Interspecific differences of leaf gas exchange and water relations of three evergreen Mediterranean shrub species

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Abstract

Leaf gas exchange and plant water relations of three co-occurring evergreen Mediterranean shrubs species, *Quercus ilex* L. and *Phillyrea latifolia* L. (typical evergreen sclerophyllous shrubs) and *Cistus incanus* L. (a drought semi-deciduous shrub), were investigated in order to evaluate possible differences in their adaptive strategies, in particular with respect to drought stress. *C. incanus* showed the highest annual rate of net photosynthetic rate (P_N) and stomatal conductance (g_s) decreasing by 67 and 69 %, respectively, in summer. *P. latifolia* and *Q. ilex* showed lower annual maximum P_N and g_s, although P_N was less lowered in summer (40 and 37 %, respectively). *P. latifolia* reached the lowest midday leaf water potential (Ψ_l) during the drought period (–3.54±0.36 MPa), 11 % lower than in *C. incanus* and 19 % lower than in *Q. ilex*. Leaf relative water content (RWC) showed the same trend as Ψ_l. *C. incanus* showed the lowest RWC values during the drought period (60 %) while they were never below 76 % in *P. latifolia* and *Q. ilex*; moreover *C. incanus* showed the lowest recovery of Ψ_l at sunset. Hence the studied species are well adapted to the prevailing environment in Mediterranean climate areas, but they show different adaptive strategies that may be useful for their co-occurrence in the same habitat. However, *Q. ilex* and *P. latifolia* by their water use strategy seem to be less sensitive to drought stress than *C. incanus*.

Additional key words: adaptive strategies; *Cistus incanus*; leaf water potential; net photosynthetic rate; *Phillyrea latifolia*; *Quercus ilex*; relative water content; stomatal conductance; water stress.

Introduction

Since under Mediterranean climate plant species are subjected to prolonged periods of drought, characterised by high air temperatures, high irradiance, and high vapour pressure deficit, Mediterranean plant species have developed both morphological and physiological adaptations to water stress (Dickson and Tomlinson 1996). Nevertheless, the degree of adaptation to drought may vary considerably within species (Torrecillas *et al.* 1996). Morphological adaptations involve leaf protective structures (*i.e.* hairs, thick cuticle, sclerenchymatic cells), steep leaf inclination, high leaf thickness, and reduced leaf surface area (Castro-Díez *et al.* 1998, Karabourniotis 1998, Gratani and Bombelli 2000). All these features improve plant drought resistance decreasing photochemical damages of the photosynthetic system and reducing transpiration rates (E) by lowering leaf temperature (T_l) under water stress (Kao and Forseth 1992, Werner *et al.* 1999). Physiological adaptations involve regulation of plant water status by stomatal control of leaf gas exchange (Faria *et al.* 1998, Jones 1998, Tognetti *et al.* 2000) and osmotic adjustment (Richter and Kikuta 1989, Scotti Campos *et al.* 1999, Sánchez-Blanco *et al.* 2002).

Performance under stress cannot be predicted from performance in non-stress conditions (Ivandic *et al.* 2000): as drought stress increases, stomatal conductance (g_s), net photosynthetic rate (P_N), leaf water potential (Ψ_l), and relative water content (RWC) decrease markedly (Grammatikopoulos 1999, Ashraf *et al.* 2001, Leidi 2002) and biochemical limitations of carbon gain appear (Angelopoulos *et al.* 1996, Tezara *et al.* 1999, Castillo *et al.* 2002).

