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Leaf anatomy, inclination, and gas exchange relationships in evergreen sclerophyllous and drought semideciduous shrub species

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Abstract

There are significant differences in leaf life-span among evergreen sclerophyllous species and drought semideciduous species growing in the Mediterranean maquis. *Cistus incanus*, which has a leaf life-span of four-eight months, was characterised by the highest net photosynthetic rates (P_N), while *Quercus ilex* and *Phillyrea latifolia*, which maintain their leaves two-three and two-four years, respectively, had a lower P_N. The longer leaf life-span of the two evergreen sclerophyllous species may be justified to cover the high production costs of leaf protective structures such as cuticle, hairs, and sclereids: cuticle and hairs screen radiation penetrating into the more sensitive tissues, and sclereids have a light-guiding function. *Q. ilex* and *P. latifolia* have the highest leaf mass/area ratio (LMA = 209 g m^{-2}) and a mesophyll leaf density (2065 cells per mm^2 of leaf cross section area) about two times higher than *C. incanus*. In the typical evergreen sclerophyllous species the steepest leaf inclination ($\alpha = 56°$) reduces 42 % of radiation absorption, resulting in a reduced physiological stress at leaf level, particularly in summer. *C. incanus*, because of its low leaf life-span, requires a lower leaf investment in leaf protective structures. It exhibits a drastic reduction of winter leaves just before summer drought, replacing them with smaller folded leaves. The lower leaf inclination ($\alpha = 44°$) and the lower LMA (119 g m^{-2}) of *C. incanus* complement photosynthetic performance. Water use efficiency (WUE) showed the same trend in *Q. ilex*, *P. latifolia*, and *C. incanus*, decreasing 60 % from spring to summer, due to the combined effects of decreased CO_2 uptake and increased transpirational water loss.

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Abbreviations: E, transpiration rate; g_s, stomatal conductance; LMA, leaf mass/area ratio; P_N, net photosynthetic rate; PAR, photosynthetically active radiation; RI, reduction of PAR incident on a sloping leaf surface; T_l, leaf temperature; WUE, water use efficiency; α, leaf inclination; η_l, leaf azimuth.

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Additional key words: *Cistus incanus*; leaf inclination; leaf life-span; leaf mass/area ratio; leaf thickness; net photosynthetic rate; *Phillyrea latifolia*; *Quercus ilex*; transpiration rate.

Introduction

Leaf life-span is related in general sense to other leaf traits such as photosynthesis, nutrient content, leaf mass/area ratio (LMA), and relative growth rate (RGR) (Chabot and Hicks 1982, Mooney and Gulmon 1982, Reich *et al.* 1992, Karlsson 1994, Kikuzawa 1995). In temperate regions, evergreen sclerophyllous leaves with high LMA are usually characterised by a longer leaf life-span whereas leaves with a lower LMA have shorter longevity (Kikuzawa 1995).

Attainment of higher photosynthetic rates may conflict with leaf life-span (Chabot and Hicks 1982), since it is necessary to invest in protective structures (Kikuzawa 1995). Leaves of evergreen woody species are characterised by a continuous CO_2 assimilation during the year, decreasing in summer at increased total daily solar radiation and air temperature (Comstock and Mahall 1985, Gratani 1995, Larcher 1995). High leaf temperatures may be avoided by steeper leaf inclination which reduces the amount of incident photons absorbed by the leaf (Medina *et al.* 1978). An advantage of reduced solar energy absorption during summer would be the reduced heat load on the leaves which results in reduced transpirational water losses by lowering leaf temperature (Berg and Heuchelin 1990, Smith *et al.* 1998). Moreover, the reduced incident flux is not only more efficiently utilised, but the potential for photoinhibition, due to excess excitation energy, is also reduced (Powles and Björkman 1981, Ludlow and Björkman 1984, Werner *et al.* 1999).

