PHOTOSYNTHETICA 42 (4): 551-558, 2004

Adaptive photosynthetic strategies of the Mediterranean maquis species according to their origin

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Abstract

In consideration of their origin the adaptive strategies of the evergreen species of the Mediterranean maquis were analysed. *Rosmarinus officinalis* L., *Erica arborea* L., and *Erica multiflora* L. had the lowest net photosynthetic rate (P_N) in the favourable period [7.8±0.6 µmol(CO$_2$) m^{-2} s^{-1}, mean value], the highest P_N decrease (on an average 86 % of the maximum) but the highest recovery capacity (>70 % of the maximum) at the first rainfall in September. *Cistus incanus* L. and *Arbutus unedo* L. had the highest P_N during the favourable period [15.5±5.2 µmol(CO$_2$) m^{-2} s^{-1}, mean value], 79 % decrease during drought, and a lower recovery capacity (on an average 54 %). *Quercus ilex* L., *Phillyrea latifolia* L., and *Pistacia lentiscus* L. had an intermediate P_N in the favourable period [9.2±1.3 µmol(CO$_2$) m^{-2} s^{-1}, mean value], a lower reduction during drought (on an average 63 %), and a range from 62 % (*Q. ilex* and *P. latifolia*) to 39 % (*P. lentiscus*) of recovery capacity. The Mediterranean species had higher decrease in P_N and stomatal conductance during drought and a higher recovery capacity than the pre-Mediterranean species. Among the pre-Mediterranean species, *P. latifolia* had the best adaptation to long drought periods also by its higher leaf mass per area (LMA) which lowered leaf temperature thus decreasing transpiration rate during drought. Moreover, its leaf longevity determined a more stable leaf biomass during the year. Among the Mediteranean species, *R. officinalis* was the best adapted species to short drought periods by its ability to rapidly recover. Nevertheless, *R. officinalis* had the lowest tolerance to high temperatures by its P_N dropping below half its maximum value when leaf temperature was over 33.6 °C. *R. officinalis* may be used as a bioindicator species of global change.

Additional key words: *Arbutus*; *Cistus*; drought period; *Erica*; *Phillyrea*; *Pistacia*; *Quercus*; recovery capacity; *Rosmarinus*; stomatal conductance.

Introduction

Mediterranean flora is a complex mixture of elements, some deriving from *in situ* evolution (indigenous elements), whereas others having colonised the region from adjacent or far-distant regions in various periods in the past (pre-Mediterranean elements) (Blondel and Aronson 1999). Among the pre-Mediterranean elements, *Phillyrea* is an Afro-tropical one originated from arid sites (Quézel 1985), *Erica* migrated from the mountain ranges of Africa, and *Pistacia* evolved in the semi-arid steppes of the central Asia (Blondel and Aronson 1999). These taxa can be considered "primitive" ones with tropical or subtropical affinities. Among the Mediterranean elements *Arbutus* (Quézel 1985), *Cistus* (Correia and Catarino 1994), *Quercus* (Blondel and Aronson 1999), and *Rosmarinus* (Munné-Bosch *et al.* 1999) are indigenous taxa evolved in more recent time under the Mediterranean climate.

Structural and physiological adaptations of pre-Mediterranean and Mediterranean taxa attain drought resistance by different traits or combination of traits; nevertheless, the extent of these adaptations varies considerably among species co-occurring in the same environments (Gratani 1995, Gratani and Bombelli 2001, Pesoli *et al.* 2003). High leaf consistency, leaf tissue density, leaf thickness, and reduced leaf area are traits improving drought resistance by decreasing photochemical damages of the photosynthetic system (Abril and Hanano 1998, Castro-Díez *et al.* 1998, Gratani and Ghia 2002).

Received 31 May 2004, *accepted* 12 July 2004.

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Abbreviations: E = leaf transpiration rate; g_s = stomatal leaf conductance; L = leaf thickness; LLF = leaf life span; LMA = leaf mass area; P_N = net photosynthetic rate; PAR = photosynthetically active radiation; RWC$_{pd}$ = relative water content at predawn; SD = stomatal density; SAI = stomatal area index; T_l = leaf temperature; WUE = instantaneous water use efficiency; ψ_{pd} = leaf water potential at predawn.

Acknowledgements: This paper was supported by the grants of University of Rome "La Sapienza" for year 2003.

