with r^2 ranging from 0.21 to 0.88 and slopes (proxy for instantaneous water-use efficiency, WUE) generally higher in *Q. pubescens* than in *Q. cerris* (data not shown).

Tree rings

The synchronous occurrence of pointer years, i.e., very narrow and very wide tree rings, in both species indicates that tree rings were measured and cross-dated correctly and that a climatic signal may be present in the growth patterns (Figure 7). In Mediterranean environments, tree-ring growth is mainly limited by soil water availability, and precipitation plays a major role in determining cambial activity. At our site, however, low correlation coefficients between total annual precipitation and specific ring width chronologies were found ($r = 0.225$ and 0.095 for *Q. cerris* and *Q. pubescens*, respectively). Although a close correlation between ring width and total annual precipitation was not found, some dry periods (early fifties, seventies and eighties, all nineties) influenced growth, as shown by the ring widths and climatic records. Low correlation coefficients between specific ring-width chronologies and precipitation for the period January–April (current year), May and August (current year) and December (previous year)–January (current year) were found ($r < 0.3$ in all cases). Analogously, BAI was scarcely correlated with precipitation patterns in either species. Differences in mean BAI between the species were strong ($P < 0.0001$); *Q. pubescens* showing a rather sensitive trend and *Q. cerris* a relatively smooth pattern (Figure 7).

Quercus pubescens has always grown faster than *Q. cerris* in the investigated stands (Figure 7). In particular, after the severe drought in the seventies, growth of *Q. pubescens* recovered completely, reaching high rates after a few years, whereas growth rates of *Q. cerris* declined dramatically without recovery until 2002. Overall, *Q. pubescens* ring-width data were more variable (Figure 8), showing that this species was better able to take advantage of favorable conditions than *Q. cerris*, as also shown by both the ring-width and the BAI responses of the species during extreme years (pointer years). During the driest years of the last decades (e.g., 1982, 1985, 1987, 1990, 1993), more negative peaks were found in *Q. cerris* than in *Q. pubescens*.