The purpose of this study was to analyse the relationships among leaf inclination, leaf anatomy, and leaf gas exchange in *Quercus ilex* L., *Phillyrea latifolia* L. (typical evergreen sclerophyllous shrub species), and *Cistus incanus* L. (a drought semideciduous shrub species) growing in the Mediterranean maquis, and to define their adaptive strategies and the degree of leaf xeromorphism. In addition, we also considered water use efficiency (WUE) and how these species utilize carbon assimilation in relation to leaf life-span.

Materials and methods

Study area: The study was conducted in the Mediterranean maquis developing along the coast near Rome, in the Castelporziano Estate (41°45'N; 12°26'E). It is under Mediterranean climate, and most of its annual rainfall (727 mm) is distributed in autumn-winter (Table 1). The average minimum air temperature of the coldest month (February) was 4.1 °C and the average maximum air temperature of the hottest month (August) was 30.8 °C (values by the Castelporziano Meteorological Station, 1987-1998, Table 1). All measurements were made during the year 1998 on randomly chosen *Q. ilex* L., *P. latifolia* L., and *C. incanus* L. shrubs (three per species), representative of the population.

Table 1. Monthly average maximum (T_{max}) and minimum (T_{min}) air temperatures, monthly average air temperature (T_m) [°C], and total monthly rainfall (R) [mm] and humidity (H) [%] for the period 1987-1998 and the year 1998. Values of the Meteorological Station of Castelporziano, Rome.

	Average 1987-1988					Study period 1998				
	T_{max}	T_{min}	T_m	R	H	T_{max}	T_{min}	T_m	R	H
Jan	13.6	4.4	9.0	52.5	78.7	13.8	5.0	9.4	101.6	82.1
Feb	14.1	4.1	9.1	50.7	77.2	15.4	4.9	10.2	100.0	76.1
Mar	15.9	5.8	10.8	43.1	71.8	15.6	4.6	10.1	66.6	64.9
Apr	17.8	7.9	12.8	78.8	76.1	18.5	9.5	14.0	81.4	73.5
May	22.2	11.7	16.9	33.7	72.3	22.8	12.3	17.6	48.8	72.0
Jun	26.2	14.6	20.4	36.0	71.1	27.3	15.5	21.4	6.6	67.6
Jul	30.0	17.7	23.8	11.9	66.8	30.4	17.7	24.1	12.2	68.3
Aug	30.8	18.5	24.6	19.6	68.6	31.7	18.8	25.3	17.2	65.5
Sep	26.9	15.6	21.2	57.6	75.3	25.8	15.0	20.4	57.2	65.5
Oct	22.6	12.8	17.7	151.2	77.3	21.6	12.3	17.0	127.8	74.5
Nov	17.1	8.4	12.8	105,1	80.8	15.4	7.2	11.3	26.4	85.4
Dec	13.6	5.4	9.5	86.5	76.7	12.5	3.4	8.0	67.0	77.0

Leaf orientation and leaf inclination: Diurnal measurements of leaf orientation (or azimuth, η_l) and leaf inclination (α) (Nobel *et al.* 1993) were recorded in the morning, at midday, and in the afternoon (Prichard and Forseth 1988), in the coldest (February and March) and hottest (July and August) months of the year.

Randomly chosen sun leaves, representative of the population, were labelled and monitored on each sampling occasion (40 leaf samples). α and η_l were obtained by measuring the angle from the horizontal and azimuth (0° = N, 90° = E, 180° = S, 270° = W) of the adaxial leaf surface (Prichard and Forseth 1988). Measurements of α were made by a hand-held clinometer (*Suunto Co.* model *PM-5/360PC*, Finland). Azimuth was measured by a compass (*Suunto Co.* model *KB-14/360R*, Finland), according to Prichard and Forseth (1988). The repeatability of both measurements was ±5°. Leaf orientation modified the angle of incidence between the direct solar beam and the leaf lamina. *C. incanus* leaves were characteristically folded along the midrib. The degree of concavity was measured by a goniometer on prints of ink-dipped leaf cross-section (n = 120).