Mediterranean maquis community repeatedly experiences high temperatures and excessive radiation during summer when low water availability limits photosynthetic energy conversion (García-Plazaola *et al.* 1997, Werner *et al.* 2002, Bombelli and Gratani 2003). Global change effects on Mediterranean region are likely to produce warmer and drier conditions, water deficit, and more frequent and stronger drought periods (Houghton *et al.* 2001, Ogaya and Peñuelas 2003a). Increased drought stress may be a discriminant of species distribution and abundance determining changes in vegetation in the long-time (Pereira and Chaves 1995, Gucci *et al.* 1999, Box and Choi 2000, Gratani and Varone 2004).

The main objective of this study was to define the adaptive strategies of the evergreen species of the Mediterranean maquis, in consideration of their origin. The most important strategy of Mediterranean plants in response to drought is to survive and persist under stress, and to be able to recover rapidly after autumn rainfall (Volaire *et al.* 1998). We analysed physiological and anatomical leaf traits of *Arbutus unedo* L., *Cistus incanus* L., *Erica arborea* L., *Erica multiflora* L, *Phillyrea latifolia* L., *Pistacia lentiscus* L., *Quercus ilex* L., and *Rosmarinus officinalis* L. co-occurring in the maquis developing along the coast near Rome and their recovery capacity after a severe drought period occurring from beginning of May to the end of August 2003. The correlation between anatomical and physiological traits may explain the co-occurrence of these species in the maquis.

Materials and methods

Study area: The study was conducted in the Mediterranean maquis developing within the Castelporziano Estate (41°45'N, 12°26'E, Rome), and characterised by 1.0 ±0.5 m tall shrubs and 2.5 leaf area index (LAI) (Gratani and Crescente 2000). The area climate was of Mediterranean type and most of its annual rainfall was distributed in autumn-winter. The average minimum air temperature of the coldest months (February) was 4.0±1.6 °C and the average maximum air temperature of the hottest month (August) was 30.8±1.4 °C. Dry period was from May to August (96.9 mm total rainfall) (data by the Castelporziano Meteorological Station for the period 1985–2003). The soil was a regosoil (Gisotti and Collamarini 1982). Soil water content was 0.5–8.0 % during the year, minimum values occurring in August and maximum ones in December (Gratani and Crescente 1997).

The year 2003 was characterised by a severe drought period from May 1th to August 20th (4 mm total rainfall and 31.4±3.8 °C average maximum air temperature) (Fig. 1). During the study period, the maximum photosynthetic photon flux density was around 1 800 μmol(photon) m^{-2} s^{-1}. Field measurements were carried out from April to October 2003.

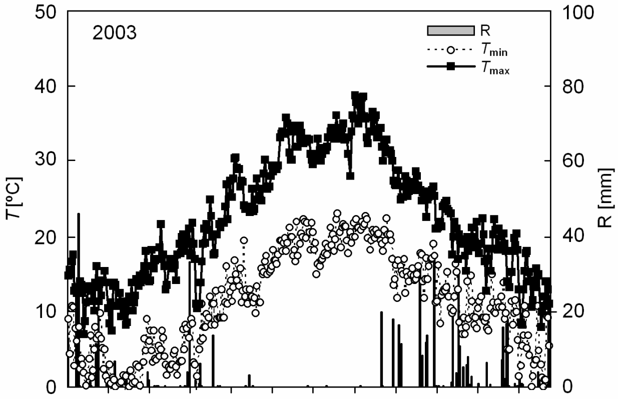

Fig. 1. Annual trends of monthly air temperatures and monthly rainfall for the study period (2003). R = total monthly rainfall; T_{min} = minimum air temperature; T_{max} = maximum air temperature (data of the Meteorological Station of Castelporziano, Rome).