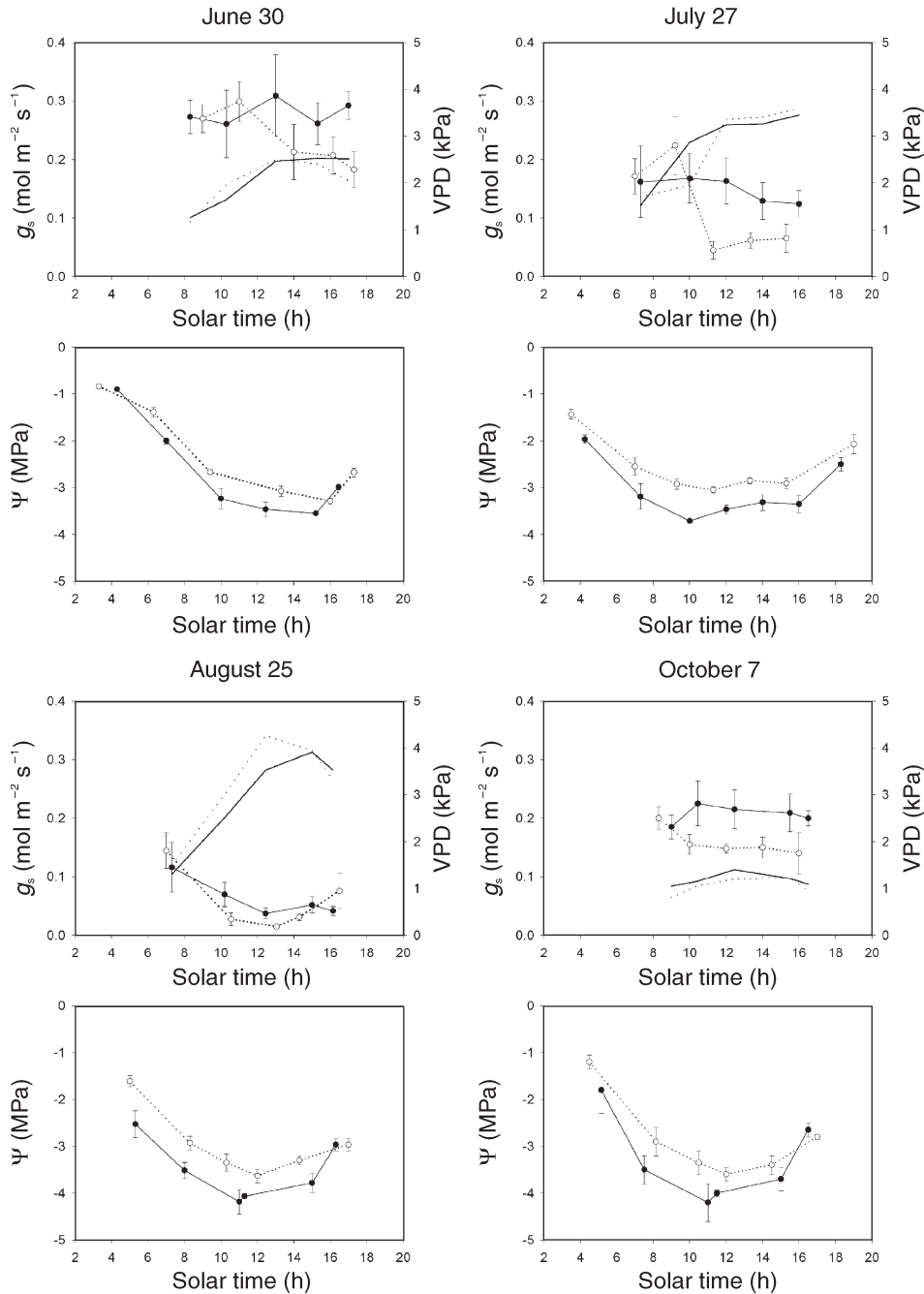


Figure 3. Representative diurnal patterns of leaf conductance (g_s) and leaf water potential (Ψ) for *Quercus cerris* (●) and *Quercus pubescens* (○). Diurnal patterns for vapor pressure deficit (VPD) are also shown (lines). Data are means ± 2 SE, bars not visible indicate SE smaller than the symbol.

Discussion

The phytoclimatic typology of these Mediterranean oak forest stands is mesotemperate subhumid/humid (Blasi 1996). Most projections for a warmer world point to significantly less rainfall in summer over the Mediterranean Basin as a whole, with an increase in annual precipitation in the region north of 40° N. Meteorological conditions in 2000 were typically subhumid Mediterranean, with annual precipitation and temperature above the mean. Nonetheless, severe summer drought caused a progressive depletion of soil water reserves, which was counterbalanced by high autumn precipitation, when soil

water content of the plots started recovering. Where the study oak species co-occurred, they differed in photosynthetic carbon gain per unit leaf area, reflecting differences in their water status. Their comparative strategies, with strategy denoting a set of traits attained through natural selection, were related to the relative distribution of each species along soil water gradients in this environment. Climatic stress and land use changes could, however, predispose these transitional high forests to decline.

Quercus pubescens probably had greater access to soil water than *Q. cerris*, based on its less negative Ψ_{pd} during most of the season (cf. Hinckley et al. 1978, Bréda et al. 1995). Greater ac-

Table 1. Repeated measures analysis of variance of physiological parameters of *Quercus cerris* and *Quercus pubescens* trees. Abbreviations: Ψ_{pd} , plant predawn water potential; Ψ_{md} , plant midday water potential; g_{smax} , maximum daily stomatal conductance; E_{lmax} , maximum daily leaf transpiration; K_{SL} , soil-to-leaf hydraulic conductance; A , net photosynthesis; g_s , stomatal conductance to water vapor; C_i , intercellular CO_2 concentration; E , leaf transpiration; and C_i/C_a , intercellular to ambient CO_2 concentration ratio. Significance values are indicated as: *, $P < 0.05$; **, $P < 0.01$; and ***, $P < 0.001$.

