Differences in leaf traits among Mediterranean broad-leaved evergreen shrubs

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Leaf morphological and physiological traits of the broad-leaved evergreen shrub species *Quercus ilex*, *Phillyrea latifolia*, *Pistacia lentiscus*, *Arbutus unedo* and *Cistus incanus* of the Mediterranean maquis were studied. Specific leaf mass (SLM), leaf tissue density (LTD), leaf life-span (LLS) and water use efficiency (WUE) were the most representative key traits resulting from discriminant analysis. Cluster analysis was used to identify the affinity among the species by statistical linkage. Dendrograms show two clusters characterised by a different integration of morphological and physiological leaf traits: *Quercus ilex*, *Phillyrea latifolia* and *Pistacia lentiscus* were in the same cluster, significantly different from that formed by *Arbutus unedo* and *Cistus incanus*.

Key words: Mediterranean maquis, broad-leaved evergreen shrubs, SLM, LTD, LLS, WUE

Introduction

The structure of leaves has important implications for the performance of plants in specific habitats (Garnier *et al*. 1999). Both between and within species, leaves are different in structure, including the plastic responses such as leaf size and mass per unit leaf area (Gutschick 1999). Specialisation has allowed plant species to co-exist in the same environment, and species with similar morphological and physiological traits reflect their evolutionary adaptations. Species with different leaf morphology and physiology are able to tolerate different levels of stress, e.g. drought and high air temperatures (Kloeppel *et al*. 1993, Abrams *et al*. 1994).

In Mediterranean ecosystems, drought, high irradiation and high air temperatures, for short or long periods, dramatically influence plant function thus limiting their production (Filella *et al*. 1998). Many structural leaf traits can be

explained as adaptations to enhance CO_2 diffusion within the leaf for photosynthesis (Parkhurst 1986). One morphological leaf trait that correlates with CO_2 assimilation is specific leaf mass (SLM) (Mooney *et al.* 1978, Field & Mooney 1983, Ellsworth & Reich 1992). SLM is at the centre of a nexus of covarying traits that together affect the ecology of plant species (Shipley 1995). High SLM, leaf tissue density, leaf thickness and reduced surface area (Abril & Hanano 1998, Castro-Díez *et al.* 1998) are features that improve Mediterranean species drought resistance, decreasing photochemical damages of the photosynthetic system and reducing transpiration rates by lowering leaf temperature under water stress (Matsuda *et al.* 1989, Kao & Forseth 1991, 1992, Abrams *et al.* 1994, Werner *et al.* 1999).

The aim of this study was to analyse differences in leaf traits among the most representative broad-leaved evergreen shrub species of the Mediterranean maquis at Castelporziano, Italy (Amadori & Gratani 1991, Gratani *et al.* 1982, Gratani 1995), and to cluster them by the affinity of those traits that are involved in adaptive strategies to drought. Consideration of adaptability involves an interest in the response of species to the forecasted increase of air temperatures and drought for the Mediterranean Basin (Merino *et al.* 1995, Filella *et al.* 1998). Therefore we analysed relationships that exist between certain leaf traits and their adaptive significance.

Material and methods

Study area

The study area is in the Mediterranean maquis developing along the coast near Rome, in the Castelporziano Estate (41°45´N, 12°26´E). The broad-leaved evergreen shrub species *Quercus ilex* L., *Phillyrea latifolia* L., *Pistacia lentiscus* L., *Arbutus unedo* L. and *Cistus incanus* L. (Gratani & Amadori 1991) were studied.

The full data set consisted of measurements of 12 variables from 6 randomly selected individual plants per species (Pyankov *et al.* 1999), representative of the population (Gratani *et al.* 1980, Gratani & Amadori 1991). All measurements were made on fully expanded "sun" leaves.

The area has a Mediterranean climate and most of the total annual rainfall (726 mm) occurs in autumn and winter. The mean minimum air temperature of the coldest month (February) is 3.9 °C, and the mean maximum air temperature of the hottest month (August) is 30.8 °C. The dry period is from mid-May to August (11% of total annual rainfall). Air humidity decreases by 15% in the summer (data by the Castelporziano Meteorological Station for the years 1987–1999). The maquis lies on young dunes; the soil is a regosoil (Gisotti & Collamarini 1982). Soil water content is in the range 0.5%–8% during the year, the annual minimum occurring in August and the annual maximum in December (Gratani 1994).

Leaf morphology

Leaf samples were collected on 15 September 1999. The projected leaf surface area (excluding petiole) (SA) was measured on fresh leaves using the Image Analysis System (Delta-T Devices, LTD, UK). Leaf dry mass (DM) was determined drying at 80 °C to constant weight. Specific leaf mass (SLM) was calculated as the ratio of leaf dry mass to unifacial leaf area (Reich *et al.* 1992). Leaf thickness was measured microscopically (Zeiss, GE) on cross sections at full leaf expansion. We restricted measurements to vein-free areas (Chabot & Chabot 1977). Leaf tissue density (LTD) was calculated as the ratio of DM and leaf volume (V) (g cm^{-3}, Witkowski & Lamont 1991), and leaf volume as leaf area × leaf thickness. Leaf age was analysed *in situ* by monitoring the number of nodes (Reich *et al.* 1992), since the flushing patterns were known (Gratani & Crescente 1997). The maximum monitored leaf life-span (LLS$_{max}$) was considered. The relative leaf area growth rate (RGR$_{la}$) was calculated as the rate of increased leaf surface area at any instant in time (Fisher 1920, Bazzaz & Harper 1977). The maximum

RGR_{la} (RGR_{lam}) rate during leaf expansion was considered.