Leaf gas exchange: Photosynthetically active radiation (PAR) [μmol(photon) m^{-2} s^{-1}], P_N [μmol(CO_2) m^{-2} s^{-1}], stomatal conductance (g_s) [mmol(H_2O) m^{-2} s^{-1}], E [mmol(H_2O) m^{-2} s^{-1}], and leaf temperature (T_l) [°C] were monitored during the study period by an infrared gas analyser *Ciras-1* open system (*PP Systems*, UK), equipped with a leaf chamber *PLC* narrow cuvette for the measurements of *E. arborea*, *E. multiflora*, and *R. officinalis*, and with a 2.5 cm^2 leaf area chamber (*Ciras-1 Parkinson* leaf cuvetes) for the other considered species. Field measurements were carried out *in situ* on the external exposed apical shoots of *E. arborea*, *E. multiflora*, and *R. officinalis* (Munné-Bosch *et al.* 1999) and on the external "sun" exposed leaves of *Q. ilex*, *P. latifolia*, *P. lentiscus*, and *C. incanus* of the selected shrubs. All the measurements were carried out under natural conditions, on cloud-free days [PAR > 800 μmol(photon) m^{-2} s^{-1}] to ensure that near-maximum daily photosynthetic rates were measured (Reich *et al.* 1995). Gas exchange measurements were carried out in April–May (favourable period), June–July (drought period), and September–October (recovery period) according to Gratani and Bombelli (2001). Instantaneous WUE [μmol(CO_2) $mmol^{-1}$(H_2O)] was calculated by the ratio P_N/E (Larcher 2003).

Stomatal density (SD) and size: Mature leaves were detached from the same, southern, upper portion of each shrub (10 "sun" leaves per 5 shrubs per species) at the end of May. SD [per mm^2] was determined from nail varnish impressions of the abaxial lamina immediately to the right of the mid-vein, according to Sack *et al.* (2003). The numbers of stomata were counted on separate impressions of the lamina (10 per species) each of 0.5×1.0 cm.

Guard cell length and width were measured on randomly selected stomata from five leaves per shrub (per species), according to Mishra (1997). Stomatal area index (SAI) was calculated by taking the product of the mean stomatal length and the SD according to Ashton and Berlyn (1994).

Statistics: All statistical tests were performed using a statistical software package (*Statistica*, *Statsoft*, USA). Differences in leaf traits were determined by analysis of variance (ANOVA) and Tukey test for multiple comparisons. Regression analysis was conducted to examine the correlation between P_N and g_s, P_N and T_l, and SD and g_s.

The considered leaf traits and species were analysed by PCA (principal component analysis) on the basis of a matrix of the normalised data. This analysis was conducted using also data from Gratani and Bombelli (2001), Gratani and Varone (2004), Gratani and Ghia (2002) for leaf mass area (LMA), leaf thickness (L), and leaf life span (LLF), and from Bombelli and Gratani (2003) for leaf water potential at predawn (ψ_{pd}), and relative water content (RWC_{pd}). The matrix was subjected to a rotated principal component analysis with the objective of summarising the main factors determining the variation of the analysed traits in the considered species, according to García-Plazaola *et al.* (2000).

Results

Leaf gas exchange: The photosynthetic activity of the considered species had the same trend during the year, nevertheless there were the same differences: *C. incanus* and *A. unedo* had the highest P_N rates [22.5±0.5 and 14.2±2.0 μmol(CO_2) m^{-2} s^{-1}, respectively] in spring, followed by *Q. ilex*, *P. lentiscus* and *P. latifolia* [13.2±2.0, 12.9±1.0, and 12.0±0.5 μmol(CO_2) m^{-2} s^{-1}, respectively], and by *E. arborea*, *E. multiflora*, and *R. officinalis* [9.3±1.1, 8.9±0.7, and 8.1±0.2 μmol(CO_2) m^{-2} s^{-1}, respectively] (Fig. 2).

Lower P_N values were measured during the drought period (beginning of May–end of August, 4 mm total rainfall and 31.4±3.8 °C average maximum air temperature) and the absolutely lowest ones in July. *R. officinalis* and *C. incanus* showed the highest P_N rate decrease (91 % of the maximum), followed by *E. multiflora* and *E. arborea* (80 % on an average), *A. unedo, Q. ilex,* and *P. lentiscus* (65 % on an average), and *P. latifolia* (58 %).