Leaf anatomy: Fresh leaf sections were hand-cut from leaves collected on 15 October 1998, dehydrated in 90 % ethanol, and analysed by light microscopy (Bolhàr-Nordenkampf and Draxler 1993). The following parameters were measured on 30 samples per species: lamina thickness, palisade and spongy layer thickness, adaxial and abaxial epidermis thickness, adaxial and abaxial cuticle thickness, number of palisade cell layers, and the length and diameter of palisade and spongy cells. Cell density was calculated as the cell number per unit leaf section area (number of cells per mm^2). The volume of leaf mesophyll intercellular spaces was calculated as a percentage of the total leaf volume (Bolhàr-Nordenkampf and Draxler 1993). All measurements were restricted to vein-free areas (Chabot and Chabot 1977). Light microscopy and image analysis system (*Lucia G Laboratory Imaging LW-LUG,* Czech Republic) were used to quantify the anatomical differences among leaf cross-sections.

Leaf morphology: Leaf samples (40 leaves per species) were collected on 15 October 1998: leaf area (excluding petiole) was determined on fresh leaves using the Image Analysis System (*Delta-T Devices*, UK). Leaf dry mass was determined by drying at 80 °C to constant mass. LMA was calculated as the ratio of leaf dry mass to unifacial leaf area (Reich *et al.* 1992). Leaf life-span was analysed *in situ* monitoring the number of nodes and leaf cohorts according to Reich *et al.* (1992), since flushing patterns were known (Gratani and Crescente 1997).

Leaf gas exchange: Field measurements were carried out on the external fully sun-exposed crown of the selected *Q. ilex*, *P. latifolia*, and *C. incanus* shrubs, representative of the population. All gas exchange measurements were taken per leaf from mid May (favourable climatic conditions) until late July (drought period) (Gratani 1995). On each sampling occasion, 15 to 25 leaves per shrub were utilised for measurements.

Photosynthetically active radiation, PAR [μmol(photon) m^{-2} s^{-1}], net CO_2 assimilation rates, P_N [μmol(CO_2) m^{-2} s^{-1}], leaf temperature, T_l [°C], stomatal conductance to water vapour diffusion, g_s [mmol(H_2O) m^{-2} s^{-1}], and transpiration rate, E [mmol(H_2O) m^{-2} s^{-1}] of sun leaves were monitored by an infrared gas analyser *Ciras-1* open system (*PP Systems*, UK), equipped with a 2.5 cm^2 leaf area chamber (*Ciras-1 Parkinson Leaf Cuvettes*, UK).

Gas exchange measurements were made *in situ* under natural conditions during morning on cloud-free days to ensure that near-maximum daily photosynthetic rates were measured, as suggested by Reich *et al.* (1991, 1995). Leaves were retained in their natural orientation during measurements. Gas exchange trends were drawn using daily averages. Instantaneous water use efficiency, WUE [μmol(CO_2) $mmol^{-1}$(H_2O)] was calculated as the ratio of the measured P_N and E (Wuenscher and Kozlowski 1971, Larcher 1995). The reduction of PAR incident on a sloping leaf surface (RI) was calculated as $RI = 100\ (1 - I_s/I_0)$, where I_0 was the fraction of PAR intercepted by a horizontal surface and I_s was the fraction of PAR incident on a sloping leaf surface (Ehleringer 1989).

Statistics: All statistical tests were performed using a statistical software package (*Statistica, Statsoft*, USA). The distributions of η_l and α were compared to a uniform distribution by χ^2 test. The differences of η_l and α during the day and between winter and summer were tested by one-way analysis of variance (ANOVA) and the Tukey test for multiple comparison. Differences in mean morphological and anatomical leaf traits were determined by *t*-test and by one-way ANOVA and Tukey test for multiple comparison.

Results

Leaf orientation and leaf inclination: Azimuth depended strictly on phyllotaxy: *C. incanus* and *P. latifolia* had opposite pattern of leaf attachment and *Q. ilex* a whorled pattern of leaf attachment. Opposite leaves of *C. incanus* and *P. latifolia* were situated at 90°, from one to another on the azimuthal projection, while *Q. ilex* leaves were situated at about 72°. η_l was random with respect to solar position, and there were no daily or seasonal changes (the deviation from randomness and the differences of means were not significant).