Leaf gas exchange

Field measurements were carried out on the external fully sun exposed crown of the selected species. All gas exchange measurements were taken from April–May (favourable period, determining maximum photosynthetic rates) to late July (drought period, minimum photosynthetic rates) to evaluate plant response to Mediterranean stress (Pereira & Chaves 1995, Gratani & Bombelli 2000). Gas exchange measurements were made *in situ* under natural conditions, 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.

Photosynthetic active radiation (PAR, µmol photon m^{-2} s^{-1}), net CO_2 assimilation rate (PN, µmol CO_2 m^{-2} s^{-1}), leaf temperature (LT, °C), stomatal conductance to water vapour diffusion (GS, mmol H_2O m^{-2} s^{-1}), and transpiration rate (*E*, mmol H_2O m^{-2} s^{-1}) were monitored with 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). The relative decrease of PN during drought (in respect to the maximum) was also considered (PN_r).

Instantaneous water use efficiency (WUE, µmol CO_2 $mmol^{-1}$ H_2O) was calculated by the ratio of the measured PN and *E* rates (Wuenscher & Kozlowski 1971, Larcher 1995).

Statistics

All statistical tests were performed with a statistical software package (Statistica, Statsoft USA). Differences in morphological and physiological means of leaf variables were determined with the analysis of variance (ANOVA) and Tukey test for multiple comparisons. The relationships among species were analysed with a multivariate analysis based on the standardised values of morphological and physiological leaf variables. Cluster analysis (dendrograms) was used to analyse similarity among species. Distance among species was Euclidean and distance between clusters were defined as an unweighted pair-group average, UPGMA. Discriminant analysis was used to determine which variables discriminated between naturally occurring clusters. Box and whisker plots were used to compare the distribution of variables.

Results

Leaf morphology

All the analysed morphological leaf traits varied among the species (Table 1). SLM was the

Table 1. Morphological leaf traits at full leaf expansion of *Quercus ilex*, *Phillyrea latifolia*, *Pistacia lentiscus*, *Arbutus unedo* and *Cistus incanus*. Means with the same letter are not significantly different (ANOVA, $p > 0.05$). Standard error is shown. DM = leaf dry mass; SA = leaf surface area; LTh = leaf lamina thickness; SLM = specific leaf mass; LTD = leaf tissue density; RGR_{lam} = maximum relative leaf area growth rate; LLS_{max} = maximum leaf life-span.

Species	DM mg	SA cm^2	LTh µm	SLM mg cm^{-2}	LTD mg cm^{-3}	RGR_{lam} cm^2 day^{-1}	LLS_{max} months
Q. ilex	181 ± 34[ac]	8.7 ± 2.1[a]	310 ± 19[a]	20.7 ± 1.7[a]	669 ± 44[a]	0.063 ± 0.003[a]	36
P. latifolia	76 ± 19[b]	3.6 ± 0.6[b]	408 ± 25[b]	20.9 ± 2.0[a]	513 ± 33[b]	0.084 ± 0.005[b]	48
P. lentiscus	206 ± 53[a]	11.0 ± 2.7[a]	396 ± 22[b]	18.7 ± 1.3[a]	472 ± 38[b]	0.063 ± 0.004[a]	30
A. unedo	172 ± 28[c]	10.8 ± 2.3[a]	384 ± 28[b]	16.0 ± 1.1[b]	416 ± 26[c]	0.065 ± 0.005[a]	11
C. incanus	59 ± 16[b]	4.1 ± 0.5[b]	267 ± 19[c]	14.3 ± 1.5[b]	535 ± 21[b]	0.036 ± 0.003[c]	7

Table 2. Leaf gas exchange during favourable and dry periods in *Quercus ilex*, *Phillyrea latifolia*, *Pistacia lentiscus*, *Arbutus unedo* and *Cistus incanus*. Intraspecific differences between optimal and drought periods are always significant (ANOVA, $p < 0.05$) except *. Within the same period (favourable or drought) means of different species with the same letter are not significantly different (ANOVA, $p > 0.05$). PN = net photosynthetic rate; GS = stomatal conductance; E = transpiration rate; WUE = water use efficiency; LT = leaf temperature. Subscripts: f = favourable and d = drought.