Source	F statistic		
	Time	Time × Species	Species
Ψ_{pd} (MPa)	21.72***	2.638	17.34***
Ψ_{md} (MPa)	20.95***	0.709	33.00***
g_{smax} ($mol\ m^{-2}\ s^{-1}$)	5.040**	0.281	0.050
E_{lmax} ($mmol\ m^{-2}\ s^{-1}$)	11.44***	0.505	0.774
K_{SL} ($mmol\ m^{-2}\ s^{-1}MPa^{-1}$)	28.27***	0.486	15.90**
A ($\mu mol\ m^{-2}\ s^{-1}$)	144.7***	3.007*	36.96***
g_s ($mmol\ m^{-2}\ s^{-1}$)	126.4***	2.436*	24.66***
C_i ($\mu mol\ mol^{-1}$)	86.63***	5.397***	0.057
E ($mmol\ m^{-2}\ s^{-1}$)	268.1***	10.05***	12.68***
C_i/C_a	77.26***	5.266***	0.000

cess to soil water could be achieved by more extensive rooting—either greater extension of laterals or greater rooting depth. Both species had extensive lateral roots, with many roots observed in the upper 15 cm. Rooting depth profiles were less certain. *Quercus pubescens* had a conservative water-use strategy compared with *Q. cerris*, based on its lower g_s and K_{SL} , even though it had less negative Ψ_{md} values. The species had similar instantaneous WUE, as indicated by comparable C_i values from gas exchange. Tree-ring data confirmed that *Q. pubescens* was better able to cope with water stress than

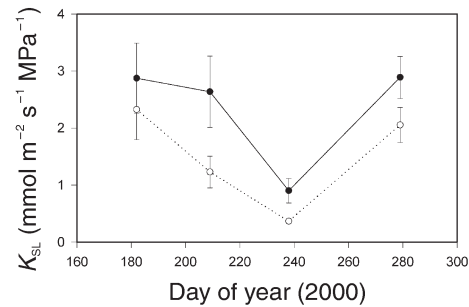


Figure 4. Seasonal variation in soil-to-leaf hydraulic conductance (K_{SL}) in *Quercus cerris* (●) and *Quercus pubescens* (○). Data are means \pm 2 SE; bars not visible indicate SE smaller than the symbol.

Q. cerris (Cherubini et al. 2003). Ring-width chronologies showed that the species responded differently to water stress during the past 65–85 years. Formerly, *Q. pubescens* grew faster than *Q. cerris*, responding more quickly to severe droughts, as shown by higher ring-width variability, and recovering in growth rate more quickly after prolonged droughts.

A more conservative water-use strategy in *Q. pubescens* (and perhaps, greater soil water access) is consistent with its dominance on xeric ridges, whereas the capacity for drought avoidance in *Q. cerris* may be exceeded in these habitats. In both species, seasonal minimum water potentials did not drop significantly below the minimum value of plants under well-watered conditions early in the season, despite decreasing Ψ_{pd} , indicating that stomatal control balanced rates of water loss with decreasing soil water potentials.

In *Q. cerris*, mid- and late-season Ψ_{md} values were considerably more negative than those of *Q. pubescens* and were accompanied by relatively high daytime values of g_s , indicating