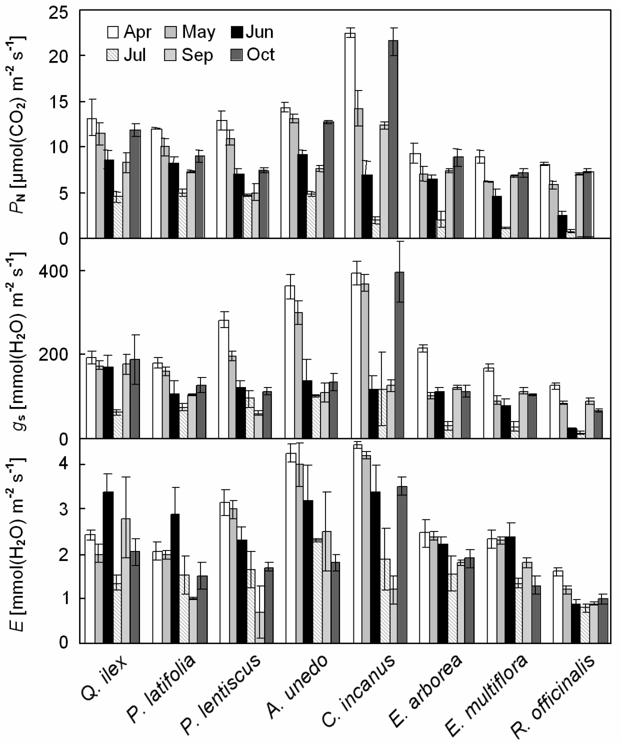

Fig. 2. Monthly trends of net photosynthetic rate (P_N), stomatal conductance (g_s), and transpiration rate (*E*) of the considered species for the study period. Means of ten measurements, standard deviations are shown. Within the same month, means of different species were significantly different (ANOVA, $p<0.05$).

The considered species recovered from the severe drought period after the first rainfall at the middle of September (66.2 mm of total rainfall from August 26th to September 15th and 22.8 °C mean air temperature). Nevertheless, the recovery pattern of the photosynthetic activity varied among the species: *R. officinalis, E. arborea*, and *E. multiflora* had the highest P_N recovery (>70 % of the maximum) followed by *Q. ilex* and *P. latifolia* (62 % on an average), *C. incanus* and *A. unedo* (54 % on an average); *P. lentiscus* showed the lowest recovery (39 % of the maximum). At the beginning of October (101 mm of total rain from September 15th up to October 9th) *C. incanus*, *E. arborea, R. officinalis, Q. ilex*, *A. unedo, E. multiflora*, and *P. latifolia* reached 88 % of the maximum P_N, but *P. lentiscus* only 57 % of the maximum.

Stomatal conductance, g_s (Fig. 2) showed the same trend as P_N, with the highest rate in April and a drastic reduction during the severe drought period. *C. incanus* had the highest yearly g_s [285±157 mmol(H_2O) m^{-2} s^{-1}] and *R. officinalis* the lowest one [66±39 mmol(H_2O) m^{-2} s^{-1}]. *R. officinalis* and *E. arborea* had the highest g_s decrease in drought (88 % on an average) and *P. latifolia* and *P. lentiscus* the lowest one (63 % on an average). Despite the high g_s reduction (70 % of the maximum) *C. incanus* and *A. unedo* had the highest *E* during drought [on an average 2.1±0.3 mmol(H_2O) m^{-2} s^{-1}] and *R. officinalis* the lowest one during the year.

There was a significant ($p<0.01$) correlation *r* between P_N and g_s in the considered species explaining on an average 90 % of the variation (Table 1). *P. latifolia* and *P. lentiscus* had the highest *r* (0.97).

R. officinalis and *E. multiflora* showed the lowest WUE (Table 2) during the drought period

[0.9±0.1 μmol(CO_2) $mmol^{-1}$(H_2O)], while *P. latifolia* and *Q. ilex* the highest one [3.3±0.01μmol(CO_2) $mmol^{-1}$ (H_2O)]. *C. incanus* and *A. unedo* showed intermediate values [1.6±0.7 μmol(CO_2) $mmol^{-1}$(H_2O)].

The polynomial relationship between P_N and T_l represented the influence of temperature on functioning (Larcher 1994). The correlation indicated that the favourable T_l enabling 90–100 % of the high P_N for the considered species was in the range 14.6–29.8 °C (Table 3). P_N dropped below half its maximum value when T_l was on an average over 32.9 °C for *C. incanus* and *A. unedo*, 34.8 °C for *R. officinalis*, *E. multiflora*, and *E. arborea*, and 36.9 °C for *Q. ilex*, *P. latifolia*, and *P. lentiscus*.

Table 1. Summary of regression analysis between net photosynthetic rate (P_N, y) or stomatal density (SD, y) and stomatal leaf conductance (g_s, x) for the considered species. The correlations were significant at $^*p<0.001$ and $^{**}p<0.05$.