Species	PN_f	PN_d	GS_f	GS_d	E_f	E_d	WUE_f	WUE_d	LT_f	LT_d
	μmol m^{-2} s^{-1}		mmol m^{-2} s^{-1}		mmol m^{-2} s^{-1}		μmol mmol^{-1}		°C	
Q. ilex	12.8 ± 2.1[a]	7.3 ± 1.2[a]	190 ± 16[a]	80 ± 7[a]	2.42 ± 0.25[a]*	2.30 ± 0.21[a]*	5.3 ± 0.5[a]	3.2 ± 0.4[a]	23 ± 0.9[a]	34 ± 1.2[a]
P. latifolia	11.5 ± 1.5[a]	5.9 ± 1.1[ab]	179 ± 20[a]	92 ± 9[a]	2.05 ± 0.18[a]*	1.84 ± 0.14[b]*	5.6 ± 0.6[a]	3.2 ± 0.3[a]	24 ± 0.8[a]	35 ± 1.5[a]
P. lentiscus	12.5 ± 1.8[a]	7.5 ± 1.5[a]	280 ± 22[b]	130 ± 18[b]	3.15 ± 0.31[b]	2.33 ± 0.28[a]	4.0 ± 0.3[b]	3.3 ± 0.3[a]	24 ± 1.0[a]	36 ± 1.6[a]
A. unedo	13.9 ± 1.8[a]	5.2 ± 1.2[b]	360 ± 33[c]	55 ± 10[c]	4.26 ± 0.36[c]	1.81 ± 0.26[b]	3.3 ± 0.5[c]*	2.9 ± 0.4[ab]*	23 ± 1.1[a]	34 ± 1.4[a]
C. incanus	22.2 ± 2.3[b]	9.6 ± 1.3[c]	394 ± 65[c]	200 ± 44[a]	4.44 ± 0.52[c]*	3.70 ± 0.39[c]*	5.0 ± 0.6[a]	2.6 ± 0.4[b]	22 ± 1.1[a]	35 ± 1.5[a]

highest in *Phillyrea latifolia* and the lowest in *Cistus incanus* (68% of the maximum). LTD was the highest in *Quercus ilex* and the lowest in *Arbutus unedo* (62% of the maximum). RGR$_{lam}$ ranged from 0.036 (*C. incanus*) to 0.084 cm^2 day^{-1} (*P. latifolia*).

Quercus ilex, Phillyrea latifolia and *Pistacia lentiscus* had a LLS$_{max}$ ranging from 2.5 to 4 years. In *Arbutus unedo* it was 11 months and *Cistus incanus* produced "summer" leaves and "winter" leaves with a LLS$_{max}$ of 5 and 8 months, respectively (*see* Table 1).

Leaf gas exchange

All the analysed physiological leaf traits varied among the species (Table 2). *Cistus incanus* showed the highest PN reduction (PN$_r$) (57%) during drought (mean LT = 35 °C), while *Pistacia lentiscus* had the lowest (40%). On average, GS showed the same trend. E_d was the highest in *Cistus incanus* (3.70 mmol m^{-2} s^{-1}) and the lowest in *Arbutus unedo* (1.81 mmol m^{-2} s^{-1}). *Cistus incanus* had the lowest WUE$_d$ (2.6 μmol mmol^{-1}) and *Pistacia lentiscus* the highest (3.3 μmol mmol^{-1}) (*see* Table 2).

Comparison among species

Morphological and physiological leaf variables were subjected to cluster analysis in order to define the affinity among the species by statistical linkage.

The dendrogram obtained with the variables SLM, LTD, RGR$_{lam}$, PN$_r$, GS$_d$, E_d, WUE$_d$ and LLS$_{max}$, showed two clusters (Fig. 1). Cluster 1 included *Quercus ilex*, *Pistacia lentiscus* and *Phillyrea latifolia*; cluster 2 included *Arbutus unedo* and *Cistus incanus*.

Quercus ilex, Phillyrea latifolia and *Pistacia lentiscus* were characterised by a higher SLM (mean 20.1 mg cm^{-2}), LTD (mean 551 mg cm^{-3}), LLS$_{max}$ (mean 38 months) and WUE$_d$ (mean 3.2 μmol mmol^{-1}), but a lower PN$_f$ (mean 12.3 μmol m^{-2} s^{-1}) and GS$_f$ (mean 216 mmol m^{-2} s^{-1}). *Arbutus unedo* and *Cistus incanus* were characterised by a lower SLM (mean 15.1 mg cm^{-2}), LTD (mean 475 mg cm^{-3}), LLS$_{max}$ (mean 9
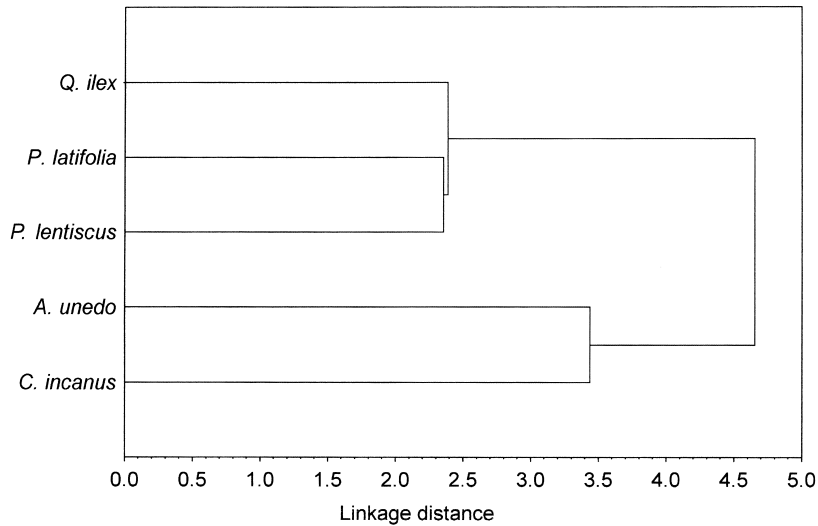
Fig. 1. Dendrogram based on Euclidean distance and UPGMA using specific leaf mass (SLM), leaf tissue density (LTD), the maximum leaf area relative growth rate (RGR_{lam}), the relative decrease of net photosynthesis during drought (PN_r), stomatal conductance during drought (GS_d), leaf transpiration rate during drought (E_d), water use efficiency during drought (WUE_d) and the maximum leaf life-span (LLS_{max}) for *Quercus ilex*, *Phillyrea latifolia*, *Pistacia lentiscus*, *Arbutus unedo* and *Cistus incanus*.

