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Canopy structure, vertical radiation profile and photosynthetic function in a *Quercus ilex* evergreen forest

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Abstract

The studied evergreen forest dominated by *Quercus ilex* showed a leaf area index (LAI) of 4.5, of which 61 % was accumulated within the tree layer, 30 % within the shrub layer, and 9 % within the herb layer. The leaves of all the species were ± horizontally oriented (41°), absorbing a relevant percentage of incident irradiance. The high LAI drastically modified the quality and quantity of solar radiation on the forest underground. The spectral distribution of the radiation under the forest was markedly deficient in blue and red wavelengths. The maximum absorption in these spectral bands was found in spring, when net photosynthetic rate (P_N) was at its maximum, and in summer, when new leaves reached 90 % of their definitive structure. The vertical radiation profile showed an evident reduction of the red-far red ratio (R/FR). Radiation quality and quantity influenced leaf physiology and morphology. Clear differences in leaf size, leaf water content per area (LWC) and specific leaf area (SLA) on the vertical profile of the forest were observed. All the shrub species showed similar SLA (12.02 m^2 kg^{-1}, mean value). The ability to increase SLA whilst simultaneously reducing leaf thickness maximized the carbon economy. The high chlorophyll (Chl) content of shrub layer leaves (1.41 g kg^{-1}, mean value) was an expression of shade adaptation. Both leaf morphology and leaf physiology expressed the phenotypic plasticity. *Q. ilex*, *Phillyrea latifolia* and *Pistacia lentiscus* of the forest shrub layer showed wide differences in leaf structure and function with respect to the same species developing under strong irradiance (low maquis): a 57 % mean increase of SLA and a 86 % mean decrease of P_N. They showed high leaf plasticity. Leaf plasticity implies that the considered sclerophyllous species has an optimum developmental pattern achieving adaptation to environments.

Additional key words: chlorophyll content; leaf area index; net photosynthetic rate; *Phillyrea latifolia*; *Pistacia lentiscus*; specific leaf area; stomatal conductance; transpiration rate; vertical light profile.

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Introduction

The structure of vegetation canopies, as determined by the spatial arrangement of its elements, is the integrated result of selection in response to a variety of environments and competitive interactions (Sala *et al.* 1994). The interactions between climate and vegetation depend on environmental variables, including solar irradiance, directly from the sun and indirectly from the sky, infrared irradiance, wind speed, and temperature (Miller *et al.* 1981). In all cases, the environmental stimulus to which the plant principally responds is radiation, either as irradiance, its duration or its product (Pereira 1994). Typical leaves transmit a small portion of incident PAR in the green band at around 550 μm, but are otherwise effectively opaque in the visible range, depending upon the type of leaves and their thickness. In general, as the climate becomes more hot and arid, the reflection coefficient of the leaves of native species increases (Fitter and Hay 1993). Variations in the radiation environment produce changes in leaf anatomical and biochemical structure (Björkman 1981). Verhagen *et al.* (1963) found that the extinction coefficient which gave the most efficient interception decreased with increasing LAI.

The vertical profile of the forest is characterized by different irradiance. The major adaptation of leaves to a lower irradiance is the formation of thinner leaves with a higher water content, which results in a higher specific leaf area, SLA (Corré 1983), a higher proportion of intercellular space, a lower ratio of internal to external surface area, wider spacing between the veins, larger epidermal cells with more undulate radial walls, and a lower stomatal density (Lewis 1972, Givnisch 1990). Species with little plasticity in leaf anatomy show little differences in structure between sun and shade leaves (Carpenter and Smith 1980). The larger area and reduced thickness of shade leaves than sun leaves may result from additive effects of low photon flux density and low R/FR (Barreiro *et al.* 1992).

Chl *a/b* ratio may be a good characteristic to express interspecific differences and adaptability of plant leaves to irradiance (Gratani 1995). The Chl or protein concentration may also serve as a basis for calculating plant growth efficiency (Šesták *et al.* 1971). Leaf age and insertion must be taken into account for these calculations (Tobias *et al.* 1995). Chloroplasts acclimate to their radiation environment by modulating the stoichiometry of the components of thylakoid membranes and stroma, changes which affect the function and structure of the chloroplasts, in accordance with the requirements of the plant for photosynthetic efficiency, under the prevailing irradiances (Anderson 1986, Smith *et al.* 1993).