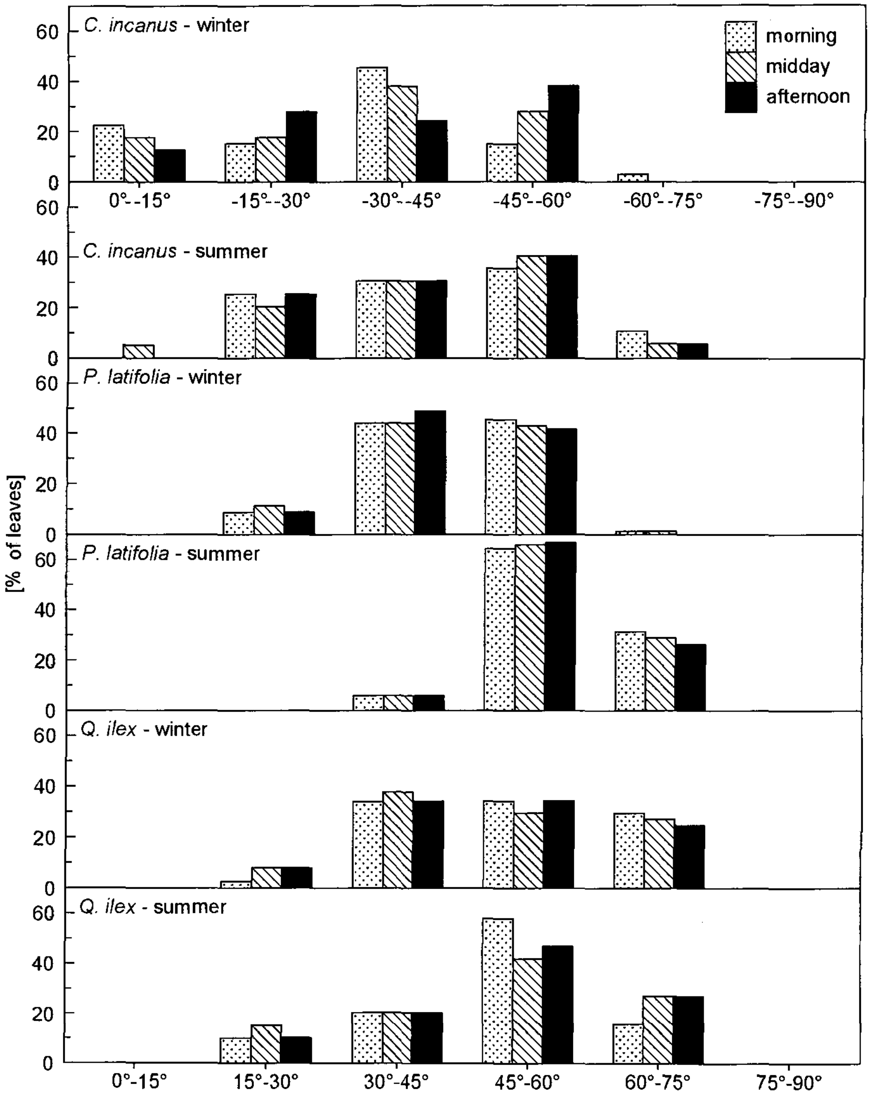

Fig. 1. Frequency histograms of *C. incanus*, *P. latifolia*, and *Q. ilex* leaf inclination (α) during three day times in winter and in summer. η_s = azimuth of sun. In winter: morning = 09:30 h (η_s = 26°), midday = 12:00 h (η_s = 37°), afternoon = 14:30 h (η_s = 28°). In summer: morning = 07:30 h (η_s = 30°), midday = 12:00 h (η_s = 72°), afternoon = 16:30 h (η_s = 35°). The increase of frequency of leaves in the steeper classes is evident from winter to summer, particularly for *P. latifolia*.