Fig. 2. Dendrogram based on Euclidean distance and UPGMA using specific leaf mass (SLM), leaf tissue density (LTD), the relative decrease of net photosynthesis during drought (PN_r), leaf transpiration rate during drought (E_d), water use efficiency during drought (WUE_d) and the maximum leaf life-span (LLS_{max}) for *Quercus ilex*, *Phillyrea latifolia*, *Pistacia lentiscus*, *Arbutus unedo* and *Cistus incanus*.
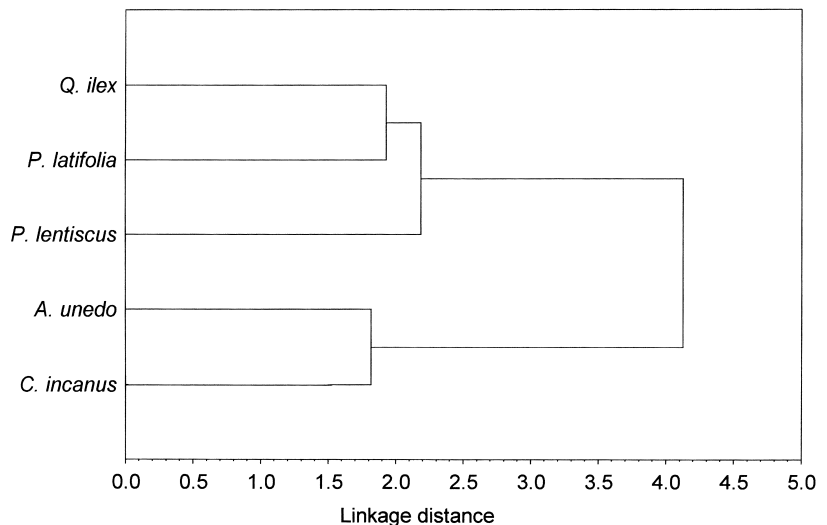
months) and WUE_d (mean 2.7 µmol mmol^{-1}), but a higher PN_f (mean 18.1 µmol m^{-2} s^{-1}) and GS_f (mean 377 mmol m^{-2} s^{-1}).

The discriminant analysis indicated that SLM, LTD, LLS_{max}, PN_r, E_d and WUE_d were the most representative leaf traits discriminating between the two clusters. A dendrogram was obtained using these variables (Fig. 2); it showed that the species within each cluster were linked to each other at a better affinity

level. Nevertheless, as WUE was inclusive of PN and *E*, the dendrogram obtained using SLM, LTD, LLS_{max} and WUE_d (Fig. 3), showed the best affinity level.

Analysis of variance (ANOVA) and Tukey test for multiple comparison showed a significant difference ($p < 0.01$) between cluster 1 and cluster 2. Box and whisker plots showed the different distribution of the variables among the species (Fig. 4).
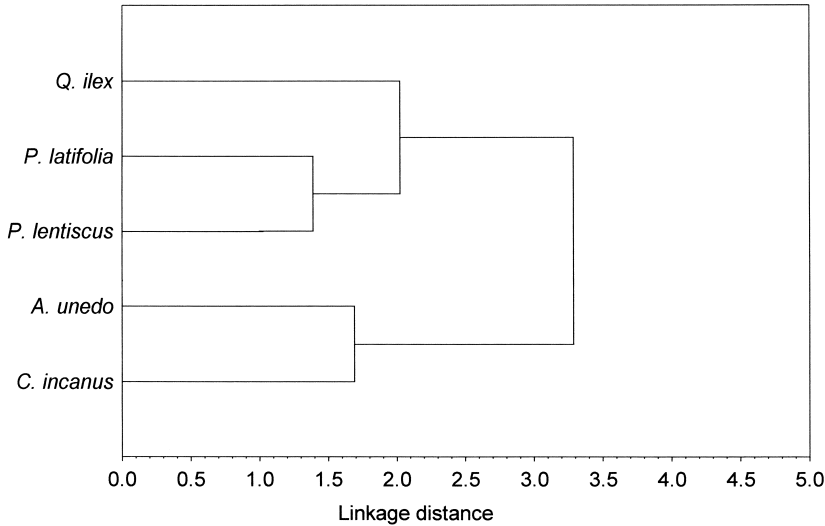
Fig. 3. Dendrogram based on Euclidean distance and UPGMA using specific leaf mass (SLM), leaf tissue density (LTD), water use efficiency during drought (WUE_d) and the maximum leaf life-span (LLS_{max}) for *Quercus ilex*, *Phillyrea latifolia*, *Pistacia lentiscus*, *Arbutus unedo* and *Cistus incanus*.
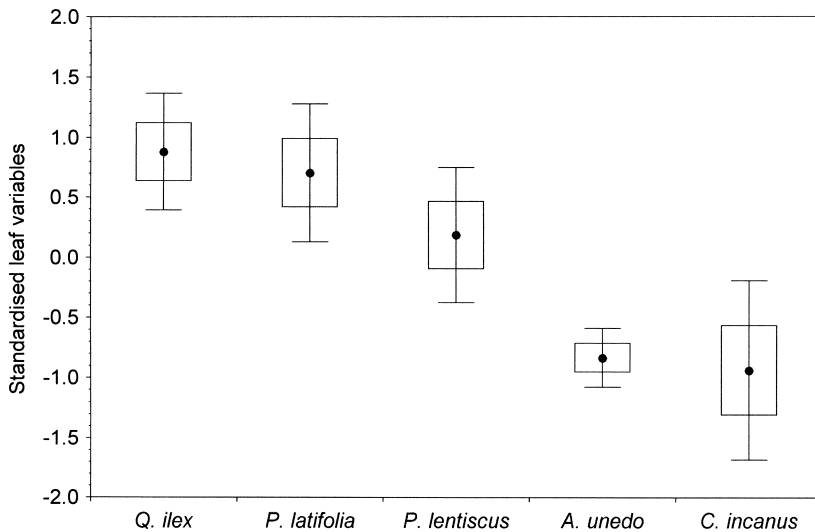