Leaf water relations data may provide a useful indication of the capacity of species to maintain growth, gas exchange, and water use during summer drought (White *et al.* 2000). Knowledge of eco-physiological responses to water stress of different species could contribute to

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Abbreviations: E = leaf transpiration rate; g_s = stomatal leaf conductance to water vapour diffusion; PAR = photosynthetically active radiation; P_N = net photosynthetic rate; RWC = relative water content; T_l = leaf temperature; VPD = leaf to air vapour pressure deficit; WUE = instantaneous water use efficiency; Ψ_l = leaf water potential; Ψ_m = minimum leaf water potential; Ψ_{pd} = predawn leaf water potential; Ψ_s = sunset leaf water potential.

better management of natural ecosystems especially in Mediterranean region where drought is an actual problem. In this context, the aim of this study was to analyse leaf gas exchange and plant water relations of three evergreen Mediterranean shrub species: *Quercus ilex, Phillyrea latifolia*, and *Cistus incanus* to test the following hypotheses: (*1*) In different environmental conditions interspecific differences in leaf traits may change during the year; (*2*) species co-occurrence in the same habitat is possible by different adaptive strategies reducing the use of limiting resources, particularly water, during summer drought. The choice of plant species was based on differences in morphological and physiological traits of *Q. ilex* and *P. latifolia* (typical evergreen sclerophyllous shrub species) and *C. incanus* (a drought semi-deciduous shrub species).

Materials and methods

Study area and climate: The study was conducted in the Mediterranean maquis developing along the coast near Rome, in the Castelporziano Estate (41°45'N; 12°26'E). The area's climate was of Mediterranean type. Most (67 %) of its annual rainfall (726 mm) was distributed in autumn-winter (Table 1). Dry period was from mid-May to the end of August (11 % of total annual rainfall); air humidity reached the minimum value in July (67.5 %) (data by the Castelporziano Meteorological Station, 1987-1999, Table 1). Soil water content (percentage ratio of water mass per dry soil mass) was in the range 0.5–8.0 % during the year, the minimum occurring in August and the maximum in December (Gratani 1994).

Table 1. Monthly average minimum air temperature (T_{min}), monthly average maximum air temperature (T_{max}), monthly average air temperature (T_{m}), monthly average air humidity (H), and total monthly rainfall (R) for the period 1987-1999 and for the study period (1999). Data of the Meteorological Station of Castelporziano, Rome.

	Average 1987-1999					Study period (1999)				
	T_{min} [°C]	T_{max} [°C]	T_{m} [°C]	H [%]	R [mm]	T_{min} [°C]	T_{max} [°C]	T_{m} [°C]	H [%]	R [mm]
Jan	4.4	13.6	9.0	78.9	51	3.8	13.7	8.8	78.5	33
Feb	3.9	13.9	8.9	77.3	49	1.6	11.8	6.7	78.8	30
Mar	5.8	15.8	10.8	72.4	44	6.0	14.9	10.5	79.0	56
Apr	8.0	17.8	12.9	76.5	78	9.0	18.3	13.7	81.6	64
May	11.8	22.3	17.1	73.0	33	13.5	23.6	18.6	81.8	23
Jun	14.7	26.3	20.5	71.0	35	15.4	27.6	21.5	69.9	21
Jul	17.7	30.0	23.8	67.5	12	17.8	29.8	23.8	76.4	8
Aug	18.5	30.8	24.7	68.6	19	19.3	31.0	25.2	69.1	17
Sep	15.7	26.9	21.3	76.1	62	17.0	27.2	22.1	75.5	121
Oct	12.8	22.6	17.7	78.7	145	13.0	23.0	18.0	84.8	77
Nov	8.4	17.1	12.7	80.3	111	8.0	17.2	12.6	81.5	178
Dec	5.4	13.6	9.5	79.5	87	5.3	13.3	9.3	81.6	90

Plants: All measurements were made on fully expanded leaves selected from the external portion of the crown of *Cistus incanus* L., *Phillyrea latifolia* L., and *Quercus ilex* L. shrubs (ten per species), representative of the population. Field measurements were made during the year 1999 on four sunny clear days, representative of the different seasons according to Infante *et al.* (1999): 21 January 1999 (winter), 19 April 1999 (spring), 21 July 1999 (summer), and 15 October 1999 (autumn).

