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Functional groups in *Quercus* species derived from the analysis of pressure–volume curves

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Abstract Oaks that occupy Mediterranean phytoclimates share common leaf features (evergreenness, high leaf dry mass per unit area, LMA). Due to this phytoclimatic, morphological, and phenological convergence it has been suggested that they might constitute a coherent functional group. To confirm this hypothesis, some physiological parameters were determined after calculating pressure–volume curves (P – V curves) using the free-transpiration method. Seventeen *Quercus* species from contrasting phytoclimates were studied: six Mediterranean evergreen species (*Q. agrifolia*, *Q. chrysolepis*, *Q. coccifera*, *Q. ilex* ssp. *ballota*, *Q. ilex* ssp. *ilex*, and *Q. suber*); seven nemoral deciduous species (*Q. alba*, *Q. laurifolia*, *Q. nigra*, *Q. petraea*, *Q. robur*, *Q. rubra* and *Q. velutina*), and four nemoro-Mediterranean deciduous species (*Q. cerris*, *Q. faginea*, *Q. frainetto*, and *Q. pyrenaica*). Two-year-old seedlings growing under homogeneous environmental conditions (no water restrictions, uniform light, and nutrient supply) were used. The statistical analyses (correlation, mean-value comparisons, principal component analysis) of leaf features and parameters derived from the P – V curves confirmed the functional homogeneity of the three phytoclimatic groups, which were characterized by their contrasting ecophysiological response to water stress. The Mediterranean oak species developed mechanisms to avoid an excessive loss of cell water (e.g. high cell-wall rigidity). Conversely, the nemoral oaks showed the opposite. The nemoro-Mediterranean oaks perform better than nemoral oaks under water-stress conditions, but they cannot perform as well as the Mediterranean oaks on relatively dry soils.

Keywords *Quercus* · Mediterranean · Phytoclimate · Pressure-volume curves

Introduction

The genus *Quercus* comprises 531 tree and shrub species distributed among contrasting phytoclimates in the Northern Hemisphere, from temperate and subtropical deciduous forests to Mediterranean evergreen woodlands (Nixon 1993; Govaerts and Frodin 1998; Manos et al. 1999). Thus, they occupy habitats of widely varying moisture-supply capacity (Kwon and Pallardy 1989; Abrams 1990). The Mediterranean climate is characterized by summer drought. In the more inland (continental) areas, summers are followed by cold winters which limit plant growth (Mitrakos 1980). This type of climate has historically been associated with sclerophyllous vegetation (Walter 1973), which would include Mediterranean oaks of various subgenera (Krüssmann 1986). Because of their similar leaf type, some authors suggested that they could form a homogeneous physiological group (Kummerow 1973).

Small sclerophyllous leaves have been regarded as a morphological adaptation of plants to drought by reducing transpiration (Morrow and Mooney 1974; Poole and Miller 1975; Levitt 1980; Turner 1994). Groom and Lamont (1997) found a link between changes in leaf structure (leaf dry mass per unit area, LMA – used here as an indication of the degree of sclerophylly) and plant function (water relations) within a single species, suggesting that sclerophylly might increase drought tolerance. In addition, Richards and Lamont (1996) also showed, in an interspecific study, that sclerophylly was positively associated with a greater drought tolerance by osmotic and elastic adjustments.

However, there are numerous studies that do not support the idea of sclerophylly as a xeromorphic functional feature related to an increased resistance to water stress (Seddon 1974; Mitrakos 1980; Ricklefs and Matthew 1982; Oertli et al. 1990). First, species with sclerophyllous leaves are widespread in both arid and humid envi-

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ronments (Turner 1994). Second, from an evolutionary point of view, sclerophylly cannot be regarded as a convergent adaptation in response to a single environmental stress (drought, herbivory, nutrient deficiency) in Mediterranean ecosystems (Nardini et al. 1996). Following this argument, Lo Gullo and Salleo (1988) showed that various species with similar degrees of sclerophylly adopted very different strategies to withstand drought. On the other hand, oak species with very different degrees of sclerophylly showed similar drought strategies (Salleo and Lo Gullo 1990). Overall, these authors found that there was no basis to support a functional relationship between sclerophylly and drought tolerance. These results require other types of studies to determine if Mediterranean oaks constitute a coherent ecophysiological group.