Fig. 4. Box and whisker plots of *Quercus ilex*, *Phillyrea latifolia*, *Pistacia lentiscus*, *Arbutus unedo* and *Cistus incanus* using specific leaf mass (SLM), leaf tissue density (LTD), water use efficiency during drought (WUE_d) and the maximum leaf life-span (LLS_{max}). Solid dot indicates mean, box gives ± standard error, and bar shows ± standard deviation.

Discussion

Evergreen shrubs of Mediterranean maquis are well-adapted to summer drought (Tenhunen *et al*. 1990, Infante *et al*. 1999). However, they are extremely sensitive to changes in length and intensity of drought stress (Strain & Thomas 1995). Although there are numerous studies dealing with leaf morphological trends in response to environmental changes, their functional interpretation should be carefully considered (Reich 1993, Smith *et al*. 1998).

The increase in CO_2 concentration is predicted to produce an increase in average global temperature, modifying the intensity and interaction of environmental stress on plants (Watson *et al*. 1990, Hope 1995, Merino *et al*. 1995, Filella *et al*. 1998). Increasing drought stress may be a major factor for the future survival of species, particularly for vegetation in the areas, such as Mediterranean type, where aridity is an actual problem.

The results of this study on the whole show significant differences between morphological and physiological leaf traits of the broad-leaved evergreen shrub species of Mediterranean maquis. The combination of morphological and physiological leaf traits provides support for the plac-

ing of these species into two separate groups: *Quercus ilex*, *Phillyrea latifolia* and *Pistacia lentiscus* form one group (below referred to as Group 1), and *Arbutus unedo* and *Cistus incanus* form another group (Group 2). These groups may be considered functional groups according to Noble and Gitay (1996), Medail *et al.* (1998), Breshears and Barnes (1999), i.e. they contain a set of species with similar morphological, physiological and phenological traits (Solbrig 1993). The identified functional groups are defined by their response to Mediterranean drought.

Species in Group 1 are evergreen sclerophyllous species characterised by a high LLS, SLM and LTD. The high SLM may be explained by different chemical composition of the leaves and cell wall constituents conferring stress resistance. The following features in particular should be emphasized: high fiber content (Castro-Díez *et al.* 1998), tannins and essential oils in *Pistacia lentiscus* (Mitrakos & Christodoulakis 1981, Castola *et al.* 2000), foliar sclereids (Heide-Jorgensen 1990, Karabourniotis 1998, Gratani & Bombelli 2000) and a thicker cuticle in *Phillyrea latifolia* (Gratani & Bombelli 2000), and monoterpenes (Delwiche & Sharkey 1993, Loreto *et al.* 1996) and polyphenol deposition (Karabourniotis *et al.* 1998) in *Quercus ilex*. The high SLM and LTD result in a higher leaf compactness, limiting leaf transpiration during drought (84% of the maximum in the favourable period) and conferring to these species high efficiency in water use during drought with respect to Group 2. Moreover, the production of secondary metabolites (terpenes, phenolics) may serve as a sink for the excess of photochemical energy (Osmond *et al.* 1982), preventing photoinhibition damages to the photosynthetic system during drought (Werner *et al.* 1999) and allowing a more efficient CO_2 assimilation under prolonged drought (L. Gratani & A. Bombelli unpubl.).

The lower SLM and LTD of species of Group 2 (mean 75% and 86%, respectively) result in a higher E_d (128%) and a lower WUE_d (85%). Nevertheless, the low LTD allows a better CO_2 movement through the air spaces between cells (Parkhurst 1986), resulting in a higher photosynthetic rate during the favourable period (mean 47% higher than in Group 1).