Leaf gas exchange: Field measurements of leaf gas exchange were carried out during the day on twenty leaves of the selected species. Leaves were retained in their natural orientation during measurements. PAR [µmol(photon) m^{-2} s^{-1}], P_{N} [µmol(CO$_2$) m^{-2} s^{-1}], T_{l} [°C], g_{s} [mmol(H$_2$O) m^{-2} s^{-1}], and E [mmol(H$_2$O) m^{-2} s^{-1}] were monitored by an infrared gas analyser *Ciras-1* open system (*PP Systems*, Hitchin, UK), equipped with a 2.5 cm^2 leaf chamber (*Ciras-1* Parkinson Leaf Cuvettes, Hitchin, UK). Instantaneous water use efficiency, WUE [mmol(CO$_2$) mol^{-1}(H$_2$O)] was calculated as the ratio of the measured P_{N} and E (Wuenscher and Kozlowski 1971). Leaf to air vapour pressure deficit (VPD) was calculated by VPD = $e_s - e_a$, where e_s was saturated vapour pressure at leaf temperature and e_a the air vapour pressure (Grantz 1990).

Water relations: The diurnal courses of Ψ_{l} [MPa] and RWC [%] were measured simultaneously at gas exchange measurements. Ψ_{l} was measured from predawn (Ψ_{pd}) to sunset (Ψ_{s}) on 10 fully expanded leaves per species, using a portable pressure chamber (*SKPM 1400*, *Skye Instruments*, Llandrindod Wells, UK) with a sheet of wet filter paper inside the chamber to avoid water loss during measurements (Lo Gullo and Salleo 1988). The minimum diurnal leaf water potential (Ψ_{m}, at midday) was monitored, and the afternoon recovery of leaf water potential ($\Delta\Psi_R$) was calculated as $\Delta\Psi_R = \Psi_s - \Psi_{pd}$.

The leaf relative water content (RWC) was calculated as 100 (fresh mass – dry mass)/(water saturated mass – dry mass) (Grammatikopoulos 1999).

Statistics: All statistical tests were performed using a statistical software package (*Statistica*, Statsoft, OK, USA). Significant differences among means of the measured leaf traits were determined by analysis of variance (ANOVA) and Tukey test for multiple comparisons. Correlation coefficients were calculated to examine relationships among the measured traits.

Results

Leaf gas exchange: The highest P_N and g_s of the considered species were found in spring and autumn, decreasing during the drought period (Fig. 1). *C. incanus* showed the highest (p<0.01) annual P_N [21.8±1.8 μmol(CO_2) m^{-2} s^{-1}] and g_s [322±28 mmol(H_2O) m^{-2} s^{-1}] values decreasing by 67 and 69 %, respectively, in summer. *P. latifolia* and *Q. ilex* showed lower annual maximum P_N [13.1±1.1 and 15.2±0.6 μmol(CO_2) m^{-2} s^{-1}, respectively] and g_s [184±13 and 189±16 mmol(H_2O) m^{-2} s^{-1}, respectively], although P_N was less lowered in summer (40 and 37 %, respectively).