Other functional leaf characteristics may offer a new basis of common performance in Mediterranean oaks. Pressure–volume (P – V) curves and their derived water-relation parameters (leaf water potential at the turgor-loss point, ψ_{tlp} ; maximum bulk modulus of elasticity, ϵ_{max} ; osmotic potential at full turgor, π_0 ; relative water content at the turgor-loss point, RWC_{tlp} ; relative symplastic water loss at the turgor-loss point, S_{tlp} ; and relative symplastic water content, S) are a very useful tool for the study of water relationships in woody plants (Cheung et al. 1975; Zine El Abidine 1994). In this way, the tolerance of water stress is mainly related to osmotic and elastic adjustments, as defined by the π_0 value and by the elastic properties of the cell wall (Dreyer et al. 1990). Significant differences in tissue elasticity and RWC_{tlp} have been found in studies considering contrasting interspecific leaf characteristics (Roberts et al. 1980; Sobrado 1986; Zobel 1996). Therefore, one way to characterize functional groups in *Quercus* species would be to study their P – V parameters.

As far as we know, there are no studies which compare the leaf parameters derived from P – V curves within a genus. This alternative approach would consist of comparing these ecophysiological characteristics in several species grown under the same environmental conditions and without water restrictions. The species selected for this study represent contrasting phytoclimatic groups (Mediterranean, nemoro-Mediterranean, and nemoral oaks) partly characterized by their different leaf features (phenology – evergreen vs deciduous – area, LMA). Our working hypothesis was that species of such different biogeographical and phytoclimatic distribution might exhibit different parameters of tissue water relations. The main objective of this study was to determine whether common functional features existed in the oaks, by considering the physiological parameters derived from the P – V curves.

Materials and methods

Experimental conditions

Seventeen *Quercus* species, occupying a wide ecological range, were studied. They belong to two different subgenera: *Quercus* (*Q. alba* L., *Q. cerris* L., *Q. chrysolepis* Liebm., *Q. coccifera* L., *Q. faginea* Lam., *Q. frainetto* Ten., *Q. ilex* ssp. *ballota* L., *Q. ilex* ssp. *ilex* L., *Q. petraea* Liebl., *Q. pyrenaica* Willd., *Q. robur* L.,

and *Q. suber* L.), and *Lobatae* (*Q. agrifolia* Née., *Q. laurifolia* Michx., *Q. nigra* L., *Q. rubra* L., and *Q. velutina* Lam.). Seed origin was described by Sisó et al. (2001).

To reduce the environmental variability, seedlings were grown in cylindrical pots under uniform nutrient supply and light conditions, with no water restrictions. The pots were filled with nutrient-free sand. Nutrient supply was ensured by using a slow-liberation fertilizer (Osmocote Plus, Sierra Chemical, Milpitas, Calif., USA) as described by Naidu and DeLucia (1997). The fertilizer (3 g l⁻¹ substratum) was applied at the start of the experiment to the top 10 cm layer of sand. The pots were placed in a shadehouse (Forest Research Unit, S.I.A., Zaragoza, Spain) covered by a shade frame to limit light intensity to a maximum of 40% of the external radiation. During the growing period plants were watered twice a day, in the early morning and evening, by using micro-sprinklers. Climatic conditions in the shadehouse were monitored by a thermohydrograph (JRI Minidisque 165–00, Jules Richard, Argenteuil, France). The mean maximum and minimum temperatures during the growing season (March–August) were 24.9°C and 10.4°C. During the same period, the relative air humidity was 58–92%, and the light regime was quite regular (only ca. 5% of the days were cloudy). At the end of the second growth cycle (July), five seedlings per species were randomly harvested for P – V measurements.

Water-relation parameters obtained from P – V curves may change according to the age and environmental conditions of a plant. For instance, changes in tissue maturity, soil water content, and nutrient status may alter tissue elasticity (Tyree and Jarvis 1982). Leaves were processed after full development. It has been found that the ranking of species, in terms of dehydration tolerance when water availability is high, is the same as the ranking when water availability is low (Tschaplinski et al. 1998). Therefore, our experimental inferences can be extrapolated to water-shortage conditions.

Morphological measurements

The area of 30 leaves per species was measured using a leaf area meter (Area Measurement System, Delta-T Devices). They were then oven dried at 70°C for 3 days, to determine their dry weight. LMA (mg cm⁻²) was calculated as the ratio of the foliage dry weight to foliage area, and was used as an estimator of the degree of sclerophylly (Witkoswski and Lamont 1991).