Objectives of this study were to characterize the structure of foliage vertical profile of a typical evergreen forest dominated by *Q. ilex* L., the radiation levels, leaf morphology, Chl content and P_N of understorey species.

Materials and methods

The research plot was situated in a natural evergreen forest dominated by *Q. ilex* L., inside the Presidential Estate of Castelporziano (S-SW of Rome, Italy). The tree layer

was composed of *Q. ilex*, 14-18 m high, whose density was 1073 trees per ha. The shrub layer, 2-5 m high, included *Q. ilex*, *Phillyrea latifolia* L., *Pistacia lentiscus* L., *Smilax aspera* L.,.*Hedera helix* L., *Ruscus aculeatus* L., and *Asparagus acutifolius* L. The herb layer was poorly developed and included *Cyclamen repandum* Sibth ex Sm., *Carex caryophyllea* Latourr., *Alliaria petiolata* (Bieb.) Cavara et Grande, *Brachypodium sylvaticum* (Hudson) Beauv., and *Asperula laevigata* L.

Field measurements were carried out during 1989-1992. Total irradiance was measured with a quantum radiometer photometer *Li-185B* (*Licor*, U.S.A.), irradiance in red, far-red and blue spectral bands with a photometer *IL 150* (*International Light*, U.S.A.), air humidity and air temperature with a thermohygrometer *HI 8564* (*Hanna Instruments*, Italy). Measurements were carried out above-canopy, below-canopy and at soil level. LAI was measured by the *LAI-2000* Plant Canopy Analyzer (*Licor*, U.S.A.). LAI estimates by this method, as with any radiation interception method, included all opaque objects, such as stems, fruit and branches (Welles and Norman 1991). LAI was estimated as a function of height, by dividing the total forest stand into three strata (tree layer, shrub layer and herb layer) and measuring LAI separately under the canopy of each stratum. Detailed ecophysiological measurements were carried out on the same position of selected branches, on one year old leaves. On each sampling, fifty leaves were collected and measured.

Measurements on plants included: average leaf surface area (SA), average leaf dry mass (DM), SLA (Beadle *et al.* 1985), specific leaf mass (SLM, Cappelletti 1954), leaf water content per area (LWC, Květ and Marshall 1971), and Chl content. Mature leaf samples were taken from fully expanded leaves of *Q. ilex* trees (from the external portion of the high layer and from the external portion of low layer of the crown) and from shrub layer, external portion of *Q. ilex, P. latifolia, P. lentiscus, S. aspera* and *H. helix*. Leaf area was determined by the Image Analysis System (*Delta-T Devices*, England). Dry mass was determined after drying leaves to constant mass at 90 °C. Chl *a*, *b*, and *a+b* concentrations and Chl *a/b* ratio were determined after macerating the leaves according to MacLachlan and Zalik (1963). Absorbance of the extracts was measured by a spectrophotometer *7800* (*LTD*, *Jasco*, Japan) at the wavelengths of 663 and 645 nm.

P_N, stomatal conductance (g_s), leaf temperature (T_l), transpiration rate (E) and PAR were measured using an infrared CO_2 gas analyser *LCA3* (*ADC*, England) open system. The highest average P_N values measured during the day were reported simultaneously with the relative values of g_s, T_l, E and PAR.

Results

The density of leaves in a canopy (or the vertical distribution of the leaves) is important in determining the extent of radiation penetration. LAI of 4.5, measured at soil level, was the sum of the different strata of the forest, of which 61 % was accumulated within the tree layer, 30 % within the shrub layer, and 9 % within the herb layer (Fig. 1). The average forest leaf angle of 41±2° means that most of the leaves are ± horizontally orientated. Leaves in the Mediterranean regions are

characteristically small and steeply inclined (Walter 1973, Cody and Mooney 1978). Vertically orientated leaves have an advantage related to uniform radiation distribution in canopies of high LAI, although the advantage disappears in situations of low LAI, or when the strength of incoming radiation is low (Williams and Soong 1961). In considering the efficiency and photosynthetic output of *Q. ilex* evergreen forest, we must take into account that during the early hours of the morning, when the sun is at lower angle and P_N is the highest (Gratani 1993), leaves have a vertical position in regard to the sun. On the contrary, at midday, when the sun is at its maximum, leaves have a horizontal position, absorbing thus most of the incident radiation.