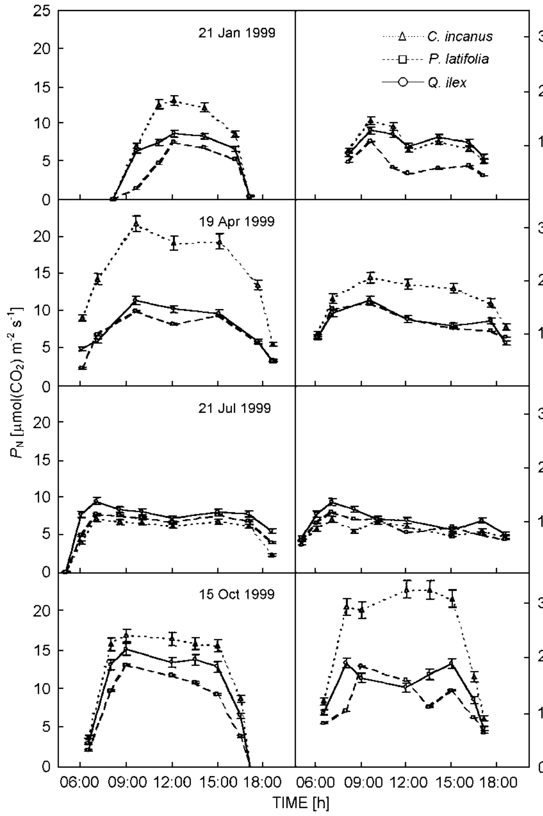

Fig. 1. Diurnal time-course of net photosynthetic rate (P_N) and stomatal leaf conductance to water vapour diffusion (g_s) of *C. incanus*, *P. latifolia,* and *Q. ilex,* on 21 January 1999, 19 April 1999, 21 July 1999, and 15 October 1999. Means±SE.

C. incanus showed the highest WUE (p < 0.01) in winter and spring for most of the day (Fig. 2). During drought, the combined effects of decreased P_N and increased E resulted in a reduced WUE [3.0±0.3, 4.1±0.5, and 4.8±0.4 μmol(CO_2) $mmol^{-1}$(H_2O) in *C. incanus*, *P. latifolia,* and *Q. ilex*, respectively], *C. incanus* showing the highest reduction (61 %) and *Q. ilex* the lowest one (29 %) (p < 0.01).

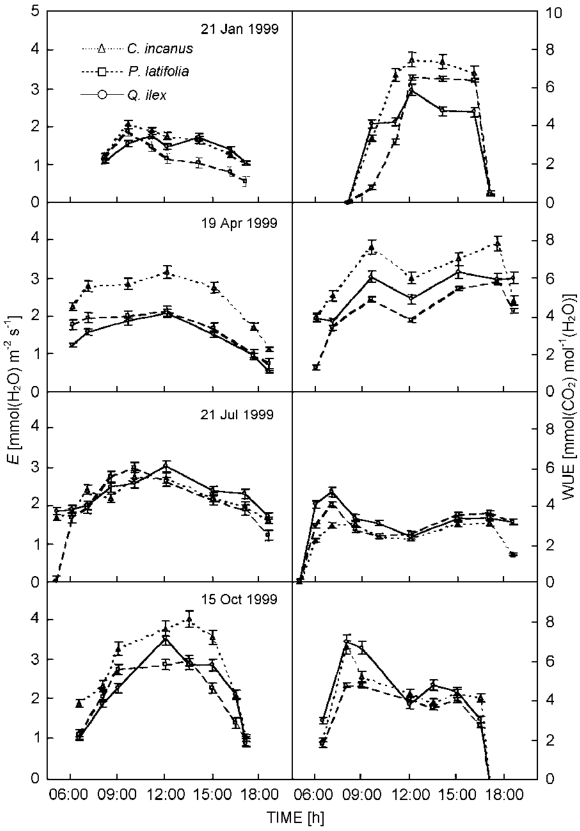

Fig. 2. Diurnal time-course of leaf transpiration rate (E) and water use efficiency (WUE) of *C. incanus*, *P. latifolia,* and *Q. ilex,* on 21 January 1999, 19 April 1999, 21 July 1999, and 15 October 1999. Means±SE.

The shape of the daily gas exchange pattern depended on the traits plotted and the degree of the drought stress. Bell-shaped daily curves of P_N were found for *C. incanus*, *P. latifolia*, and *Q. ilex* in winter, spring, and autumn, while in summer they were nearly flat with a slight maximum at early morning [7.2±1.0, 7.8±0.9, and 9.5±0.8 μmol(CO_2) m^{-2} s^{-1} in *C. incanus*, *P. latifolia,* and *Q. ilex*, respectively], a depression at midday [6.3±0.9, 6.8±1.2, and 7.3±1.1 μmol(CO_2) m^{-2} s^{-1} in *C. incanus*, *P. latifolia*, and *Q. ilex*, respectively], and a small but significant ($p<0.05$) recovery during the afternoon (6.9±0.6, 7.7±0.8, and 8.1±0.6 μmol(CO_2) m^{-2} s^{-1} in *C. incanus*, *P. latifolia*, and *Q. ilex*, respectively). Under water stress, *P. latifolia* and *Q. ilex* maintained relatively high P_N with respect to the annual maximum (60 and 62 %, respectively) just early in the morning, when T_l and VPD were relatively low (Fig. 3) and irradiance was saturating [PAR > 1 000 μmol(photon) m^{-2} s^{-1}].