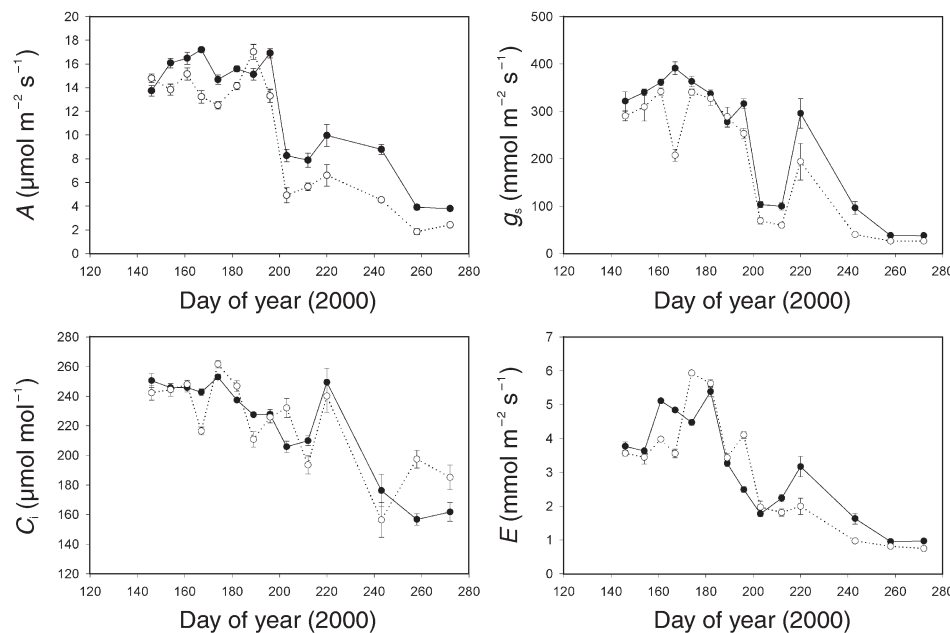


Figure 5. Seasonal changes in gas exchange parameters (photosynthesis (A), stomatal conductance (g_s), intercellular CO_2 concentration (C_i) and leaf transpiration (E)) in *Quercus cerris* (●) and *Quercus pubescens* (○). Data are means \pm 2 SE; bars not visible indicate SE smaller than the symbol.

Table 2. Repeated measures analysis of variance for positional and seasonal characteristics for *Quercus cerris* and *Quercus pubescens* trees. Abbreviations: g_s , stomatal conductance; A , net photosynthesis; C_i , intercellular CO_2 concentration; and E , leaf transpiration. Significance values are indicated as: *, $P < 0.05$; **, $P < 0.01$; and ***, $P < 0.001$. Species \times position and species \times position \times time interactions were never significant; position \times time interactions were always significant (**); and species \times time interactions were significant only for A (**).

Source	F statistic		
	Position	Time	Species
g_s ($\text{mmol m}^{-2} \text{s}^{-1}$)	82.86***	69.02***	2.159
A ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	97.96***	182.4***	37.57***
C_i ($\mu\text{mol mol}^{-1}$)	5.063**	68.31***	11.69***
E ($\text{mmol m}^{-2} \text{s}^{-1}$)	72.25***	137.1***	14.51***

limited stomatal closure. This behavior may indicate a non-conservative water-use pattern with a tendency to use water from progressively deeper soil layers thereby avoiding marked stomatal closure. Weak stomatal control at low Ψ_{md} could lead to excessive water loss during particularly dry summers, resulting in low A because of non-stomatal inhibition and xylem cavitation during drought (Pezeshki and Chambers 1986, Bragg et al. 1993, Donovan et al. 2000), and exclusion from xeric sites. However, this interpretation was not supported by our observation that high g_s was associated with high A . The greater efficiency in hydraulic transport by the xylem of *Q. cerris* shoots (higher K_{SL}) may have allowed higher E in this species compared with *Q. pubescens*, thus facilitating higher A .