Table 2. Average *C. incanus*, *P. latifolia*, and *Q. ilex* leaf inclinations α [°] during morning, midday, and afternoon in winter and in summer. From winter to summer, leaf inclinations in *P. latifolia* significantly increased ($p<0.01$) and in *C. incanus* changed their values from negative to positive ($p<0.01$) . No significant change occurred during the day. Standard error is shown. In winter: morning = 09:30 h, midday = 12:00 h, afternoon = 14:30 h; in summer: morning = 07:30 h, midday = 12:00 h, afternoon = 16:30 h.

		Morning	Midday	Afternoon
C. incanus	winter	-35±12	-37±11	-39±12
	summer	44±13	45±13	44±13
P. latifolia	winter	46±8	45±8	45±7
	summer	59±7	59±7	58±7
Q. ilex	winter	52±11	51±11	51±11
	summer	52±13	52±13	52±13

C. incanus showed a seasonal trend of α: in winter α was negative (-37°±12°) and in summer positive (44°±13°) (the difference of means was significant, $p<0.01$) and it remained constant throughout the day (the difference of means was not significant) (Fig. 1, Table 2). *C. incanus* showed, moreover, a particular trend of leaf concavity: its leaves had a marginal leaf folding along the midrib axis, which was more pronounced in summer (76°±11°) than in winter (29°±9°) ($p<0.01$).

Table 3. Reduction of photosynthetically active radiation, PAR [μmol(photon) m^{-2} s^{-1}] incident on a sloping leaf surface (RI) [%]. I_0 = fraction of PAR intercepted by an horizontal plane, was always 1900±50. I_s = fraction of PAR incident on a sloping leaf. Standard error is shown.

	C. incanus	*P. latifolia*	*Q. ilex*
I_s	1291	999	1206
I_s/I_0	0.68	0.53	0.63
RI	32	47	37

P. latifolia showed a seasonal trend of α: in summer α was significantly steeper than in winter (59°±7° and 45°±8°, respectively; $p<0.01$), but in both seasons it remained constant throughout the day (the difference of means was not significant) (Fig. 1, Table 2). In winter 90 % of *P. latifolia* leaves were equally distributed in the 30°-60° α classes, while in summer 95 % of the leaves were in the 45°-75° α classes (Fig. 1). *Q. ilex* did not show a seasonal or a daily trend of α (the differences of means were not significant), nevertheless, in summer the leaf distribution was concentrated in the 45°-60° α classes (Fig. 1, Table 2). In summer, *P. latifolia* had the highest RI (47 %), due to its steeper α, while *C. incanus* had the lowest (RI = 32 %), due to its lower α (Table 3).

Table 4. Morphological and anatomical leaf traits of *C. incanus*, *P. latifolia*, and *Q. ilex*. Standard error is shown.

	C. incanus	*P. latifolia*	*Q. ilex*
Surface area per leaf [cm^2]	3.5±1.0	3.0±0.6	9.9±2.6
Dry mass per leaf [mg]	41±12	61±12	209±66
Leaf mass/area ratio [g m^{-2}]	11.9±1.7	20.9±2.5	20.9±1.7
Leaf lamina thickness [µm]	201.3±13.8	329.5±14.8	305.3±18.4
Adaxial cuticle [µm]	6.8±0.8	17.1±1.4	9.7±1.9
Adaxial epidermis [µm]	20.7±3.1	19.6±3.3	13.9±1.4
Palisade parenchyma thickness [µm]	86.8±8.7	136.8±17.9	160.4±15.1
Spongy parenchyma thickness [µm]	74.7±12.0	134.2±17.0	104.8±15.2
Abaxial epidermis [µm]	9.7±0.9	15.4±2.0	9.1±0.9
Abaxial cuticle [µm]	2.7±0.9	6.5±0.8	7.4±0.8
Number of palisade cell layers	1	3	2
Palisade cell length [µm]	68.7±4.8	41.3±5.6	67.1±3.9
Spongy cell length [µm]	24.1±4.7	22.9±5.5	15.9±3.1
Palisade cell diameter [µm]	17.1±2.1	10.5±1.2	10.4±1.8
Spongy cell diameter [µm]	24.5±4.8	10.9±2.3	9.6±1.1
Palisade density [cell mm^{-2}]	860±50	1850±100	1600±80
Spongy density [cell mm^{-2}]	900±180	2070±250	2730±130
Volume of intercellular spaces [%]	36	29	32