Species of Group 1 may be at a competitive advantage relative to species of Group 2 in regard to drought stress. Leaves with a higher amount of biomass per unit of area (i.e. high SLM and LTD) may be more efficient in water use during drought. Moreover, the high leaf longevity may enhance resource use efficiency and the better WUE may be advantageous in drought stress conditions.

These types of studies demonstrate that there are plant functional groups which include one or more species in the same habitat. The groups can be used to identify general processes at ecosystem level, thus developing a good understanding of the major trends in trait variations and trait-environment correlations (Parker *et al.* 1989, Shipley *et al.* 1989, Barkman 1990, Kull *et al.* 1995, Gratani & Foti 1998, Wilson *et al.* 1999). Moreover, the use of functional groups may give the largest possible amount of information on plants and ecosystem functioning using only a limited number of key traits (Wilson *et al.* 1999).

SLM, LTD, WUE and LLS seems to be the key traits characterising the broad-leaved evergreen shrub species we studied. Other species of the maquis, such as *Smilax aspera* (a liana) should be studied to determine their inclusion in the groups. The functional groups may be suggested for a structural classification of the Mediterranean maquis in addition to a floristic one.

References

Abrams, M. D., Kubiske, M. E. & Mostoller, S. A. 1994: Relating wet and dry year ecophysiology to leaf structure in contrasting temperate tree species. — *Ecology* 75: 123–133.

Abril, M. & Hanano, R. 1998: Ecophysiological responses of three evergreen woody Mediterranean species to water stress. — *Acta Oecol.* 19: 377–387.

Amadori, M. & Gratani, L. 1991: Response of some maquis species to anthropic perturbation. — In: Ravera, O. (ed.), *Terrestrial and aquatic ecosystems: perturbation and recovery*: 206–212. Ellis Horwood Ltd., Chichester.

Barkman, J. J. 1990: A tentative typology of European scrub and forest communities based on vegetation texture and structure. — *Vegetatio* 86: 131–141.

Bazzaz, F. A. & Harper, J. L. 1977: Demographic analysis of the growth of *Linus usitatissimum*. — *New*

Phytol. 78: 193–208.

Breshears, D. D. & Barnes, F. J. 1999: Interrelationship between plant functional types and soil moisture heterogeneity for semiarid landscapes within the grassland/forest continuum: a unified conceptual model. — *Landscape Ecol.* 14: 465–478.

Castola, V., Bighelli, A. & Casanova, J. 2000: Intraspecific chemical variability of the essential oil of *Pistacia lentiscus* L., from Corsica. — *Biochem. Syst. Ecol.* 28: 79–88.

Castro-Díez, P., Villar-Salvador, P., Pérez-Rontomé, C., Maestro-Martínez, M. & Montserrat-Martí, G. 1998: Leaf morphology, leaf chemical composition and stem xylem characteristics in two *Pistacia* (Anacardiaceae) species along a climatic gradient. — *Flora* 193: 195–202.

Chabot, B. F. & Chabot, J. F. 1977: Effects of light and temperature on leaf anatomy and photosynthesis in *Fragaria vesca*. — *Oecologia* 26: 363–377.

Delwiche, C. F. & Sharkey, T. D. 1993: Rapid appearance of ^{13}C in biogenic isoprene when $^{13}CO_2$ is fed to intact leaves. — *Plant Cell Environ.* 16: 587–591.

Ellsworth, D. S. & Reich, P. B. 1992: Leaf mass per area, nitrogen content and photosynthetic carbon gain in *Acer saccharum* seedlings in contrasting forest light environments. — *Funct. Ecol.* 6: 423–435.

Field, C. & Mooney, H. A. 1983: Leaf age and seasonal effects on light, water, and nitrogen use efficiency in a California shrub. — *Oecologia* 56: 348–355.

Filella, I., Llusìa, J., Piñol, J. & Peñuelas, J. 1998: Leaf gas exchange and fluorescence of *Phillyrea latifolia* and *Quercus ilex* saplings in severe drought and hight temperature conditions. — *Environ. Exp. Bot.* 39: 213–220.

Fisher, R. A. 1920: Some remarks on the methods formulated in a recent article on "The quantitative analysis of plant growth?". — *Ann. Appl. Biol.* 7: 376.

Garnier, E., Farrar, J., Poorter, H. & Dale, J. 1999: Editorial. — *New Phytol.* 143: 1.

Gisotti, G. & Collamarini, D. 1982: Suolo e vegetazione nella tenuta di Castelporziano. — *Genio Rurale* 9: 35–56.

Gratani, L. 1994: Risposta fotosintetica ed adattamenti morfologici fogliari di alcune specie arbustive sempreverdi a variazioni microclimatiche. — *Ecol. Medit.* 20: 61–71.

Gratani, L. 1995: Structural and ecophysiological plasticity of some evergreen species of the Mediterranean maquis in responses to climate. — *Photosynthetica* 31: 335–343.

Gratani, L. & Amadori, M. 1991: Post-fire resprouting of shrubby species in Mediterranean maquis. — *Vegetatio* 96: 137–143.