The C_i/C_a ratio declined over the season from about 0.7 to less than 0.5 in both species (data not shown), a consequence of drought-induced stomatal closure and the subsequent readjustment between the supply and demand for CO_2 . We used C_i as a comparative estimate of instantaneous WUE, because ambient CO_2 concentration, leaf temperature and leaf-to-air vapor pressure deficit (calculated from leaf temperature during measurements and air temperature and relative humidity from open chamber readings) did not differ between species on any sampling date (Donovan and Ehleringer 1994). A higher C_i reflects a lower instantaneous WUE. The decrease in g_s throughout the season resulted in a general increase in instantaneous WUE in both species, though it was higher in *Q. pubescens*. Čermák et al. (1998) reported that seasonal total transpiration was significantly lower in *Q. pubescens* than in *Q. cerris*. In our study, although *Q. pubescens* showed little variation in total transpiration throughout the season, transpiration of *Q. cerris* was high early in the season but decreased dramatically with the midsummer drought. Chiesi et al. (2002) observed a wider range of measured and simulated transpiration values in *Q. cerris* than *Q. pubescens* that they attributed to higher LAI and g_s in the former species than in the latter species.

Our values of gas exchange and water potential were similar to those reported for *Quercus* species at Mediterranean latitudes (e.g., Goulden 1996, Damesin et al. 1997). In Mediterranean climates, *Quercus* species routinely achieve Ψ_{pd} values below -1.5 MPa. In contrast, Ψ_{pd} of eastern North American *Quercus* species rarely falls below -1 MPa except during extreme droughts (Kubiske and Abrams 1992, Bragg et al. 1993, Vaitkus and McLeod 1995, Donovan and Pappert 1998, Donovan et al. 2000). Based on their Ψ_{pd} values, we conclude that

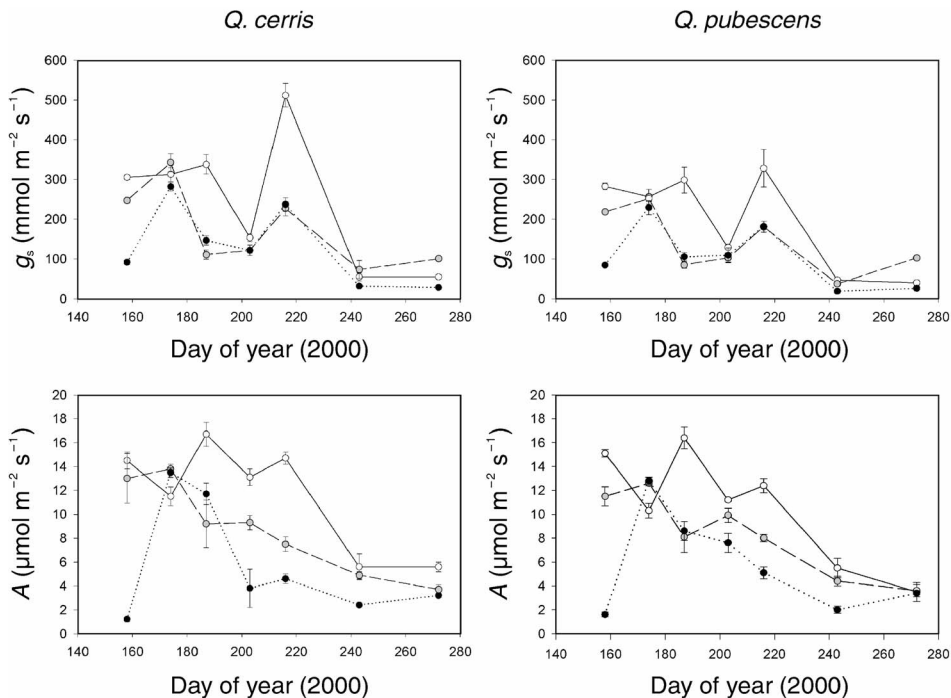


Figure 6. Seasonal changes in gas exchange parameters (photosynthesis (A) and stomatal conductance (g_s)) for *Quercus cerris* and *Quercus pubescens*, measured between 1000 and 1700 h at three different positions along the canopy profile following a gradient of decreasing irradiance from upper (○), through middle (●), to lower (●) levels. Data are means ± 2 SE; bars not visible indicate that the SE is smaller than the symbol.