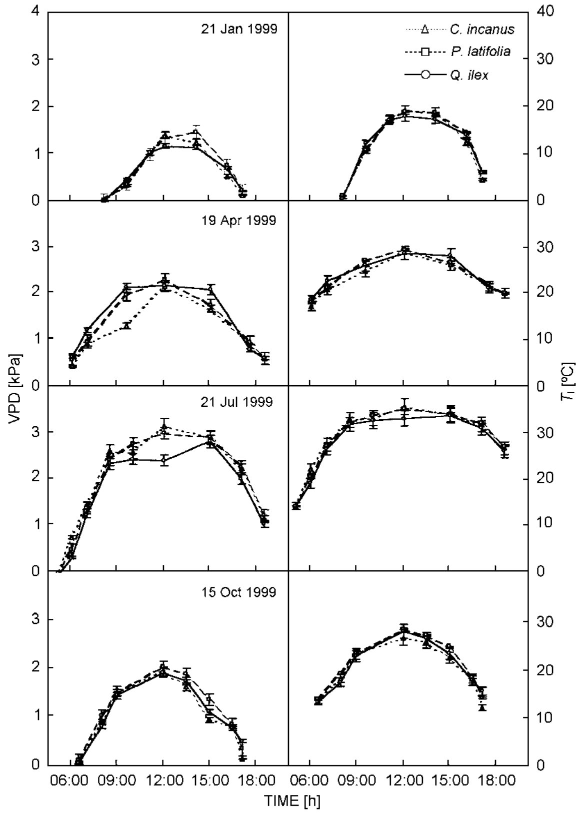

Fig. 3. Diurnal time-course of leaf to air vapour pressure deficit (VPD) and leaf temperature (T_l) of *C. incanus*, *P. latifolia*, and *Q. ilex*, on 21 January 1999, 19 April 1999, 21 July 1999, and 15 October 1999. Means±SE.

Daily pattern of g_s generally showed two peaks (one in the morning and another in the afternoon separated by a slight depression at midday) flattening out as drought stress increased. In summer, g_s was relatively high only at early morning [101±8, 114±11, and 133±16 mmol(H_2O) m^{-2} s^{-1} in *C. incanus*, *P. latifolia,* and *Q. ilex*, respectively] decreasing gradually during the day in *C. incanus* and *P. latifolia*, while *Q. ilex* showed a lower maximum in the afternoon.

