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Long-time variations in leaf mass and area of Mediterranean evergreen broad-leaf and narrow-leaf maquis species

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Abstract

Morphological (dry mass, DM; surface area, LA; leaf mass per area, LMA), anatomical (leaf thickness, L), phenological (leaf life span, LL), and physiological (net photosynthetic rate, P_N) leaf traits of the evergreen species co-occurring in the Mediterranean maquis developing at Castelporziano (Rome) were tested. The correlation analysis indicated that LMA variation was tightly associated with LL variations: *Cistus incanus* and *Arbutus unedo* had a short LL (4±1, summer leaves, and 11±1 months, respectively) and low LMA (153±19 g m^{-2}) values, *Quercus ilex, Phillyrea latifolia*, and *Pistacia lentiscus* high LMA (204±7 g m^{-2}) and long LL (22±3 months), *Erica arborea*, *Erica multiflora*, and *Rosmarinus officinalis* a short LL (9±2 months) and an either high (213±29 g m^{-2}, *R. officinalis* and *E. multiflora*) or low (115±17 g m^{-2}, *E. arborea*) LMA. LMA values were significantly ($p \le 0.05$) correlated with P_N ($r \ge 0.68$). In the tested species, LMA increased in response to the decrease of the total rainfall during the leaf expansion period. LMA variation was due to the unequal variation of DM and LA in the considered species. LMA is thus a good indicator of evergreen maquis species capability to respond to climate change, in particular to total rainfall decrease in the Mediterranean basin.

Additional key words: dry mass; *Erica*; leaf life span; leaf mass per area; *Phillyrea*; *Pistacia*; *Quercus*; rainfall; *Rosmarinus*.

Introduction

Sclerophylly is a recurrent plant trait in areas with Mediterranean climate, protecting plants facing drought stress and resulting from selection for increased leaf life-span (LL) under resource shortage (Turner 1994, Salleo and Nardini 2000, Gratani and Ghia 2002). The leaf mass per area (LMA) characteristic has been suggested as a measure of sclerophylly (Stocker 1931). Cowling and Campbell (1983) use the LMA value of 70 g m^{-2} to distinguish sclerophylls from non-sclerophylls. Species with a low LMA have a higher photosynthetic capacity per unit leaf mass (LM), that results from a larger photon-capture area per mass (Wright *et al.* 2001). A higher internal competition for photons and CO_2 (Poorter *et al.* 1990), a higher internal resistance to CO_2 transfer (Lloyd *et al.* 1992), a low proportion of leaf nitrogen in photosynthetic enzymes (Evans 1989, Niinemets 1999), and an unequal distribution of N in the different enzymes involved in CO_2 assimilation (Poorter and Evans 1998) have been proposed as factors responsible for the low photosynthetic rates in leaves of high LMA.

In growth models, many authors have considered LMA either as a constant (Gratani 1995), as a function of plant developmental stage (Gratani and Crescente 1997), or dependent on climate fluctuations (Bertin and Gary 1998). Slow leaf turnover (*i.e.* long LL) is associated with structural investment measured as LMA (Reich *et al.* 1992, Wright and Cannon 2001, Gratani and Varone 2004a). Species with high LMA have long LL, both in comparison with coexisting species, than species from many different habitats (Gratani and Crescente 1997, Reich *et al.* 1997, Diemer 1998a,b). The chief reason why species with high LMA achieve long LL is because LMA is related to leaf strength, and the more sturdy the leaves, the more tolerant they are (Chabot and Hicks 1982, Grubb 1986, Coley 1988, Reich *et al.* 1991, Gratani and Bombelli 2001, Wright and Cannon 2001). An overview of LL-LMA combinations in co-occurring species at dry sites suggests that there are relative advantages enjoyed by various species along the whole spectrum (Wright *et al.* 2002, Gratani and Varone 2004a). Thus, the relationship LL-LMA should be analysed considering a broad set of structural and functional leaf traits. Search

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Abbreviations: DM – leaf dry mass; L – leaf thickness; LA – leaf area; LL – leaf life span; LMA – leaf mass per area; P_N – net photosynthetic rate; PAR – photosynthetically active radiation; R_{LE} – total rainfall during the leaf expansion period; R_{tot} – total yearly rainfall; T_{max} – mean maximum air temperature during the period of leaf expansion; T_{min} – mean minimum air temperature during the period of leaf expansion.