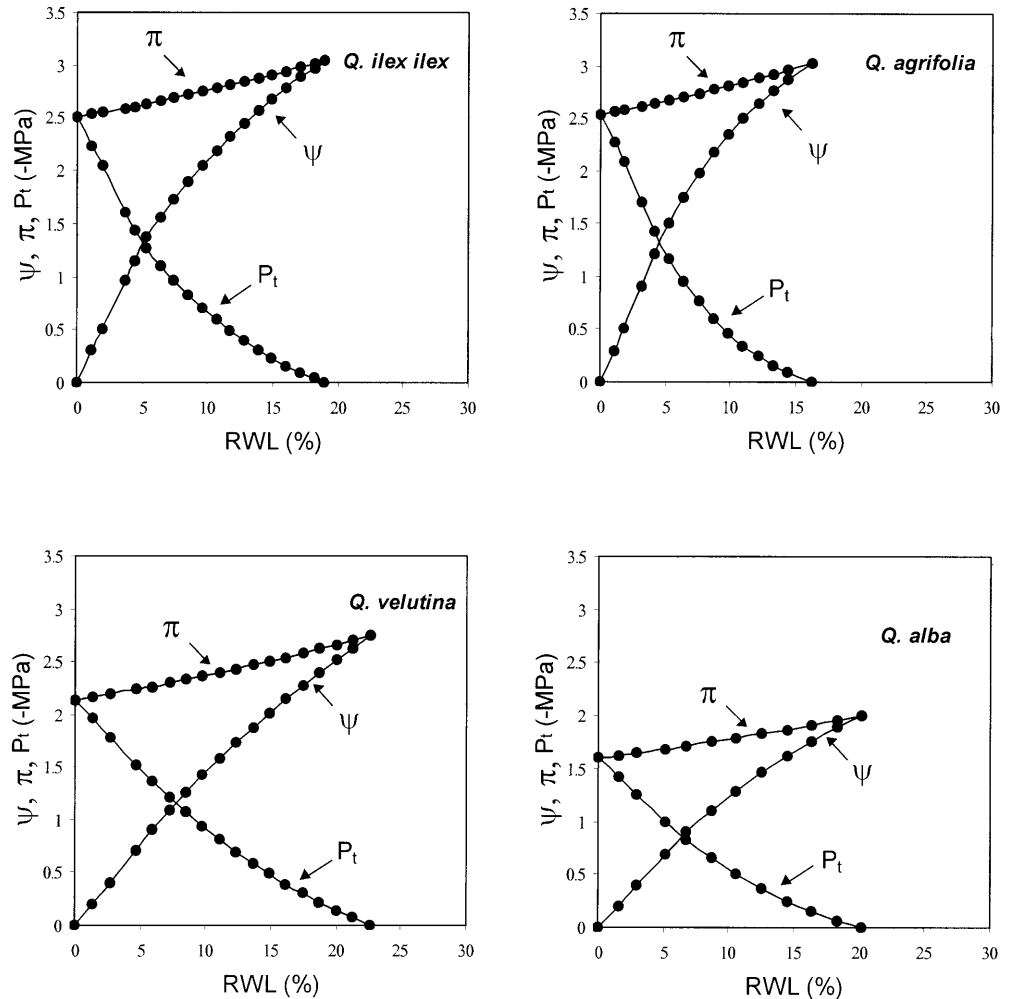
In order to obtain a wide range of foliar phenology and morphology in *Quercus* (Tutin et al. 1964; Krüssmann 1986; Castroviejo et al. 1990), evergreen (*Q. agrifolia*, *Q. chrysolepis*, *Q. coccifera*, *Q. ilex* ssp. *ballota*, *Q. ilex* ssp. *ilex*, and *Q. suber*) and deciduous species (*Q. alba*, *Q. laurifolia*, *Q. cerris*, *Q. faginea*, *Q. frainetto*, *Q. nigra*, *Q. petraea*, *Q. pyrenaica*, *Q. robur*, *Q. rubra* and *Q. velutina*) were studied.

Three different groups were established a priori according to their phytoclimate (Walter 1973): Mediterranean oaks (*Q. agrifolia*, *Q. chrysolepis*, *Q. coccifera*, *Q. ilex* ssp. *ballota*, *Q. ilex* ssp. *ilex*, and *Q. suber*; see Pignatti 1982; Allué-Andrade 1990; Burns and Honkala 1990; Castroviejo et al. 1990; Rivas-Martínez and Sáenz-Lain 1991); transitional nemoro-Mediterranean oaks (*Q. cerris*, *Q. faginea*, *Q. frainetto*, and *Q. pyrenaica*; Pignatti 1982; Allué-Andrade 1990; Castroviejo et al. 1990; García-López 2000); and nemoral oaks (*Q. alba*, *Q. laurifolia*, *Q. nigra*, *Q. petraea*, *Q. robur*, *Q. rubra* and *Q. velutina*; see Tutin et al. 1964; Burns and Honkala 1990).