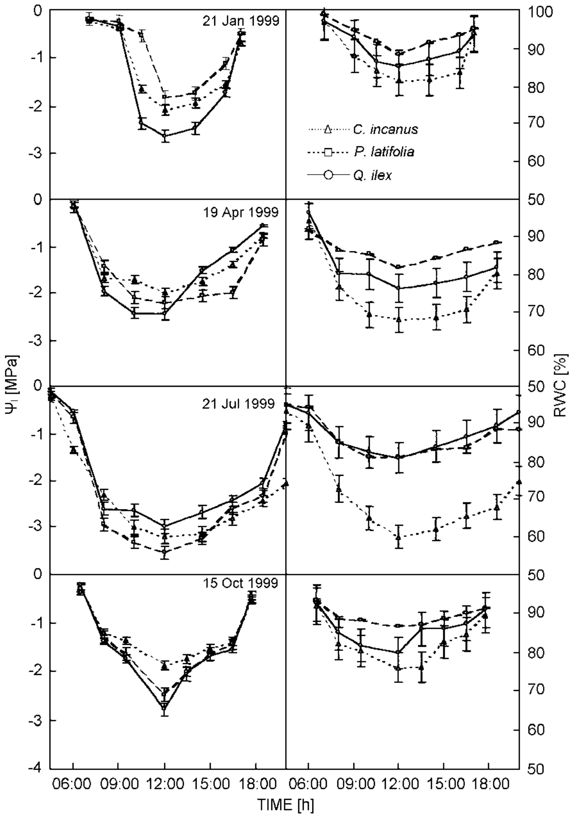

Fig. 4. Diurnal time-course of leaf water potential (Ψ_l) and relative water content (RWC) of *C. incanus*, *P. latifolia,* and *Q. ilex,* on 21 January 1999, 19 April 1999, 21 July 1999, and 15 October 1999. Means±SE.

Table 2. Summary of correlations among the analysed leaf traits: stomatal leaf conductance to water vapour diffusion (g_s), net photosynthetic rate (P_N), leaf relative water content (RWC), leaf to air vapour pressure deficit (VPD), leaf water potential (Ψ_l). Correlation coefficients are significant at $p<0.05$ (*), $p<0.01$ (**), and $p<0.001$ (***); NS = not significant (all values for *P. latifolia*). $n = 30$.

y – x	*C. incanus*	*Q. ilex*
g_s – VPD	-0.48^{**}	-0.52^{**}
g_s – RWC	0.49^{**}	NS
g_s – Ψ_l	0.70^{***}	NS
P_N – VPD	-0.56^{**}	NS
P_N – RWC	0.43^{*}	NS
P_N – Ψ_l	0.79^{***}	NS

Water relations: In the considered species, Ψ_l and RWC changed both on a diurnal and on a seasonal time-scale (Fig. 4), decreasing during the warmest hours of the day and during the drought period. There were considerable differences among the species. The diurnal maximum Ψ_l was always recorded at predawn, when values were higher than –0.4 MPa. The lowest leaf water potential (Ψ_m) values were reached at midday when VPD reached the highest values. At sunset Ψ_l recovered to near predawn values, except in summer, when it recovered only partially and *C. incanus* showed a $\Delta\Psi_R$ of –1.82 MPa (the lowest recovery) and *Q.* ilex of –0.69 MPa (the highest recovery). Nevertheless, a complete recovery was reached during the night for the three species. In winter, spring, and autumn *Q. ilex* showed a lower Ψ_m (on an average –2.62±0.17 MPa) than the other two species ($p<0.05$). The lowest Ψ_m ($p<0.05$) was reached by *P. latifolia* in summer (–3.54±0.36 MPa), being 11 % lower than in *C. incanus* and 19 % lower than in *Q. ilex*. In this time VPD reached the highest annual values (3.1±0.5, 3.0±0.4, and 2.4±0.2 kPa in *C. incanus*, *P. latifolia,* and *Q. ilex*, respectively).

RWC showed the same trend as Ψ_l: higher values were monitored at predawn (over 90 %), decreasing at midday when Ψ_l reached the lowest values. *C. incanus* had the greatest RWC decrease (31 %) during drought, twice as large as in *P. latifolia* and *Q. ilex* ($p<0.01$). The diurnal RWC was never below 74 % in *P. latifolia* and *Q. ilex*, while in *C. incanus* (which showed the lowest values) it reached 65 % in summer.

Statistics: The result of correlation analysis is showed on Table 2. In different species leaf variables did not correlate in the same way: in *C. incanus* g_s and P_N significantly correlated with VPD, Ψ_l, and RWC; in *Q. ilex* g_s and P_N significantly correlated with VPD; in *P. latifolia* g_s and P_N did not correlate with VPD, Ψ_l, and RWC.

Discussion

Although evergreen shrub species growing in the Mediterranean climate show similar basic leaf structure and photosynthetic activity (Kummerow 1973, Mitrakos and Christodoulakis 1981, Tenhunen *et al.* 1987, Gratani and Bombelli 2000, Flexas *et al.* 2001), there are significant intra- and inter-specific variations in the measured leaf traits for the considered Mediterranean species, resulting in different adaptive strategies.