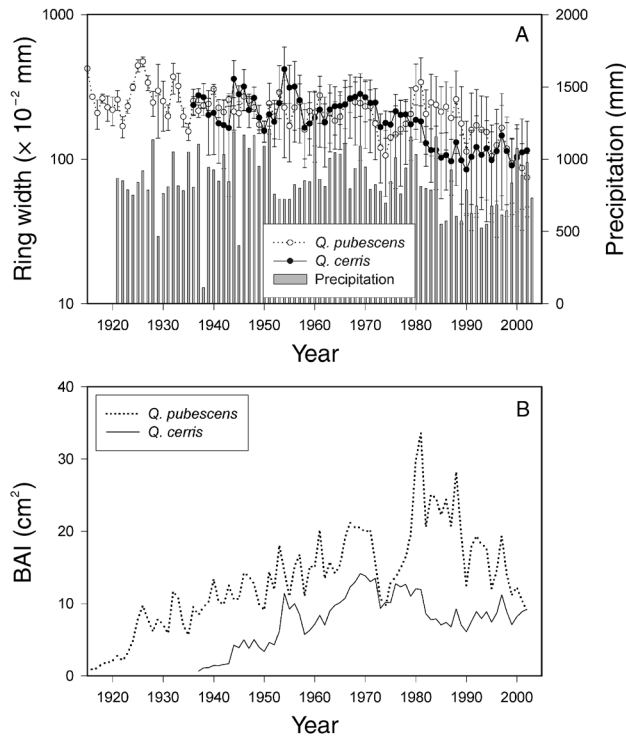


Figure 7. (A) Mean ring-width chronologies (logarithmic scale) for all trees (*Quercus cerris* and *Quercus pubescens*) at Radicondoli (mean \pm SD), and total annual precipitation (Servizio Idrologico Regionale, Pisa, Tuscany, Italy) for the period 1921–2003 (overall mean 850.8 mm). (B) Averaged basal area increment (BAI).

Q. cerris and *Q. pubescens* in the hilly habitats where we studied them, quite regularly experience severe limitations of soil water availability even though the area is apparently sub-humid. Superficial and incoherent soil layers did not serve to store enough soil water. As in other *Quercus* species of Mediterranean ecosystems (Sala and Tenhunen 1994, Gallego et al.

1994, Tognetti et al. 1998a), $\Delta\Psi$ of *Q. cerris* and *Q. pubescens* reached up to 2.7 and 2.5 MPa, respectively, whereas in eastern North American *Quercus* species $\Delta\Psi$ values are generally below 1.5 MPa (Bahari et al. 1985, Abrams and Knapp 1986, Abrams et al. 1990, Kubiske and Abrams 1992, Kloeppe et al. 1993).

Examination of relationships between parameters revealed a strong correlation between A and g_s in both species, as previously documented (e.g., Tognetti et al. 1998b). Similarly, Ψ_{pd} and g_{smax} , Ψ_{pd} and Ψ_{md} , and g_{smax} and K_{SL} showed close relationships (cf. Reich and Hinckley 1989, Acherar and Rambal 1992), suggesting a possible controlling effect of K_{SL} on g_s , mediated by root or soil water potentials. Soil water deficits could trigger root signals stimulating stomatal reactivity (Davis and Zhang 1991). Bréda et al. (1993) and Tognetti et al. (1998a) suggested that, in oak trees subjected to drought, seasonal changes in hydraulic conductance were mainly attributable to modifications in hydraulic properties at the soil–root interface rather than to changes in xylem embolism in apical twigs. As observed by Donovan et al. (2000), K_{SL} was not significantly correlated with Ψ_{md} (data not shown). The relationship of K_{SL} to threshold water potentials for stomatal closure may provide more insight into stomatal control in these species (Bond and Kavanagh 1999).