P – V curves

P – V curves were determined using a Scholander pressure chamber (Scholander et al. 1965) and following the free-transpiration method described in previous studies (Talbot et al. 1975; Hinckley et al. 1980; Turner 1988; Dreyer et al. 1990). The weight and water potential were measured at constant time intervals until values close to –6 MPa were reached. This methodology allowed us to conduct simultaneously up to five analyses per day (Tyree and Hammel 1972).

Fig. 1 Höfler diagrams relating symplastic water loss (RWL, %) to turgor pressure (P_t), osmotic potential (π_o), and leaf water potential at the turgor-loss point (ψ_{tlp}) in shoots of two typical Mediterranean (*Quercus ilex* ssp. *ilex*, *Q. agrifolia*) and nemoral (*Q. velutina*, *Q. alba*) oak species



The short petioles of Mediterranean oaks did not protrude beyond the rubber seal of the pressure pump. Therefore, in order to standardize the measurements, shoots bearing 5–6 leaves were used in all the species, instead of single leaves. Sample leafiness (% leaf dry weight) differed slightly between species, from *Q. suber* with about 79% of dry weight in leaves to *Q. alba* with 82%. As long as variations in the foliage weight are kept at a moderate level, the use of foliated shoots for P – V curves seems justified, as insignificant variation in their parameter estimates (<0.2 MPa in π_o and Ψ_{tlp} , and 12–16% in RWC_{tlp}) was found (Neufeld and Teskey 1986; Parker and Pallardy 1987; Zobel 1996).

Five terminal shoots were used per species. Their extremes were carefully cut and submerged in distilled water until full rehydration. Afterwards, they were wrapped in plastic seal and left overnight in the refrigerator. Special care was taken to prevent leaf oversaturation by detecting eventual water outflow from the sample when water potential (Ψ) was equal to zero (Kubiske and Abrams 1991). In order to calculate each pressure-volume curve, a scatter diagram was plotted using the values of $1/\Psi$ and the volume of expressed symplastic water (V_e). After these measurements, shoots were oven dried at 70°C for 72 h. Then, they were weighed with a resolution of 1 mg, so as to calculate the parameters related to the volume of water.

Statistical analysis

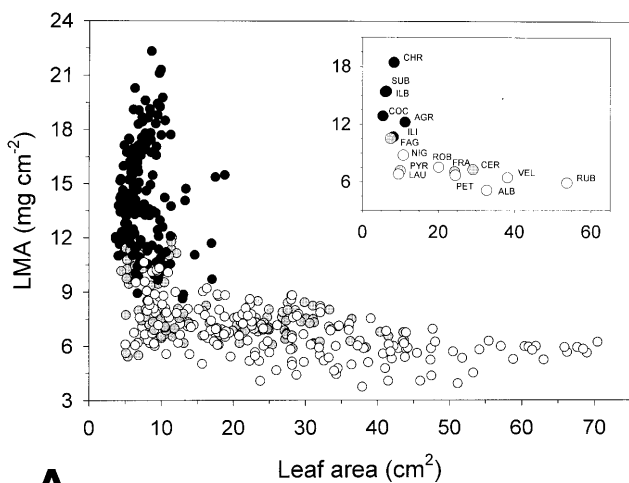
Data were previously transformed (logarithm, square root) to follow normality. This was checked using the Kolmogorov-Smirnov test. Simple one-way ANOVA was used to check and find differences between mean values in different species and phytoclimatic

species groups. Species values, both the individual ($n=92$) and mean ones ($n=17$), were normal for all variables ($P>0.25$), including LMA. In order to determine which groups were significantly different from each other, unplanned comparisons were carried out using the Tukey HSD (honest significant difference) test. This is a very conservative test offering the least amount of protection against the increased alpha error rate due to multiple a posteriori comparisons. The relationship between variables was assessed using the Pearson (r) coefficient (Sokal and Rohlf 1995), and considering the individual values of all plants ($n=92$).

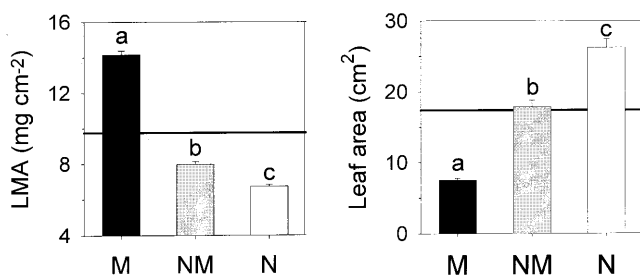
In order to present the interspecific variability of P – V parameters and sclerophylly in a few dimensions, a principal component analysis (PCA) was carried out. We assumed that the relationship between variables was linear (Ter Braak 1995). The mean values of P – V parameters and sclerophylly ($n=30$ leaves per species), for each species, were used in the PCA. The graphical display of the ordination diagram was simplified showing only the vectors (arrow) for the P – V parameters (ϵ_{max} , π_o , Ψ_{tlp} , S , S_{tlp} , RWC_{tlp}) and the degree of sclerophylly (Legendre and Legendre 1998). All statistical analyses were performed using the statistical package SPSS (version 6.1.2.), except the PCA which was done using Canoco 4.0 (Ter Braak 1988; Ter Braak and Smilauer 1998).