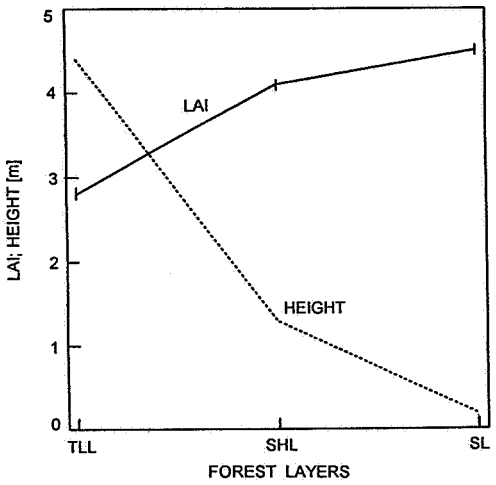

Fig. 1. Vertical distribution of LAI (TLL = tree low layer; SHL = shrub layer; SL = soil layer) and height for each layer of the forest. Standard error of LAI (|) is shown.

Table 1 and Fig. 2 show microclimate profile of the forest. The maximum absorption in red and blue regions at the tree crown level was found in spring, when P_N was the highest and when old leaves were substituted by new (Gratani and Crescente 1993), photosynthetically more active leaves. In this season the light transmittance to the shrub layer was the lowest. The same trend is observed in summer, when new leaves form 90 % of their definitive size (Gratani and Crescente 1993). During winter, when P_N is at its minimum (Eckardt *et al.* 1975, Gratani 1994) the light transmittance to the shrub layer is at its maximum. The R/FR trend during the year was not marked, due to its low influence on P_N. On the contrary, the vertical profile of the forest was evidently reduced in R/FR, from the upper layer of the crown (1.4) to the soil level (1.0). Air temperature during winter was lower at the upper layer of the crown due to cool winds from the sea. In summer, air temperature and humidity were lower in the shrub layer, due to the closed structure of the forest.

Table 2 shows the vertical leaf profile of average SA, DM, LWC, SLW, SLA, and Chl content. SLA of shrubs ranged between 1.166 and 1.277 $m^2\ kg^{-1}$. SLA of tree high layer was 55.4 % of tree low layer. The larger area and the reduced SLW of tree low layer might result from the additive effect of low irradiance and low R/FR,

whereas the decrease in the number of cells of the palisade and spongy mesophyll was brought about mostly by decreased irradiance, with little effect of R/FR (Barreiro *et al.* 1992).

Table 1. Microclimatic vertical profile of the forest (I = total irradiance; R = red spectral band; FR = far red spectral band; B = blue spectral band; R/FR = red-far red ratio; H = air humidity; T = air temperature; THL = tree high layer; TLL = tree low layer; SL = soil level). Percentage of transmission of each band is shown. All measurements were made at the same hours (09:30 - 11:30) in representative days for each month during 1991. June 21, variable weather.