Leaf area index and its distribution in forest canopies are important attributes influencing canopy energy and water exchange with the atmosphere (Jarvis and Leverenz 1983). Many studies that have examined leaf gas exchange throughout a canopy profile have focused on the light environment of the foliage in closed-canopy forests (e.g., Schoettle and Smith 1999, Rijkers et al. 2000). Although a link exists between liquid and vapor phase conductances, g_s varied with canopy height to a lesser extent and irregularly compared with A , suggesting that stomata were responsive to changes in hydraulic conductance of the soil-to-leaf flow path. Cochard et al. (1997) examined the vertical profile of leaf gas exchange in 15–18-m tall *Fraxinus excelsior* L. growing in an open stand and found little

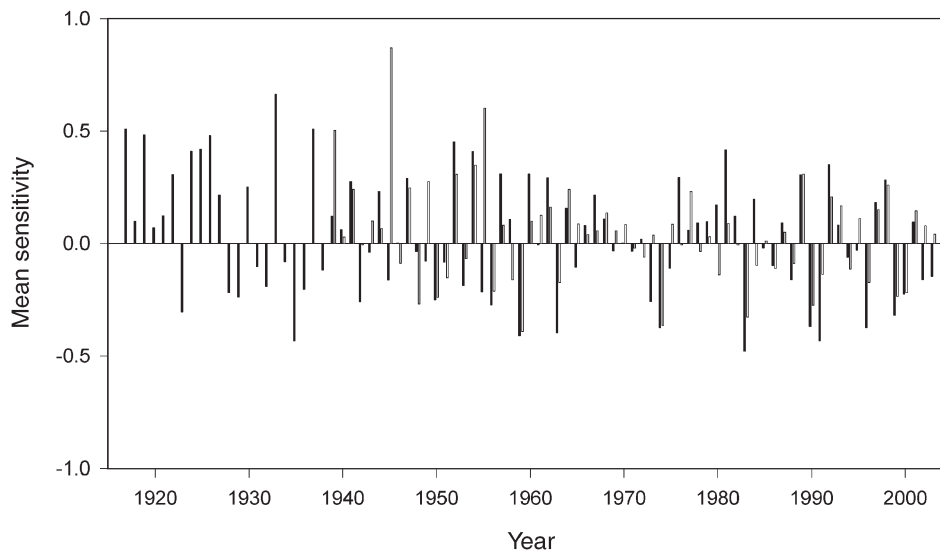


Figure 8. Mean sensitivity for all trees (*Quercus cerris* (open bars) and *Quercus pubescens* (filled bars)) at Radicondoli.

variation in g_s and E with canopy position. Likewise, Oliveira et al. (1996) found that g_s did not vary with crown position in *Q. suber* L. Tognetti et al. (2003) observed that leaf dry mass per area was more variable for *Q. pubescens* (75–89 to 153–173 g m⁻²) than for *Q. cerris* (106–147 g m⁻²).

The fairly open canopy of the *Q. pubescens* site resulted in more uniform sharing of light among leaves and smaller differences in leaf gas exchange between upper and lower branches within the crown. The relatively dense canopy of the *Q. cerris* site resulted in greater gas exchange in the upper-canopy than in the lower canopy. Ecophysiological data collected and simulated for the ongoing and the predicted climate in Tuscany, and tree-ring records, are consistent with the interpretation that both of these *Quercus* species are drought tolerant but that *Q. pubescens* is found on more xeric sites than *Q. cerris* because of its greater access to, and its more conservative use of, soil water. Under severely dry conditions, the lack of stomatal response to drought in *Q. cerris* may result in earlier depletion of available water. Although other adaptations of *Quercus* species and environmental factors may be important, the interaction of water-use strategy of *Q. pubescens* and *Q. cerris* and water availability of topsoils is a strong determinant of the performance and distribution of these species in the hilly area of Tuscany. The integrated use of instantaneous measurements and temporal reconstructions to understand current and past tree responses to environmental stress point to the favorable competitive status of *Q. pubescens* compared with *Q. cerris* in a predicted harsher climate in the Mediterranean region.

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