Results

To illustrate the results obtained in the Höfler diagrams, two contrasting sets of oak species, according to their phytoclimate, are shown in Fig. 1. Two strictly Mediterranean



A



B

Fig. 2 A Relationship between leaf area and leaf dry mass per unit area (*LMA*) values in all *Quercus* individuals studied, and the mean value per species (*inset graph*). The color of the points indicates the phytoclimate where each species is mostly found: Mediterranean (*M* black), nemoro-Mediterranean (*NM* gray), and nemoral (*N* white). **B** Comparison of mean values of these variables according to the phytoclimate of each *Quercus* species. Different letters refer to significant differences between groups ($P \leq 0.05$; Tukey HSD test). The horizontal lines indicate the mean value of each variable in all the individuals studied. The color of bars is the same as that of points in Fig. 2A. The species abbreviations are: *Q. agrifolia* (*AGR*), *Q. alba* (*ALB*), *Q. cerris* (*CER*), *Q. chrysolepys* (*CHR*), *Q. coccifera* (*COC*), *Q. faginea* (*FAG*), *Q. frainetto* (*FRA*), *Q. ilex* ssp. *ilex* (*ILI*), *Q. ilex* ssp. *ballota* (*ILB*), *Q. laurifolia* (*LAU*), *Q. nigra* (*NIG*), *Q. petraea* (*PET*), *Q. pyrenaica* (*PYR*), *Q. robur* (*ROB*), *Q. rubra* (*RUB*), *Q. suber* (*SUB*), and *Q. velutina* (*VEL*)

nean species (*Q. ilex* ssp. *ilex*, *Q. agrifolia*) and two typically nemoral species were selected (*Q. alba*, *Q. velutina*). At a small symplastic water loss (5%), both the osmotic-potential and turgor-pressure drop were greater in the Mediterranean species than in the nemoral ones. These contrasting results could be explained in terms of differences in ϵ_{\max} , whose values for the evergreen species were on average almost twice those for the deciduous ones.

The Mediterranean oak species showed small leaf-area and high *LMA* values (Fig. 2A, B). They also showed a low dispersion in their leaf-area values, but their *LMA* values were much more scattered. In contrast, individuals belonging to nemoral species showed a wide

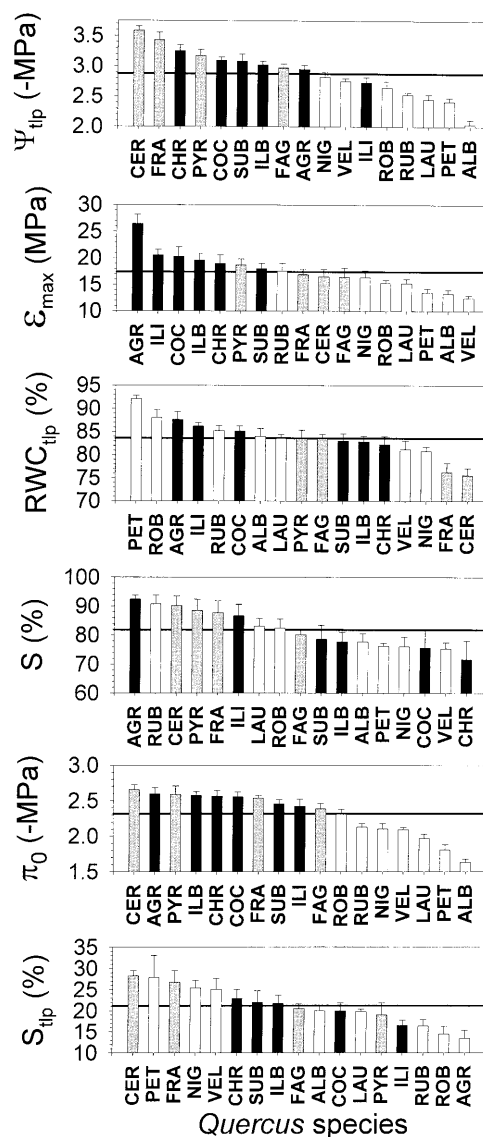


Fig. 3 Parameters derived from the pressure–volume curves for the *Quercus* species studied (mean values and standard errors). The species are arranged in decreasing order according to their mean value of each variable. The horizontal lines indicate the mean value of each parameter for all the studied individuals. Abbreviations as in Table 1 and Fig. 2 and colors as in Fig. 2