Leaf anatomy (Table 4): Among the examined species, the thickness of adaxial epidermis varied between 13.9 and 20.7 µm. There were significant differences in cuticle and in epidermis thickness between the adaxial and abaxial surfaces ($p<0.01$). *P. latifolia* had a particularly thick adaxial cuticle (17.1±1.4 µm) while *C. incanus* the thinnest one (6.8±0.8 µm). Adaxial *plus* abaxial epidermis (protective tissues) constituted 7, 11, and 15 % of the leaf thickness in *Q. ilex*, *P. latifolia* and *C. incanus*, respectively. The thickness ratio of cuticle to whole leaf was higher in *P. latifolia* (0.072±0.005) than in *Q. ilex* (0.056±0.008) and *C. incanus* (0.047±0.007). *P. latifolia* leaves were glabrous, *Q. ilex* leaves were covered with a dense pubescence on the abaxial surface and *C. incanus* leaves on both the adaxial and the abaxial surfaces.

P. latifolia showed three layers of palisade parenchyma cells, *Q. ilex* two, and *C. incanus* one layer. On the average, *Q. ilex* and *P. latifolia* leaves showed a densely packed mesophyll cells (2063 cells mm^{-2}) with 31 % of intercellular spaces; on the contrary, *C. incanus* showed a lower leaf density (880 cells mm^{-2}) and larger intercellular spaces (36 % of the total leaf volume), but its cells were the largest. In *C. incanus* the spongy and palisade cells contributed about equally to mesophyll thickness. On the average the spongy parenchyma cells were smaller than palisade parenchyma cells, and they had a more irregular shape, almost spherical in *C. incanus* (Table 4).

The *P. latifolia* foliar sclereids occurred diffusely within the mesophyll and were vertically oriented, occupying 5 % of total mesophyll volume. *P. latifolia* had the highest total leaf thickness (329.5±14.8 µm), 8 % higher than *Q. ilex* and 64 %

higher than *C. incanus* ($p<0.01$). The ratio of palisade parenchyma thickness to mesophyll thickness was 0.55 (for the three species).