Sampling day		I [W m^{-2}]	R [μW m^{-2}]	R [%]	FR [μW m^{-2}]	FR [%]	B [μW m^{-2}]	B [%]	R/FR	H [%]	T [°C]
January 31	THL	270.7	862.5		700.0		1210.0		1.23	46.2	7.6
	TLL	7.1	92.0	10.67	100.0	14.29	104.5	8.64	0.92	52.8	7.6
	SL	6.3	92.0	10.67	93.0	13.29	100.0	8.26	0.99	60.6	8.8
February 15	THL	400.0	471.5		340.0		1045.0		1.39	75.3	13.7
	TLL	6.1	57.5	12.20	70.0	20.59	71.5	6.84	0.82	83.0	14.0
	SL	5.9	<0.5	-	<0.5	-	<0.5	-		84.8	14.3
March 31	THL	700.0	1898.0		1150.0		1760.0		1.65	49.0	17.0
	TLL	7.9	120.8	6.36	100.0	8.70	88.0	5.00	1.21	51.0	17.6
	SL	7.5	118.0	6.22	97.0	8.43	80.0	4.55	1.22	58.0	18.1
May 20	THL	950.0	12650.0		8500.0		11000.0		1.49	42.0	18.8
	TLL	150.0	149.0	1.18	180.0	2.12	121.0	1.10	0.83	45.0	19.6
	SL	12.0	140.0	1.11	170.0	2.00	116.0	1.05	0.82	52.0	19.8
June 21	THL	750.0	5290.0		3400.0		5500.0		1.56	65.1	25.0
	TLL	28.5	92.0	1.74	140.0	4.12	71.5	1.30	0.66	66.8	24.2
	SL	27.0	90.8	1.72	140.0	4.12	71.5	1.30	0.65	70.8	23.3
July 18	THL	2400.0	7935.0		4500.0		3850.0		1.76	53.0	27.3
	TLL	54.0	138.0	1.74	130.0	2.89	115.5	3.00	1.06	57.0	26.1
	SL	34.5	120.8	1.52	122.0	2.71	115.5	3.00	0.99	57.0	26.2
September 10	THL	1800.0	2185.0		2000.0		2750.0		1.09	-	-
	TLL	24.0	80.5	3.68	90.0	4.50	<0.5	-	0.89	-	-
	SL	19.5	80.5	3.68	85.0	4.25	<0.5	-	0.95	-	-
October	THL	660.0	3105.0		2900.0		3740.0		1.07	70.5	23.9
	TLL	130.0	115.0	3.70	140.0	4.83	110.0	2.94	0.82	75.4	23.5
	SL	10.0	97.8	3.15	90.0	3.10	55.0	1.47	1.09	83.3	24.4
November 16	THL	290.0	1955.0		1300.0		2530.0		1.50	61.4	12.0
	TLL	42.0	149.5	7.65	110.0	8.46	132.0	5.22	1.36	61.9	12.4
	SL	20.0	136.0	6.96	100.0	7.69	125.0	4.94	1.36	62.0	12.7
December 21	THL	250.0	1495.0		1100.0		1980.0		1.36	72.4	15.1
	TLL	37.5	115.0	7.69	100.0	9.09	121.0	6.11	1.15	73.7	15.5
	SL	37.5	108.0	7.22	95.0	8.64	119.0	6.01	1.14	74.8	16.0

The adaptation of the considered evergreen sclerophyllous species to high irradiance showed the formation of twice thicker leaves with a higher LWC (155.6

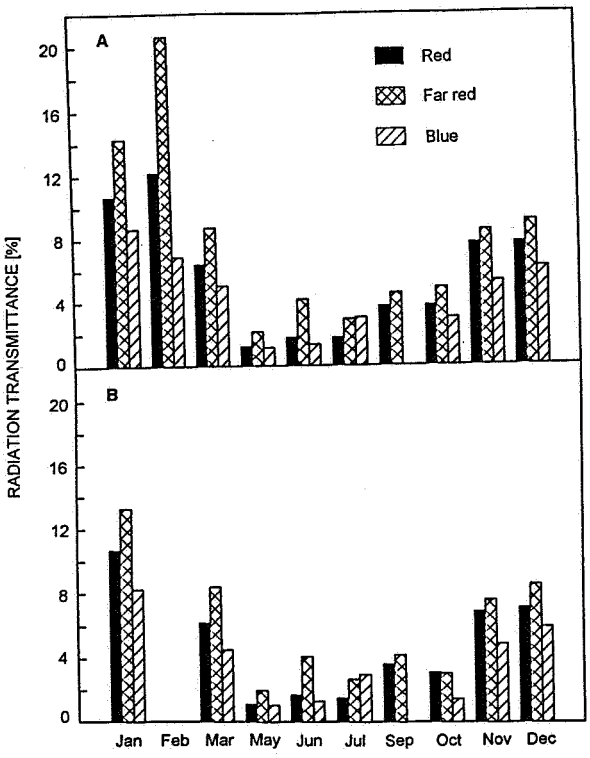

Fig. 2. Seasonal course of relative transmittance of red, far-red and blue spectral bands at tree low layer (*A*) and at soil level (*B*).