range of leaf-area but a narrow range of *LMA* values. The nemoro-Mediterranean species showed intermediate values of both variables, but these were always closer to those shown by the nemoral oaks. Considering mean species values, the relationship between sclerophylly and mean leaf area was significantly negative ($r = -0.67$; $P = 0.003$; Fig. 2A). Thus, the typically Mediterranean species constitute a group morphologically different from the nemoral and nemoro-Mediterranean species, as regards their leaf features (Fig. 2B).

Significant differences between species were found for *LMA*, leaf area, and the parameters derived from the *P*–*V* curves (ANOVA, *F* ratio=3.03–24.14, $P \leq 0.001$, $n = 92$).

Table 1 Correlation values (Pearson's r) of different parameters derived from the pressure-volume curves considering all individuals studied ($n=92$). Probability values are shown in parenthesis (values in bold: $P \leq 0.05$). Abbreviations of the $P-V$ curve parameters: maximum bulk modulus of elasticity (ϵ_{\max}), osmotic potential

	ϵ_{\max}	π_o	ψ_{tlp}	RWC_{tlp}	S
π_o	0.60 (0.001)				
ψ_{tlp}	0.37 (0.001)	0.84 (0.001)			
RWC_{tlp}	0.03 (0.78)	-0.28 (0.009)	-0.60 (0.001)		
S	0.48 (0.001)	0.34 (0.002)	0.16 (0.131)	-0.18 (0.098)	
S_{tlp}	-0.39 (0.001)	-0.15 (0.162)	0.32 (0.003)	-0.54 (0.001)	-0.39 (0.001)

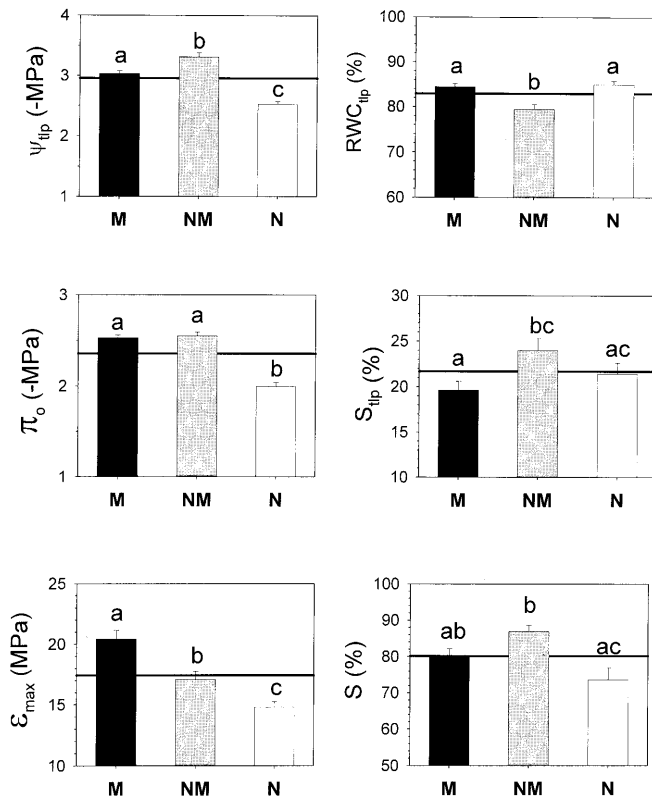


Fig. 4 Parameters derived from the pressure-volume curves for the *Quercus* species studied (mean values and standard errors) according to the phytoclimate of each species. The horizontal lines indicate the mean value for all the individuals studied. Different letters refer to significant differences between groups ($P \leq 0.05$; Tukey HSD test). Abbreviations as in Table 1 and colors as in Fig. 2

The nemoral oak species showed the lowest ϵ_{\max} values as well as the highest π_o and ψ_{tlp} values (Figs. 3, 4). The Mediterranean and nemoro-Mediterranean species showed the reverse trend. These differences were significant between phytoclimatic species groups for ϵ_{\max} and ψ_{tlp} (Tukey HSD test, $P \leq 0.05$; Fig. 4). From their ϵ_{\max} values, the oak species studied could be arranged from Mediterranean to nemoro-Mediterranean and to nemoral. The lowest mean ψ_{tlp} values were found in the nemoro-Mediterranean species. The rest of parameters, which were mostly related to the relative symplastic water content (RWC_{tlp} , S_{tlp} , S), showed no evident trend.