Species	Relationship	*r*
Q. ilex	$P_N = 0.0556\, g_s + 0.5345$	0.86^*
P. latifolia	$P_N = 0.0580\, g_s + 1.2455$	0.97^*
P. lentiscus	$P_N = 0.0396\, g_s + 2.1634$	0.96^*
E. arborea	$P_N = 0.0378\, g_s + 2.4673$	0.86^*
E. multiflora	$P_N = 0.0476\, g_s + 0.9205$	0.91^*
R. officinalis	$P_N = 0.0630\, g_s + 1.2862$	0.89^*
A. unedo	$P_N = 0.0285\, g_s + 4.8445$	0.86^*
C. incanus	$P_N = 0.0430\, g_s + 1.9722$	0.87^*
All the species	$SD = -0.0056\, g_s^2 + 3.5450\, g_s - 246.4300$	-0.50^{**}

Table 2. Monthly values of water use effficiency (WUE) [μmol(CO_2) mol^{-1}(H_2O)] for the considered species during the study period. Standard deviations are showed. Within the same month means of different species with the same letter are not significantly different (ANOVA, $p>0.05$).

	Q. ilex	*P. latifolia*	*P. lentiscus*	*A. unedo*	*C. incanus*	*E. arborea*	*E. multiflora*	*R. officinalis*
Apr	5.5±1.1a	5.9±0.6b	4.1±1.1c	3.4±1.5d	5.1±0.8e	3.8±0.1f	3.8±1.0f	5.1±2.0g
May	5.7±0.8a	5.1±1.1b	3.7±0.8c	3.3±1.0d	3.4±0.6d	2.9±0.2e	2.7±0.5e	4.8±1.2f
Jun	2.5±0.3a	2.9±0.2a	3.0±0.2a	2.9±0.9a	2.0±0.1b	2.9±0.3a	1.9±0.1b	2.8±0.6a
Jul	3.3±0.6a	3.3±0.7a	2.9±0.1a	2.1±0.3b	1.1±0.01c	1.3±0.2d	0.8±0.03e	0.9±0.04e
Sep	3.8±2.0a	7.4±0.1b	5.2±2.7c	6.5±2.1d	11.1±2.0e	4.1±0.02f	3.9±0.4f	7.8±0.4g
Oct	5.9±1.1a	6.2±1.2b	4.4±0.4c	6.0±0.6d	6.1±0.7d	4.6±0.9c	5.4±0.5e	7.0±1.0f

Table 3. Correlation analysis between net photosynthetic rate (y) and leaf temperature (x) [°C] of the considered species, during the study period. $T_{100\%}$ = leaf temperature enabling 100 % of high photosynthetic rates; $T_{100\text{-}90\%}$ = leaf temperature enabling 100–90 % of high photosynthetic rates; $T_{90\text{-}50\%}$ = leaf temperature enabling 90–50 % of high photosynthetic rates.

Species	Relationship	$T_{100\%}$	$T_{100–90\%}$	$T_{90–50\%}$
Q. ilex	$y = -0.0269\, x^2 + 1.1418\, x - 1.2598$	21.2	14.6–27.7	7.1–35.3
P. latifolia	$y = -0.0235\, x^2 + 1.0815\, x - 2.8458$	23.0	16.2–29.8	8.7–37.3
P. lentiscus	$y = -0.0184\, x^2 + 0.8528\, x - 1.5746$	23.2	16.6–29.6	7.9–38.3
E. arborea	$y = -0.0188\, x^2 + 0.8501\, x - 1.5440$	22.6	16.2–28.9	8.1–37.2
E. multiflora	$y = -0.0386\, x^2 + 1.8453\, x - 14.6000$	23.9	19.7–28.0	14.2–33.6
R. officinalis	$y = -0.0363\, x^2 + 1.7154\, x - 12.8550$	23.6	18.7–28.6	13.7–33.6
A. unedo	$y = -0.0479\, x^2 + 2.1228\, x - 10.9540$	22.1	17.2–26.6	10.4–33.4
C. incanus	$y = -0.0851\, x^2 + 3.7261\, x - 22.1500$	21.9	17.1–26.6	11.3–32.5

SD and SAI: SD varied significantly among the considered species: *Q. ilex* showed the highest value (468±88 stomata per mm^2), followed by *P. lentiscus* and *P. latifolia* (325±20 and 251±12 stomata per mm^2, respectively), *A. unedo* and *C. incanus* (on an average 217±20 stomata per mm^2), and *E. arborea*, *E. multiflora,* and *R. officinalis* (on an average 179±14 stomata per mm^2), the last ones showing the lowest SD (Fig. 3). The regression analysis showed a significant ($p<0.05$) correlation ($r = 0.50$) between SD and g_s (Table 1).