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for those leaf traits, indicative of plant species adaptability to environmental constraints, is crucial for understanding their functional ecology. It involves an interest in the response of plant species to the increasing length and intensity of drought stress in the Mediterranean Region (IPCC 2001, Gulías *et al.* 2002).

The main objective of this study was to analyse morphological (dry mass – DM, leaf area – LA, leaf mass per area – LMA), anatomical (L – leaf thickness), phenological (LL – leaf life span), and physiological (net photosynthetic rate – P_N) leaf traits of the evergreen species co-occurring in the Mediterranean maquis developing at Castelporziano (Rome), by addressing the following questions: (*1*) Do leaf traits differ among species co-occurring in the same environment? (*2*) Do leaf traits change in response to changing climatic factors? (*3*) What is the most discriminating trait influencing LMA variation among different species?

Moreover, the ecological interpretation of LMA variation considers the associated traits (Castro-Díez *et al.* 2000). High LMA values improve drought resistance of sclerophyllous species (Abril and Hanano 1998, Castro-Díez *et al.* 1998, Gratani and Bombelli 1999, Werner *et al.* 1999, Gratani and Ghia 2002, Gratani and Varone 2004a). Therefore we hypothesise that increasing drought stress may lead to an increase of LMA in Mediterranean evergreen species. LMA may be used to monitor long-term species response to the increasing drought stress.

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). A detailed description of the vegetation type is given in Gratani and Crescente (2000). The climate of the area is of Mediterranean type (Fig. 1) and most of its annual rainfall is distributed in autumn-winter. The average minimum air temperature of the coldest months (January and February) was 4.00±0.01 °C and the average maximum air temperature of the hottest month (August) was 30.80±1.40 °C. Total annual rainfall was 714 mm, and dry period was from May to August (98.2 mm total rainfall) (data by the Castelporziano Meteorological Station for the period 1985–2004).

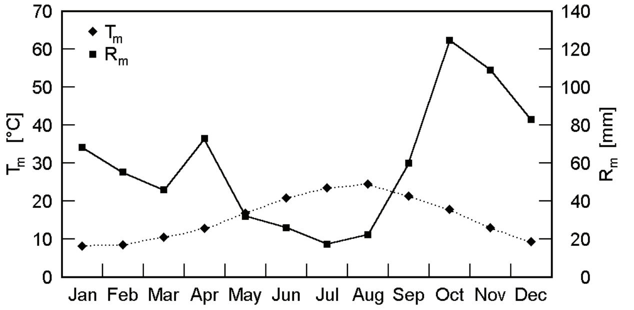

Fig. 1. Ombrothermic diagram of Castelporziano for the period 1985–2004, according to Bagnouls and Gaussen (1953). Data of the Meteorological Station of Castelporziano, Rome. T_m = monthly air temperature; R_m = monthly total rainfall.

The years 2000–2004 were characterised by an 11 % decrease of total rainfall with respect to the general trend. The year 2003 was characterised by a severe drought period from May 1th to August 20th (4 mm total rainfall and 31.1 °C average maximum air temperature), and the year 2004 by a moderate stress period (121.8 mm total rainfall and 27.4 °C average maximum air temperature) (Fig. 2).

Field measurements were carried out in the period January 2000–December 2004, on *Quercus ilex* L., *Phillyrea latifolia* L., *Pistacia lentiscus* L., *Arbutus unedo* L., *Cistus incanus* L., *Erica arborea* L., *Erica multiflora* L., and *Rosmarinus officinalis* L. (twelve individuals per species).

Leaf morphology and anatomy: Measurements of leaf morphology included LA [cm^2], obtained by the Image Analysis System (*Delta–T Devices*, UK), and DM [mg] when oven-dried at 80 °C to constant mass. LMA [g m^{-2}] was calculated from leaf DM and one-sided leaf area (Gratani and Varone 2004a). L [μm] was measured by leaf sections ($n = 20$ per species) from twenty fresh, fully expanded leaves from the selected shrubs and measured by light microscope. Measurements were carried out on mature leaves each year in September.