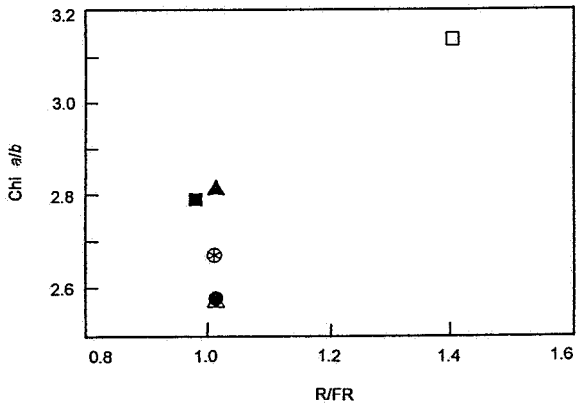

Fig. 3. Distribution of mean yearly chlorophyll (Chl) *a*/*b* in response to mean yearly red/far-red (R/FR) radiation. *Quercus ilex* (□ THL = tree high layer, ■ TLL = tree low layer, Δ SHL = shrub layer), *Phillyrea latifolia* (▲), *Smilax aspera* (○), *Hedera helix* (●), and *Pistacia lentiscus* (∗).

g m^{-2}, tree high layer), with respect to shade leaves (92.8 g m^{-2}, tree low layer). Typical sclerophyllous species were distinguished by mean SLW of 80.2 g m^{-2}, *Q. ilex* had the highest value (83.8 g m^{-2}) and *S. aspera* the lowest one (71.1 g m^{-2}); on the contrary *H. helix* showed a value of 40.6 g m^{-2}. LWC was highest in *Smilax* (150.3 g m^{-2}) and lowest in *Q. ilex* (81.0 g m^{-2}). The decreased leaf size at the top of

the tree canopy was advantageous in terms of thermoregulation and heat dissipation (Gates 1980), as a high air humidity inside the forest (Table 1) can help thermoregulation of high surface area of the undergrowth.

The 61 % of the total LAI, accumulated within the tree layer, was characterized by leaves of 140 g m^{-2} mean SLW, 124.2 g m^{-2} mean LWC, and SLA of 7.79 m^2 kg^{-1}. The 30 % of the total LAI, accumulated within the shrub layer, was characterized by leaves of 72.3 g m^{-2} mean SLW, 109.8 g m^{-2} LWC and a mean SLA of 14.95 m^{-2} kg^{-1}.

Table 2. Vertical leaf profile of surface area (SA), dry mass (D.M.), leaf water content per area (LWC), specific leaf mass (SLM), specific leaf area (SLA), contents of chlorophyll (Chl) *a*, *b*, and *a+b*, and ratio Chl *a/b* of one year old leaves, mean of the years 1989-92. THL = tree high layer; TLL = tree low layer.

	SA [cm^2]	D.M. [mg]	LWC [g m^{-2}]	SLM [g m^{-2}]	SLA [m^2 kg^{-1}]	Chl *a* [g kg^{-1}]	Chl *b* [g kg^{-1}]	Chl (*a+b*) [g kg^{-1}]	Chl (*a/b*)
TREE LAYER									
Quercus ilex THL	6.42±0.7	115.70± 9.7	155.6	180.22	5.549	0.66±0.05	0.21±0.02	0.87±0.07	3.14
Quercus ilex TLL	17.57±1.2	175.28±11.7	92.8	99.76	10.024	0.92±0.05	0.33±0.02	1.25±0.07	2.79
SHRUB LAYER									
Quercus ilex	18.99±1.6	159.11±15.8	81.0	83.78	11.936	0.90±0.06	0.35±0.04	1.25±0.10	2.57
Phillyrea latifolia	7.16±0.6	57.40± 5.7	103.3	80.17	12.474	1.04±0.08	0.37±0.03	1.41±0.10	2.81
Pistacia lentiscus	21.09±1.8	180.96±19.4	123.8	85.80	11.655	1.15±0.08	0.43±0.03	1.58±0.10	2.67
Smilax aspera	27.42±2.5	195.00±21.6	150.3	71.12	14.062	0.96±0.05	0.36±0.03	1.32±0.07	2.67
Hedera helix	15.93±1.6	64.68± 6.3	90.6	40.60	24.629	1.03±0.08	0.40±0.04	1.43±0.11	2.58