Gratani, L., Amadori M. & Veri, L. 1982: A preliminary study of the maquis at Castelporziano (Lazio) structure and biomass with the use of the phytosociological table. — *Ann. Bot. Roma* 40: 163–170.

Gratani, L., Amadori, M., Veri, L., Bruno, F. & Porri, M. 1980: Determinazione di un metodo di stima della biomassa nella macchia di Castelporziano (Lazio). — *Ann. Bot. Roma* 39: 131–151.

Gratani, L. & Bombelli, A. 2000: Correlation between leaf age and other leaf traits in three Mediterranean maquis shrub species: *Quercus ilex*, *Phillyrea latifolia* and *Cistus incanus*. — *Environ. Exp. Bot.* 43: 141–153.

Gratani, L. & Crescente, M. F. 1997: Phenology and leaf adaptative strategies of Mediterranean maquis plants. — *Ecol. Medit.* 23: 11–19.

Gratani, L. & Foti, I. 1998: Estimating forest structure and shade tolerance of the species in a mixed deciduous broad-leaved forest in Abruzzo, Italy. — *Ann. Bot. Fennici* 35: 75–83.

Gutschick, V. P. 1999: Biotic and abiotic consequences of differences in leaf structure. — *New Phytol.* 143: 3–18.

Heide-Jorgensen, H. S. 1990: Xeromorphic leaves of *Hakea suaveolens* R. Br. IV. Ontogeny, structure and function of the sclereids. — *Austr. J. Bot.* 38: 25–43.

Hope, A. S. 1995: Monitoring ecosystems response to global change: high spatial resolution digital imagery. — In: Moreno, J. M. & Oechel, W. C. (eds.), *Global change and Mediterranean-type ecosystems*: 239–253. Ecological Studies 117, Springer-Verlag, New York, Berlin, Heidelberg.

Infante, J. M., Damesin, C., Rambal, S. & Fernández-Alés, R. 1999: Modelling leaf gas exchange in holmoak trees in southern Spain. — *Agric. For. Meteorol.* 95: 203–223.

Kao, W. Y. & Forseth, I. N. 1991: The effect of nitrogen, light and water avalaibility on tropic leaf movements in soybean (*Glycine max*). — *Plant Cell Environ.* 14: 287–293.

Kao, W. Y. & Forseth, I. N. 1992: Diurnal leaf movement, chlorophyll fluorescence and carbon assimilation in soybean growth under different nitrogen and water availability. — *Plant Cell Environ.* 15: 703–710.

Karabourniotis, G. 1998: Light-guiding function of foliar sclereids in the evergreen sclerophyll *Phillyrea latifolia*: a quantitative approach. — *J. Exp. Bot.* 49: 739–746.

Karabourniotis, G., Kofidis, G., Fasseas, C., Liakoura, V. & Drossopoulos, I. 1998: Polyphenol deposition in leaf hairs of *Olea europea* (Oleaceae) and *Quercus ilex* (Fagaceae). — *Am. J. Bot.* 85: 1007–1012.

Kloeppel, B. D., Abrams, M. D. & Kubiske, M. E. 1993: Seasonal ecophysiology and leaf morphology of four successional Pennsylvania barren species in open versus undestorey environments. — *Can. J. For. Res.* 23: 181–189.

Kull, O., Aan, A. & Sõelsepp, T. 1995: Light interception, nitrogen and leaf mass distribution in a multi-layer plant community. — *Funct. Ecol.* 9: 589–595.

Larcher, W. 1995: *Physiological plant ecology.* 3rd ed. — Springer-Verlag, Berlin, Heidelberg. 506 pp.

Loreto, F., Ciccioli, P., Cecinato, A., Brancaleoni, E., Frattoni, M. & Sharkey, T. D. 1996: Different sources of reduced carbon contribute to form three classes of terpenoid emitted by *Quercus ilex* L. leaves. — *Proc. Natl. Acad. Sci. USA* 93: 9966–9969.

Matsuda, K., McBride, J. R. & Kimura, M. 1989: Seedling growth form of oaks. — *Ann. Bot.* 64: 439–446.

Médail, F., Roche, P. & Tatoni T. 1998: Functional groups in phytoecology: an application to the study of isolated plant communities in Mediterranean France. — *Acta Oecol.* 19: 263–274.

Merino, O., Villar, R., Martin, A., Garcia, D. & Merino, J. 1995: Vegetation response to climatic change in a dune ecosystems in Southern Spain. — In: Moreno, J. M. & Oechel, W. C. (eds.), *Global change and Mediterranean-type ecosystems*: 225–238. Ecological Studies 117, Springer-Verlag, New York, Berlin, Heidelberg.

Mitrakos, K. & Christodoulakis, N. S. 1981: Leaf structure diversity in Mediterranean evergreen sclerophyllous. — In: Margaris, N. S. & Mooney, H. A. (eds.), *Components of productivity of Mediterranean-climate regions. Basic and applied aspects*: 21–25. W. Junk Publ., The Hague.

Mooney, H. A., Ferrar, P. J. & Slatyer, R. O. 1978: Photosynthetic capacity and carbon allocation patterns in diverse growth forms of *Eucalyptus*. — *Oecologia* 36: 103–111.