at full turgor (π_o), leaf water potential at the turgor-loss point (ψ_{tlp}), relative water content at the turgor-loss point (RWC_{tlp}), relative symplastic water content (S), and relative symplastic water loss at the turgor-loss point (S_{tlp})

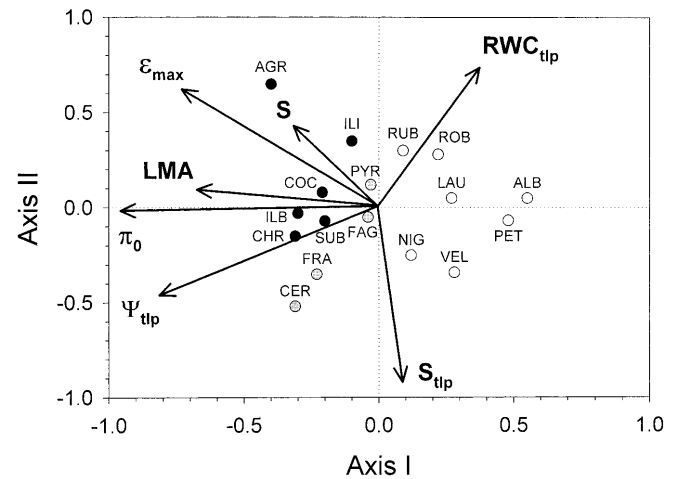


Fig. 5 Principal component analysis (PCA) for several *Quercus* species according to their leaf dry mass per unit area (LMA; mean value per species) and the parameters derived from pressure-volume curves ($P-V$ curves). For visual clarity, only the vectors for LMA and $P-V$ curves parameters are displayed. The two first axes of the ordination are presented (I, horizontal; II, vertical). Abbreviations as in Table 1 and Fig. 2 and colors as in Fig. 2

In the oak species studied, high cell-wall rigidity was associated with low π_o , low ψ_{tlp} , and high S . However, it was associated with low S_{tlp} (Table 1). Considering the mean species values of the parameters derived from the $P-V$ curves, the first component of the PCA (axis I) explained 42.7% of the total amount of variation, while the second component (axis II) explained 29.1% (Fig. 5). Axis I was related negatively to π_o , ψ_{tlp} , ϵ_{\max} , and LMA. Axis II was also related negatively to S_{tlp} , but positively to RWC_{tlp} . In the PCA, there was a neat separation between nemoral oaks and the rest of species (Mediterranean and nemoro-Mediterranean; Fig. 5).

Discussion

In this investigation, we grouped the *Quercus* species a priori, according to their phytoclimatic distribution (Mediterranean, nemoro-Mediterranean and nemoral). We were interested in determining if this biogeographical distribution was related to a functional grouping. As regards leaf features (leaf area and leaf mass area) two

evident sets of species were found (Fig. 2A). The Mediterranean oak species could be characterized by their small leaves and high LMA. Conversely, the nemoral and nemoro-Mediterranean oaks showed bigger leaves and relatively low LMA values.

However, the analysis of some parameters derived from the P - V curves suggested that the studied *Quercus* species constituted three distinct functional groups. The Mediterranean oak species were characterized by higher ϵ_{\max} values, and lower ψ_{tip} values (Figs. 3, 4). The nemoral oak species showed the reverse trend. These relationships have also been reported previously (Sobrado 1986; Dreyer et al. 1990; Eamus and Narayan 1990; Wan et al. 1993; Richards and Lamont 1996; Zobel 1996; Groom and Lamont 1997; Hietz and Briones 1998; Zhang et al. 1998; Fernández et al. 1999). Furthermore, the ordination produced by the PCA was coherent with the phytoclimatic classification of the oak species (Fig. 5). In addition, when specifically considering the ϵ_{\max} or ψ_{tip} values (Fig. 4), a third intermediate group appeared, comprising the nemoro-Mediterranean oak species (*Q. cerris*, *Q. faginea*, *Q. frainetto*, and *Q. pyrenaica*). Nevertheless, parameters related to the cellular water content did not distinguish the phytoclimatic oak groups, which is in agreement with the results reported by Sobrado (1986). The latter variables must be interpreted with caution because the use of P - V curves to estimate them might not be very accurate. For instance, values of these variables greater than 100% have been reported in leaves (Richter et al. 1980) and defoliated twigs (Neufeld and Teskey 1986).