SAI (Fig. 3) was the highest in *Q. ilex* (11.7) and *P. latifolia* (7.7) and the lowest in *E. arborea*, *E. multiflora* and *R. officinalis* (on an average 3.2±0.4); *C. incanus* and *A. unedo* showed intermediate values (5.2±1.7 on an average).

Principal component analysis (PCA): P_N, g_s, E, WUE (measured in favourable period, during drought, and at recovery), SD, and SAI of the considered species were subjected to PCA (Fig. 4) using also data from Gratani and Bombelli (2001), Gratani and Varone (2004), and Gratani and Ghia (2002) for LMA, L, and LLF, and from Bombelli and Gratani (2003) for ψ_{pd} and RWC_{pd}.

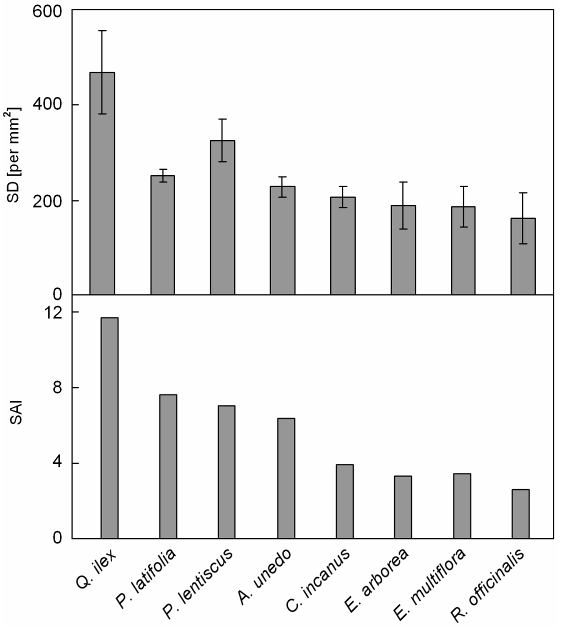

Fig. 3. Stomatal density (SD) and stomatal area index (SAI) of the considered species. Each point is the mean of ten measures, standard deviations are shown. All differences are significant (ANOVA, $p<0.05$).

PCA showed a main trend of the considered species along the first axis related negatively to the decrease of P_N, g_s, and WUE during drought and positively to SD, SAI, and RWC at predawn during drought and to LLF, and a trend along the second axis (orthogonal to the first). This last value was negatively related to P_N and g_s during the favourable period and positively to P_N recovery and E in the favourable period. The two axes accounted for 66 % of the total variance (35 and 31 %, respectively). The analysis showed a separation between the considered species along the two axes: *Q. ilex*, *P. latifolia*, *A. unedo*, and *P. lentiscus* were characterised by higher values of the first axis than *C. incanus*, *E. arborea*, *E. multiflora*, and *R. officinalis*. Moreover, *Q. ilex*, *P. latifolia*, *E. arborea*, *E. multiflora*, and *R. officinalis* showed higher values along the second axes than *P. lentiscus*, *A. unedo*, and *C. incanus*.

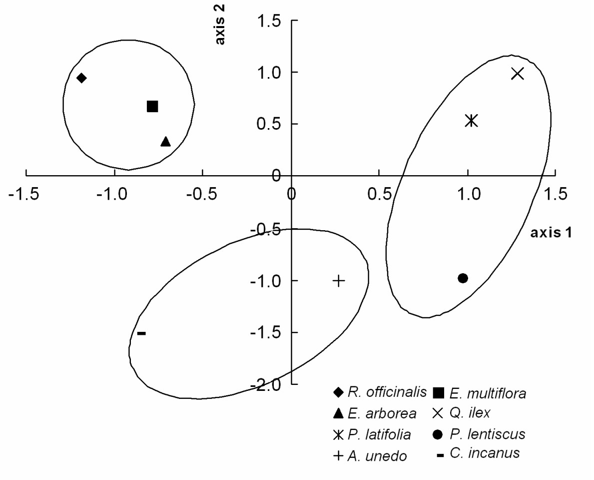

Fig. 4. Principal component analysis (PCA) of leaf functional traits (P_N, g_s, E, WUE, ψ_{pd}, RWC_{pd}) measured in favourable, drought, and recovery period. Phenological traits (LLF) and leaf morpho-anatomical traits (LMA, L, SD, SAI) for the considered species. The species within cluster circles have similar leaf functional and morpho-anatomical traits.