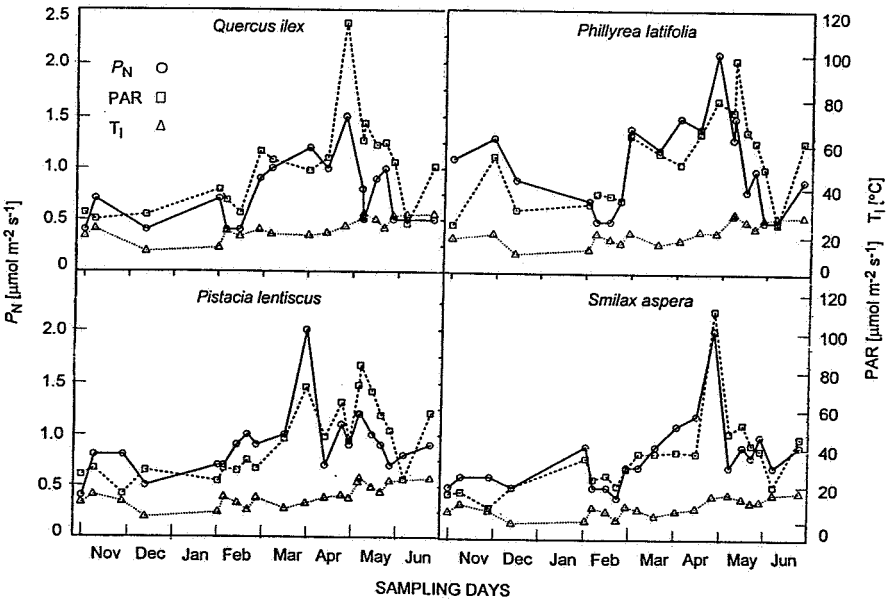

Fig. 4. Mean highest values of net photosynthetic rate (P_N) and corresponding PAR and leaf temperature (T_l) during the day (means of three-four measurements).

Radiation as an ecological factor evidently influences leaf Chl content. By considering the vertical distribution of Chl content per fresh matter (Table 2), the leaves of *Q. ilex* shrubs, that developed under low irradiance, had a total Chl content (fresh mass) higher than the leaves of *Q. ilex* trees. The preferential allocation of C and N to Chl in shade is an adaptation to maximize photon harvesting in radiation-poor environments (Barreiro *et al.* 1992). The Chl *a/b* ratio may be a useful indicator of the physiological state of a plant, as Chl is an unstable molecule, with a relatively short life (Gracia 1984). Fig. 3 shows Chl *a/b versus* mean yearly R/FR in the vertical profile of evergreen forest.