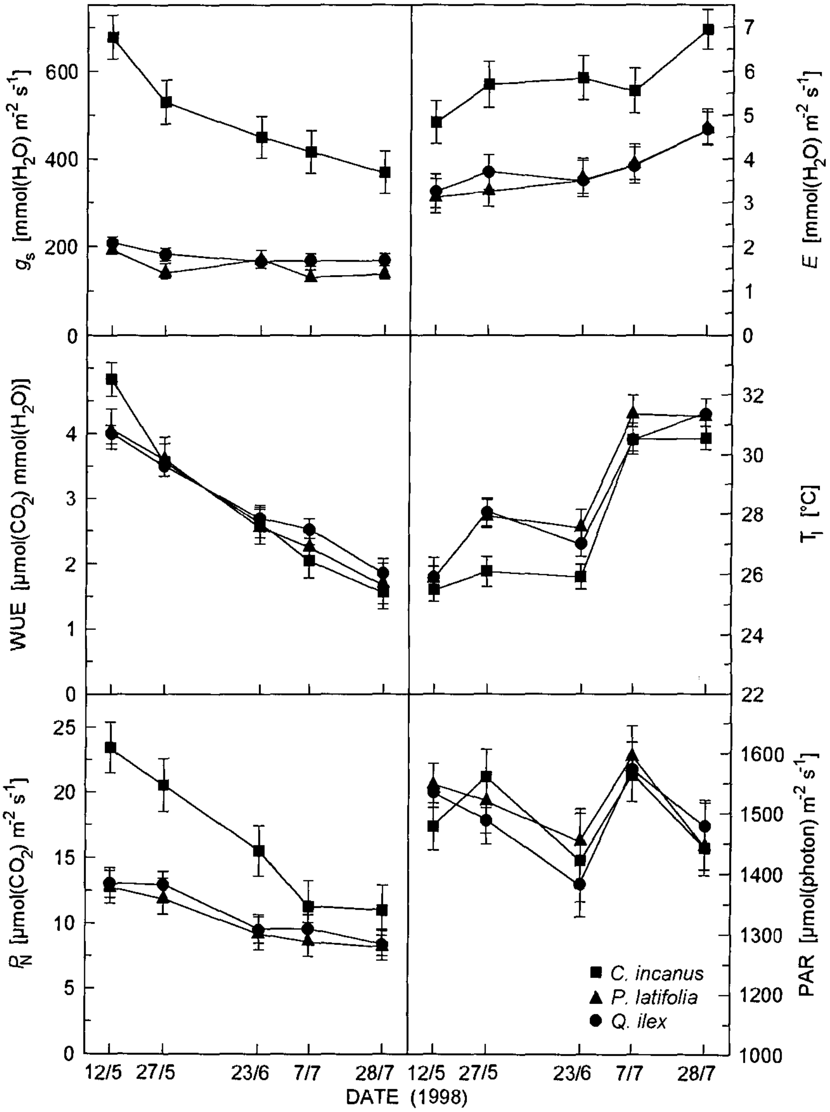

Fig. 2. Trends of photosynthetically active radiation (PAR), leaf temperature (T_l), stomatal conductance (g_s), leaf transpiration rate (E), net photosynthetic rate (P_N), and water use efficiency (WUE) from spring to summer for *C. incanus*, *P. latifolia*, and *Q. ilex*.

Leaf morphology: The highest number of cells per unit leaf area, the highest cuticle thickness, and the highest proportion of sclerenchymatic cells (*P. latifolia*) contribute to the highest LMA in *Q. ilex* and *P. latifolia* (209 g m^{-2}), almost two times that of *C. incanus* ($p<0.01$). Leaf life-span of the considered species ranged from four months to four years: *Q. ilex* and *P. latifolia* maintained their leaves for two to four years whilst *C. incanus* had a leaf life-span of four to eight months.

Gas exchange trends: P_N, g_s, E, T_l, and WUE average daily trends are shown in Fig. 2. Average leaf temperatures were 1.0-1.5 °C higher than air temperatures (values not shown). *C. incanus* showed the highest P_N and g_s in May ($T_l = 25.5$ °C), they decreased about 50 % in July when T_l was 30.6 °C. *P. latifolia* and *Q. ilex* showed the same trends as *C. incanus*, although their rates were less lowered (P_N 36 % and g_s 28 %) (Fig. 2). The three species showed an increase of E from May to the end of July. *C. incanus*, *P. latifolia,* and *Q. ilex* showed the same WUE trend during the study period (Fig. 2). During drought, the combined effects of decreased assimilation and increased water loss per transpiration resulted in a reduced WUE in all three species; nevertheless, *Q. ilex* had the lowest reduction (55 %) and *C. incanus* the highest one (67 %).

Discussion

Evergreen sclerophyllous and semideciduous shrub species growing in the Mediterranean climate are basically xerophytes. Their leaves are 45° or steeper inclined (Werner *et al.* 1999), or folded along the midrib (Ehleringer and Comstock 1987) and possess similar basic anatomical organization (Kummerow 1973, Catarino *et al.* 1981, Mitrakos and Christodoulakis 1981, Turner 1994, Karabourniotis 1998) which requires high construction costs (Ehleringer and Mooney 1983). Sclerenchymatic cells are located in distinct regions of the lamina or diffusely within the mesophyll (Fahn 1990, Turner 1994, Karabourniotis 1998), not only in the form of sclereids, but they are also abundant in the vascular bundle sheaths and leaf margin (Turner 1994). Sclerenchymatic cells might be the main factor determining the interspecific variation in LMA (Van Arendonk and Poorter 1994). The thickness of cuticle often corresponds with the degree of leaf xeromorphism (Bolhàr-Nordenkampf and Draxler 1993), and is considered part of the leaf construction costs (Koike 1988). Protective compounds indirectly affect leaf longevity by reducing the photosynthetic rate as a result of diluting photosynthetic tissues with non-photosynthetic tissues (Williams *et al.* 1989). Photosynthetic activity is continuous during the year and it decreases as drought increases (Oechel *et al.* 1981, Tenhunen *et al.* 1987, Damesin and Rambal 1995, Gratani *et al.* 1998, Peñuelas *et al.* 1998).