Discussion

The overall results of this research underline that the evergreen species of the Mediterranean maquis had different photosynthetic responses to drought and a different recovery capacity by their morpho-anatomical and physiological traits. *R. officinalis*, *E. arborea*, and *E. multiflora* had the lowest P_N in the favourable period [7.8±0.6 μmol(CO_2) m^{-2} s^{-1}, mean value] and the highest decrease (on an average 86 % of the maximum) but the highest recovery capacity (>70 % of the maximum) at the first rainfall in September. *C. incanus* and *A. unedo* had the highest P_N during the favourable period [15.5± 5.2 μmol(CO_2) m^{-2} s^{-1}, mean value], 79 % decrease during drought, and a low recovery capacity (on an average 54 %). *Q. ilex*, *P. latifolia*, and *P. lentiscus* had intermediate P_N in the favourable period [9.2±1.3 μmol(CO_2) m^{-2} s^{-1}, mean value], a low reduction during drought (on an average 63 %), and a 62 % (*Q. ilex* and *P. latifolia*)–39 % (*P. lentiscus*) recovery capacity.

Q. ilex, *P. latifolia*, and *P. lentiscus* had the highest WUE during drought [3.2±0.2 μmol(CO_2) $mmol^{-1}$(H_2O)]; *E. arborea*, *E. multiflora,* and *R. officinalis* the lowest one [1.0±0.3 μmol(CO_2) $mmol^{-1}$(H_2O)]; *C. incanus* and *A. unedo* had an intermediate value [1.6±0.7 μmol(CO_2) $mmol^{-1}$(H_2O) on an average].

Under Mediterranean field conditions chlorophyll content loss acted as a supplementary defence along increased reflectance (Kyparissis and Manetas 1993) reducing photon absorbance and alleviating the adverse effects of drought (Kyparissis *et al.* 2000). Moreover, the increased carotenoid/chlorophyll ratio during drought reduced the risk of over-excitation and photo-oxidative damage. *R. officinalis* shows the highest chlorophyll reduction (72 %) and the highest carotenoid/chlorophyll ratio increase (Gratani and Varone 2004) contributing to reduction of the damage to the photosynthetic machinery. Changes in pigment contents explain *R. officinalis* ability to recover more rapidly to the first rainfall than the other considered species. Among the other species, *E. arborea* and *E. multiflora* show a substantial decrease of chlorophyll content during drought (62 % on an average) (Gratani and Varone 2004) while *Q. ilex*, *P. latifolia*, *P. lentiscus*, and *A. unedo* show a lower (9 %) one (Gratani 1995).

Moreover, *R. officinalis* showed the highest g_s decrease (90 %) during drought. Stomatal closure during drought might avoid dehydration and therefore major tissue damage (Pereira and Chaves 1995).

SD and SAI varied in the considered species, with the highest values in *Q. ilex*, *P. lentiscus*, and *P. latifolia* (348±110 and 8.8±2.5 stomata per mm^2, respectively) and the lowest values in *R. officinalis*, *E. multiflora*, and *E. arborea* (179±14 and 3.2±0.4 stomata per mm^2, respectively). *C. incanus* and *A. unedo* showed intermediate values (217.0±20.0 and 5.2±1.7 stomata per mm^2, respectively). SD and stomata size influence g_s (Wong *et al.* 1979), contributing to the adaptive strategy to drought confirmed by the correlation between SD and g_s ($r = 0.50$). The sclerophyllous species (*Q. ilex*, *P. latifolia*, and *P. lentiscus*) by the highest SD and SAI (79 and 121 %, respectively, higher than the other species) and the high stomatal control (Flexas *et al.* 2001, Ogaya and Peñuelas 2003a) are able to have a more efficient water use during all the year and in drought.