Noble, I. R. & Gitay, H. 1996: A functional classification for predicting the dynamics of landscapes. — *J. Veg. Sci.* 7: 329–336.

Osmond, C. B., Winter, K. & Ziegler H. 1982: Functional significance of different pathways of CO_2 fixation in photosynthesis. — In: Lange, O. L., Nobel, P. S., Osmond, C. B. & Ziegler, H. (eds.), *Physiological plant ecology II. Water relations and carbon assimilation. Encyclopedia of plant physiology* 12 B: 479–547. Springer-Verlag, Berlin, Heidelberg, New York, Tokyo.

Parker, G. G., O'Neill, J. P. & Higman, J. P. 1989: Vertical profile and canopy organization in a mixed deciduous forest. — *Vegetatio* 85: 1–11.

Parkhurst, D. F. 1986: Internal leaf structure: a three-dimensional perspective. — In: Givnish, T. J. (ed.), *On the economy of plant form and function*: 215–249. Cambridge Univ. Press, Cambridge.

Pereira, J. S. & Chaves, M. M. 1995: Plant responses to drought under climate changes in Mediterranean-type ecosystems. — In: Moreno, J. M. & Oechel, W. C. (eds.), *Global change and Mediterranean-type ecosystems*: 140–160. Ecological Studies 117, Springer-Verlag, New York, Berlin, Heidelberg.

Pyankov, V. I., Kondratchuk, A. V., Shipley, B. 1999: Leaf structure and specific leaf mass: the alpine desert plants of the Eastern Pamirs, Tadjikistan. — *New. Phytol.* 143: 131–142.

Reich, P. B. 1993: Reconciling apparent discrepancies among studies relating life span, structure and function of leaves in contrasting plant life forms and climates: 'the blind men and the elephant retold'. — *Funct. Ecol.* 7: 721–725.

Reich, P. B., Kloeppel, B. D., Ellsworth, D. S & Walters, M. B. 1995: Different photosynthesis-nitrogen relations in deciduous hardwood and evergreen coniferous tree species. — *Oecologia* 104: 24–30.

Reich, P. B., Walters, M. B. & Ellsworth, D. S. 1991: Leaf age and season influence the relationship between leaf nitrogen, leaf mass per area, and photosynthesis in maple and oak trees. — *Plant Cell Environ.* 14: 251–259.

Reich, P. B., Walters, M. B. & Ellsworth, D. S. 1992: Leaf life-span in relation to leaf, plant, and stand characteristics among diverse ecosystems. — *Ecol. Monogr.* 62: 365–392.

Shipley, B. 1995: Structured interspecific determinants of specific leaf area in 34 species of herbaceous angiosperms. — *Funct. Ecol.* 9: 312–319.

Shipley, B., Keddy, P. A., Moore, D. R. J. & Lemky, K. 1989: Regeneration and establishment strategies of emergent macrophytes. — *J. Ecol.* 77: 1093–1110.

Smith, W. K., Bell, D. T. & Shepherd, K. A. 1998: Association between leaf structure, orientation, and sunlight exposure in five Western Australian communities. — *Am. J. Bot.* 85: 56–63.

Solbrig, O. T. 1993: Plant traits and adaptative strategies: their role in ecosystem function. — In: Schulze, E. D. & Mooney, H. A. (eds.), *Biodiversity and ecosystem function*: 97–116. Ecological Studies 99, Springer Verlag, Berlin, Heidelberg, New York.

Strain, B. R. & Thomas, R. B. 1995: Anticipated effects of elevated CO_2 and climate change on plant from Mediterranean-type ecosystems utilizing results of studies in other ecosystems. — In: Moreno, J. M. & Oechel, W. C. (eds.), *Global change and Mediterranean-type ecosystems*: 121–139. Ecological Studies 117, Springer-Verlag, New York, Berlin, Heidelberg.

Tenhunen, J. D., Sala Serra, A., Harley, P. C., Dougherty R. L. & Reynolds, J. F. 1990: Factor influencing carbon fixation and water use by Mediterranean sclerophyll shrubs during summer drought. — *Oecologia* 82: 381–393.

Watson, R. T., Rodhe, H., Oescheger, H. & Siegenthaler, U. 1990: Greenhouse gases and aerosols. — In: Houghton, J. T., Jenkins, G. J. & Ephraums, J. J. (eds.), *Climate change: the IPCC scientific assessment*: 1–40. Cambridge Univ. Press, Cambridge.

Werner, C., Correia, O. & Beyschlag, W. 1999: Two

different strategies of Mediterranean macchia plants to avoid photoinhibitory damage by excessive radiation levels during summer drought. — *Acta Oecol.* 20: 15–23.

Wilson, P. J., Thompson, K. & Hodgson, J. G. 1999: Specific leaf area and leaf dry matter content as alternative predictors of plant strategies. — *New Phytol.* 143: 155–162.

Witkowski, E. T. F. & Lamont, B. B. 1991: Leaf specific mass confounds leaf density and thickness. — *Oecologia* 88: 486–493.

Wuenscher, J. E. & Kozlowski, T. T. 1971: Relationship of gas-exchange resistance to tree-seedling ecology. — *Ecology* 52: 1016–1023.