The analysis of morphological, anatomical, and physiological leaf traits may explain the different strategies of *Q. ilex*, *P. latifolia,* and *C. incanus* growing in the Mediterranean maquis. Leaf life-span is an "ecological integrator" of plant processes, it is an important life-history trait of plants with respect to their response to irradiance, nutrient availability, drought, and other factors (Chapin 1980, Gray and Schlesinger 1983, Reich *et al.* 1987, 1991, Codey 1988). Leaf life-span is one of several interrelated and mutually supporting traits and another is photosynthetic capacity (Reich *et al.* 1991). *C. incanus*, which has a leaf life-span of four-eight months (summer and winter leaves, respectively, Gratani and Crescente 1997) is characterised by the highest photosynthetic capacity. *Q. ilex* and *P. latifolia*, which maintain their leaves two-three and two-four years, respectively, are characterised by lower P_N. Photosynthetic activity of *Q. ilex* and *P. latifolia* requires a long period of time to cover the high production cost of their leaf protective structures and sclereids and to achieve a net profit in lifetime carbon gain, according to Miller and Stoner (1979) for *Ceanothus* sp. Even if non-photosynthesizing external structures, such as leaf hairs, polyphenol leaf deposition (in *Q. ilex*), and foliar sclereids (in *P. latifolia*) increase the intrinsic costs of the leaf, they are part of an effective stress defence mechanism, the first screening radiation penetrating into more sensitive tissues and the second suggesting a light-guiding function (Karabourniotis *et al.* 1992, Skaltsa *et al.* 1994, Karabourniotis 1998, Karabourniotis *et al.* 1998).

LMA is intrinsically variable among species and plastic within species (Reich *et al.* 1991). In the examined species, it is 120-210 g m^{-2} and its variations are related to leaf anatomy. In the examined species the increased LMA is paralleled by significantly increased leaf thickness, particularly in cuticle thickness and palisade parenchyma thickness (in *Q. ilex* and *P. latifolia* two and three layers, respectively), and by increased leaf mesophyll cell density.

In Mediterranean climate water stress is often accompanied by other limiting factors such as high temperature, leaf-to-air vapour pressure deficit, nutrient depletion, and irradiance. The combination of these factors favours photoinhibition of leaves, limiting the photosynthetic capacity of plants (Björkman and Powles 1984, Valladares and Pearcy 1997). The steeper leaf inclination could significantly decrease carbon gain (Nobel 1986), nevertheless, associated with thicker cuticles (Abril and Hanano 1998), it reduces over 42 % leaf radiation absorption in *Q. ilex* and *P. latifolia*. This may be a prevention mechanism against photoinhibition of the photosynthetic system and a means of reducing *E* by lowering T_l, in accordance with the results of Ludlow and Björkman (1984), Kao and Forseth (1991, 1992), and Werner *et al.* (1999). *Q. ilex* and *P. latifolia* pay the higher construction cost of leaf protective structures by a longer leaf life-span; they are the more xeromorphic species having the highest leaf thickness, cuticle thickness, LMA, and mesophyll cell density. *C. incanus*, which exhibits a drastic leaf drop of its winter leaves just before summer drought and which substitutes them with smaller folded leaves, does not require further leaf protective structures. Leaf folding under extreme water stress may effectively reduce the surface area exposed to direct sun rays by up to 73 % (Ehleringer and Comstock 1987), resulting in a reduced physiological stress at leaf level during drought. The evergreen sclerophyllous and drought semideciduous shrub species have similar WUE suggesting that the different interaction of morphological, anatomical, and physiological leaf traits may explain their co-presence in the Mediterranean maquis.

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