Water availability is an important factor affecting photosynthetic activity of Mediterranean species (Llorens *et al.* 2003). Gratani and Varone (2003) underline that *Q. ilex*, *P. latifolia*, *P. lentiscus*, and *E. arborea* have sufficiently high leaf water potential and relative water content during drought. The lower leaf water potential (ψ) variation during the year and the highest ψ and RWC during drought are also due to their ability to access water from those parts of the soil profile which are subjected to narrow changes in soil water. All these species are characterised by a deep root system (data not shown). *P. lentiscus* has the lowest ψ and RWC variation during the year. On the contrary, the large ψ variation during the year and the low ψ and RWC during drought of *R. officinalis*, *C. incanus*, and *E. multiflora* (shallow root system, data not shown) are also the result of the species accessing part to the superficial soil profile that is subjected to large changes in water content.

Leaf morphology and anatomy influence the photosynthetic activity (Wright *et al.* 2001). Gratani and Ghia (2002) and Gratani and Varone (2004) indicate that variations in leaf mass area (LMA) are tightly associated with variations in leaf tissue density (LTD) and leaf thickness (L): the higher LMA values in *P .latifolia*, *Q. ilex*, and *P. lentiscus* (209±20, 207±17, and 187±13 g m^{-2}, respectively) result in a higher leaf compactness (higher sclerophylly) improving drought resistance. *C. incanus* and *A. unedo* had low LMA values (143±15 and 160±11 g m^{-2}, respectively) decreasing drought resistance, nevertheless, the shorter diffusion pathway from stomata to chloroplasts (Parkhurst 1994) favoured higher photosynthetic capacity during drought: *E. arborea*, *E. multiflora*, and *R. officinalis* are characterised by a small leaf size and by a range of LMA from 126 to 259 g m^{-2}.

The species which are considered of the same origin may have different morpho-anatomical traits and physiological responses to drought stress, reflecting different adaptive strategies. The considered species have different traits or assemblages of traits converging on the control of the transpiration. Patterns among individual species that belong to a closely related assemblage and patterns among the assemblage themselves may prove useful to understand species habitat specialisation (Ashton and Berlyn 1994). The results of this research underline that the Mediterranean species have a higher P_N and g_s decrease during drought and a higher recovery capacity than the pre-Mediterranean species. Among the pre-Mediterranean species, generally characterised by a deep root system, *P. latifolia* is best adapted to long drought periods also by its higher LMA which lowers leaf temperature, decreasing *E* during drought. Moreover, its long longevity (3–4 years) (Gratani and Bombelli 2001) determines a more stable leaf biomass during the year. And the polynomial correlation between T_l and P_N showed a lower sensibility of this species to the highest temperatures. The cumulative carbon assimilation available for plant growth is drastically reduced when T_l is above 37 °C.

Among the Mediteranean species, generally characterised by a shallow root system, *R. officinalis* is the best adapted species to short drought periods by its ability to rapidly recover. Nevertheless, *R. officinalis* has the lowest tolerance to high temperatures by its P_N dropping below half its maximum value when T_l is over 33.6 °C. It loses *ca.* 50 % of its leaves at the end of severe drought periods (Gratani and Varone 2004). *R. officinalis* may be used as a bioindicator species of global change.

The PCA confirms these results, underlining three groups of species co-existing in Mediterranean maquis: one group is formed by *E. arborea*, *E. multiflora*, and *R. officinalis*; a second one by *Q. ilex*, *P. latifolia*, and *P. lentiscus*; and a third one by *C. incanus* and *A. unedo*. According to Soares *et al.* (1995) the species having similar factor scores are grouped together, showing similar morpho-anatomical and physiological leaf traits.

Drought stress is the climatic factor essentially responsible for growth and survival of evergreen woody species in the Mediterranean Region. The intrinsic link between photosynthesis and biomass production suggests that photosynthesis and its response to drought probably play a major role in determining the ability of these species to persist in drought-prone areas (Lambers *et al.* 1998, Gulías *et al.* 2002), also in consideration of global change. The physiological responses could be followed by changes in carbon acquisition of Mediterranean forests

(Reichstein *et al.* 2002) and in a long-term by changes in species distribution conferred by the different capacity of different species to survive under the new climatic constraints (Ogaya and Peñuelas 2003b). Thus, an important task for comparative environmental physiology should be the precise and long-term monitoring of environments and functional traits of the most representative species of this region (Larcher 2000).

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