C. incanus was characterised by a maximum P_N, 43 % higher than in *Q. ilex* and 66 % higher than in *P. latifolia,* and by g_s being 70 % higher than in *Q. ilex* and 75 % than in *P. latifolia*. During the drought period it showed the highest g_s decrease causing the highest P_N decrease (67 %). In spite of its low g_s, *C. incanus* showed the highest *E*, the lowest RWC, and the lowest afternoon recovery of Ψ_l, due to the lack of protective structure (Gratani and Bombelli 1999, 2000). Leaf gas exchange of *C. incanus* seems to be more dependent on drought stress than the other considered species (g_s significantly correlated with Ψ_l, RWC, and VPD). For these reasons *C. incanus* may be considered a drought avoiding species (according to Sánchez-Blanco *et al.* 2002, for *Cistus* spp.), trying to conserve water by progressive stomatal closure with decreasing Ψ_l and by the high reduction of leaf evaporative surface (leaf drop and smaller summer leaves – Gratani and Bombelli 2000).

Q. ilex maintains relatively high g_s and P_N even at low Ψ_l (according to Tenhunen *et al.* 1985 and Acherar and Rambal 1992): leaf gas exchange does not significantly correlate with Ψ_l and RWC. Although *Q. ilex* showed the highest g_s with respect to *C. incanus* and *P. latifolia* in July, the RWC values were the highest, showing a rapid recovery of Ψ_l at sunset. This suggests that *Q. ilex* can recover at least partly from water loss (according to the results of Salleo and Lo Gullo 1990), maintaining a favourable ratio between water loss and uptake during the drought period and resulting in a relatively constant RWC. The responsive stomatal behaviour (g_s significantly correlated with VPD) of *Q. ilex* in addition to the leaf protective structure (Gratani and Bombelli 1999, 2000) allows a fine regulation of *E* and high P_N in each moment of the day and during the year. This behaviour seems to optimise daily WUE in a fluctuating microclimate (Acherar and Rambal 1992). These results confirm that *Q. ilex* is a drought avoiding species with a water spending or water saving strategy (Lo Gullo and Salleo 1988) according to circumstances, resulting in a regulator species (Rambal 1992).

P. latifolia undergoes a much higher Ψ_l drop in July than *C. incanus* and *Q. ilex*, but shows a rapid recovery at sunset. The rapid drop of Ψ_l as soon as the leaves begin to lose water in the early hours of the day is probably allowed by the high bulk modulus of elasticity (*i.e.* the high "rigidity" of the living cell walls) (Nardini *et al.* 1999). *P. latifolia* shows the lowest P_N and the lowest stomatal control in respect to *C. incanus* and *Q. ilex* (g_s is not correlated with VPD), determining the lowest WUE; the relative inability to control water loss by their stomata is confirmed by the larger daily and annual variations in Ψ_l (according to Miller *et al.* 1993 for *Juniperus occidentalis*). Nevertheless, leaf gas exchange is independent from Ψ_l (Ψ_l is not correlated with P_N and g_s): P_N remains rather high even at low Ψ_l. These physiological features in addition to the high presence of leaf protective structures (Gratani and Bombelli 1999, 2000) allow *P. latifolia* to tolerate the lowest Ψ_l, suggesting a drought tolerance strategy.

These results suggest that *Q. ilex* and *P. latifolia*, by their water use strategy, are less sensitive to drought stress in respect to *C. incanus* and might be at a competitive advantage considering a drought stress increase in the Mediterranean Basin. Our study indicates that the considered species are well adapted to the prevailing environment in Mediterranean climate areas, but show different adaptive strategies. These might be useful for their co-occurrences in the same habitat: in Mediterranean ecosystems, during drought period, complementary water use strategies may minimise plant competition, optimising productivity of the stand.

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