In the case of the Mediterranean oaks, a low cell-wall elasticity would allow a rapid recovery after a decrease in soil water content; this could be regarded as an efficient mechanism to overcome water stress. This implies a decrease in the turgor and water potential with a small decrease in plant water content (Patakas and Noitsakis 1997). The latter does not bear a high degree of energy loss, which is important in plants growing on soil poor in organic matter (Lo Gullo et al. 1986). Both environmental conditions, of soils poor in water resources and organic matter, are found in Mediterranean-region forests. The water-potential gradient created in these environments would allow some water uptake from dry soil and thus a minor decrease in the relative cellular water content (Cheung et al. 1975; Salleo and Lo Gullo 1985; Lo Gullo et al. 1986; Lo Gullo and Salleo 1988; Abrams et al. 1990; Abrams and Menges 1992).

The causal relationship between a high modulus of elasticity and LMA is still unclear (Lo Gullo and Salleo 1988; Salleo and Lo Gullo 1990; Nardini et al. 1996; Salleo et al. 1997). Specifically, a positive correlation between them has also been reported in several *Quercus* species (Salleo and Lo Gullo 1990). Nevertheless, LMA and elasticity modulus are not related to the same environmental phenomenon qualitatively or quantitatively. The LMA values depend on the amount of mechanical tissue (mainly lignin), while the elasticity modulus is more closely related to cell-wall thickness and cell cellu-

lose content. Therefore, their association cannot be regarded as a functional relationship.

The Mediterranean evergreen *Quercus* species studied showed low osmotic potential. Similar results were reported by Calkin and Percy (1984) and Roberts et al. (1980). Low osmotic potential permits the development of positive turgor at low water potential, allowing cellular stretching under conditions of water stress (Cheung et al. 1975; Tyree 1976; Morgan 1984). This would allow plants to tolerate greater water stress, reaching lower leaf water potential (Ranney and Skroch 1991). In general, more negative osmotic potential is found in oak species growing in more arid regions (Parker et al. 1982; Bahari et al. 1985; Abrams and Knapp 1986). Overall, our results are in agreement with those findings. Thus, the decrease in osmotic potential at the turgor-loss point would be a characteristic trait in *Quercus* species adapted to climates with water-stress periods.

Under water stress, the elastic cell walls of the deciduous oaks experience a greater water loss in leaves than those of the evergreens. If the closure of stomata is activated by the loss of cellular turgor, the greater the elasticity modulus of the cell wall the quicker the closure of stomata, and therefore, the greater the symplastic cell water content. This is confirmed by our results which show that a higher cell-wall rigidity is associated with a lower S_{tip} , and with a higher S value (Table 1, Fig. 5). A positive relationship between cell-wall rigidity and S value has also been found by other authors (Cutler et al. 1977; Düring 1986; Rascio et al. 1988; Kubiske and Abrams 1991; Wan et al. 1993; Fan et al. 1994). The capacity to maintain an adequate amount of water in the cell at low water potential could be an adaptive characteristic in species which experience moderate water stress (e.g. nemoral oaks). A high degree of cell-wall elasticity would therefore permit positive turgor pressure in the cells.

The set of traits found in the Mediterranean evergreen oaks has been regarded as characteristic of plant species adapted to high water stress (Turner 1994). These species, as compared to the deciduous ones, are able to develop a higher turgor pressure, as water potential decreases, and to lose turgor at lower leaf water potential. This would be related to species showing a *water-saver* strategy (sensu Levitt 1980). Nemoral deciduous species would tend to maintain turgor pressure at the expense of more water being lost at the turgor-loss point (Jane and Green 1983; Wan et al. 1998). The nemoro-Mediterranean oaks showed more elastic cell walls than the Mediterranean species, but similar π_0 and lower ψ_{tip} values than the nemoral ones. This allows them to perform better than nemoral oaks under water-stress conditions such as those experienced during Mediterranean summers. However, the nemoro-Mediterranean oaks cannot grow as well as Mediterranean oaks on relatively dry soils because they are unable to create high water-potential gradients in the soil-plant-atmosphere continuum. Thus, they constitute a coherent ecophysiological group in itself, according to certain parameters derived from the P - V curves (e.g. ϵ_{\max}).

In summary, we have established three consistent functional groups of oaks according to their leaf features and some of the parameters derived from the pressure-volume curves. This grouping agrees well with the phytoclimatic situation of these species. The oaks studied could be arranged according to their phytoclimate by their ϵ_{\max} and ψ_{tip} values. This study confirms that the nemoro-Mediterranean oaks occupy an intermediate niche between nemoral and Mediterranean oaks, according to their tissue water relations, as previously suggested by phytoclimatologists (Allué-Andrade 1990).

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