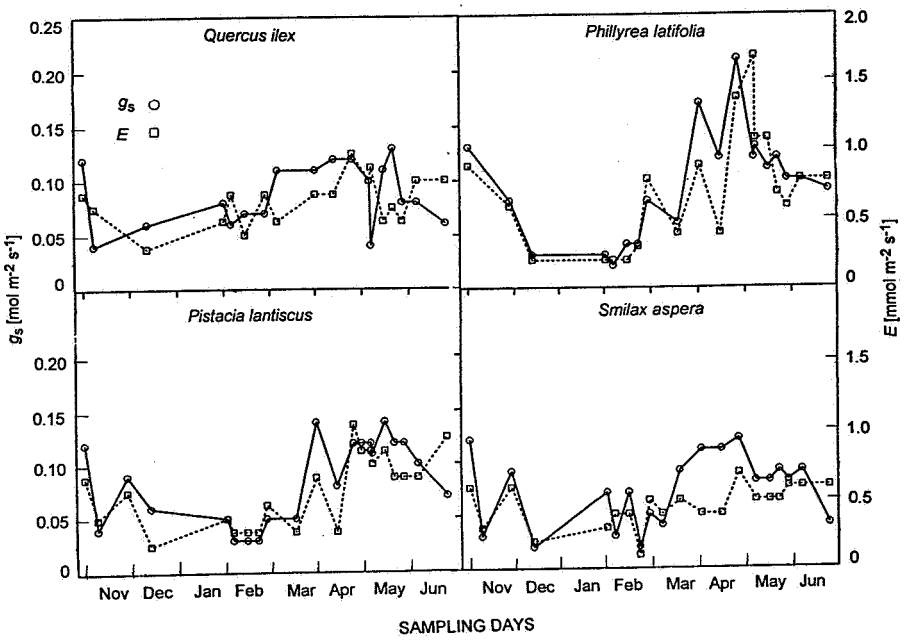

Fig. 5. Mean stomatal conductance (g_s) and transpiration rate (E) values corresponding to the highest values of P_N measured.

Figs. 4 and 5 show P_N, PAR, T_l, g_s, and E during the study period. The P_N was maximum in spring in all the species. g_s was the highest in autumn and spring, while E maintained high values in summer. P_N strongly depended on PAR. At PAR as high as 115 μmol m^{-2} s^{-1} *Q. ilex* shrubs, for example, were capable of P_N of 1.5 μmol m^{-2} s^{-1} at a leaf temperature of 20 °C.

Discussion

The interception of solar radiation depends on the forest structure, which includes the inclination of leaves, stems and LAI (Miller *et al.* 1981). LAI describes the size of the assimilatory apparatus of a plant stand and serves as a primary value for the calculation of the growth characteristics and leaf morphology characteristics. LAI of

4.5 is typical for the dense canopy of *Q. ilex* evergreen forest. It denotes microclimate influence on undergrowth plant morphology and function.

One of the expressions of the plant phenotypic plasticity is the modification of leaf morphology and anatomy by irradiance (Dengler 1980), and the major adaptation of leaf morphology to changed irradiance is the variation in SLA. The SLA reflects leaf thickness (Dole and Causton 1992) and the relative proportions of assimilatory, conductive or mechanical tissue of leaves (Květ *et al.* 1969). Experiments of Nobel (1976) indicate that leaf thickness does not respond to irradiance *per se*, but rather reflects the total daily irradiance received by a leaf during its development. Sun leaves thus develop in parts of the canopy exposed to full sun radiation during much of the day, while the total daily irradiance received by shade leaves is correspondingly low (Nobel 1977).

The plasticity of SLA implies that the plants have an optimum developmental pattern in terms of dry mass distribution achieving adaptation to irradiance (Fitter and Hay 1993). While typical shade plants adapt to low irradiances by being able to increase leaf area, with only a slight reduction in photosynthetic rate per unit leaf area (Evans and Hughes 1961), the considered sclerophyllous species of the evergreen forest shrub layer respond to a decrease in irradiance by both a high reduction of net assimilation rate and a high increase of SLA. Comparing the considered evergreen sclerophyllous species of the forest shrub layer (under low irradiance) with the same species developing in the low maquis (under strong irradiance), SLA shows a difference of 57 % in *Q. ilex*, 62 % in *P. latifolia* and 53 % in *P. lentiscus*; total Chl content shows a difference of 63 % in *Q. ilex*, 58 % in *P. latifolia* and 64 % in *P. lentiscus*; the maximum values of P_N during the year give for all the species a mean difference of 86 %. The SLA of tree high and low layers differs by 45 %. *Q. ilex*, *P. latifolia* and *P. lentiscus* therefore widely differ in structure and function of sun and shade leaves. Species that show little difference in structure between sun and shade leaves are less plastic in leaf anatomy (Carpenter and Smith 1980). The high adaptability of the considered sclerophyllous species is conferred by high plasticity of both leaf morphology and leaf physiology.

Plasticity may be therefore an important ecological factor that can explain the coexistence of the considered evergreen sclerophyllous species in these communities. *Q. ilex, P. latifolia, P. lentiscus* and *S. aspera* are fundamental constituents of Mediterranean maquis and evergreen forest. These communities have developed under Mediterranean climate. The evergreen sclerophyllous species probably have colonized the Mediterranean Regions by high morphological and physiological plasticity. To achieve such high distribution, evergreen sclerophyllous species have evidently evolved a high optimization of their structure, function and economy of resource use.

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