Leaf life-span: For repeated non-destructive measurements of LL [months], one hundred shoots (per species) of the selected shrubs were labelled with nylon tape and monitored at weekly intervals during the study period (from January 2000 to December 2004), according to Gratani and Crescente (1997).

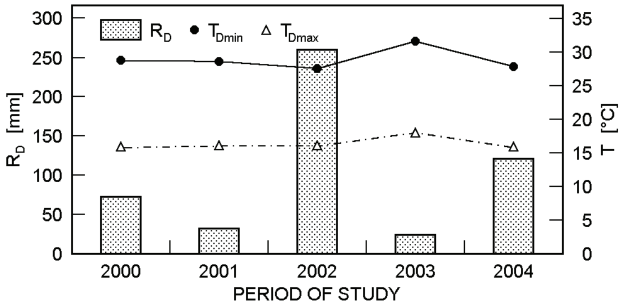

Fig. 2. Trend of air temperature and total rainfall during the drought period (May–August) for the study period (2000–4). R_D = total rainfall during drought period; T_{Dmin} = minimum air temperature during drought period; T_{Dmax} = maximum air temperature during the drought period (data of the Meteorological Station of Castelporziano, Rome).

Photosynthetic activity: PAR [μmol(photon) m^{-2} s^{-1}] and $P_{\rm N}$ [μmol(CO$_2$) m^{-2} s^{-1}] were monitored with 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 cuvette) for the other 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 the selected shrubs of *Q. ilex*, *P. latifolia*, *P. lentiscus*, and *C. incanus*. All the measurements were carried out in 2004, under natural conditions, on cloud-free days [PAR>800 μmol(photon) m^{-2} s^{-1}], according to Reich *et al.* (1995).

Statistics: All statistical tests were performed using a statistical software package (*Statistica*, *Statsoft*, USA). The differences in leaf traits were determined by analysis of variance (ANOVA) and Tukey's test for multiple comparisons. Correlation analysis was carried out using also data from Gratani and Crescente (1997), Crescente (1998), Gratani and Bombelli (1999, 2001), Gratani and Ghia (2002), and Gratani and Varone (2004a,b).

Results

Leaf morphology and anatomy: Leaf morphological traits for the considered species significantly differed between the study period (January–December 2004; Table 1). All the considered species had the highest LMA in the year 2003 (characterised by a severe drought from May 1th to August 20th). *E. multiflora* had the highest LMA [g m^{-2}] (263±23), followed by *P. latifolia* (254±29), *P. lentiscus* (223±19), *Q. ilex* (209±29), *R. officinalis* (206±8), *A. unedo* (185±6), *C. incanus* (165±3), and *E. arborea* (140±1) (Fig. 3).

Comparing LMA values measured in the broadleaf species in the year 2004 (850 mm total rainfall) with those measured in the year 2003 (596 mm total rainfall), LMA increased by 7 % in *Q. ilex* and *P. lentiscus* due to a 6 % increase of DM, by 37 % in *P. latifolia* due to a 54 % increase of DM, and by 19 % in *A. unedo* due to an 11 % LA decrease. The 15 % LMA increase in *C. incanus* was justified by a 7 % DM decrease associated with a strong decrease of LA by 24 % (Fig. 4).

Table 1. Results of ANOVA analysis for the leaf mass per area (LMA) and leaf thickness (L). For the considered study years the means of each species with the same letters are not significantly different ($p \geq 0.05$). p-values were always 0.0001, with the exception of value 0.01 for *Q. ilex* LMA.

Species	LMA 2000	2001	2002	2003	2004	F	L 2000	2001	2002	2003	2004	F
Q. ilex	abc	abc	c	b	ac	4.9	ab	a	b	c	c	27.0
P. latifolia	a	b	ab	c	a	23.5	a	b	c	d	e	1363
P. lentiscus	a	b	b	c	b	23.7	a	b	a	c	d	80.8
A. unedo	a	b	a	b	a	19.7	a	b	b	b	c	188.4
C. incanus	a	b	a	b	c	65.8	a	b	b	c	d	276.7
E. arborea	a	b	c	d	c	42.2	a	b	ac	b	ac	26.7
E. multiflora	a	b	c	b	a	52.4	a	a	a	b	a	98.5
R. officinalis	a	b	c	b	b	23.7	a	b	c	bd	bd	73.2

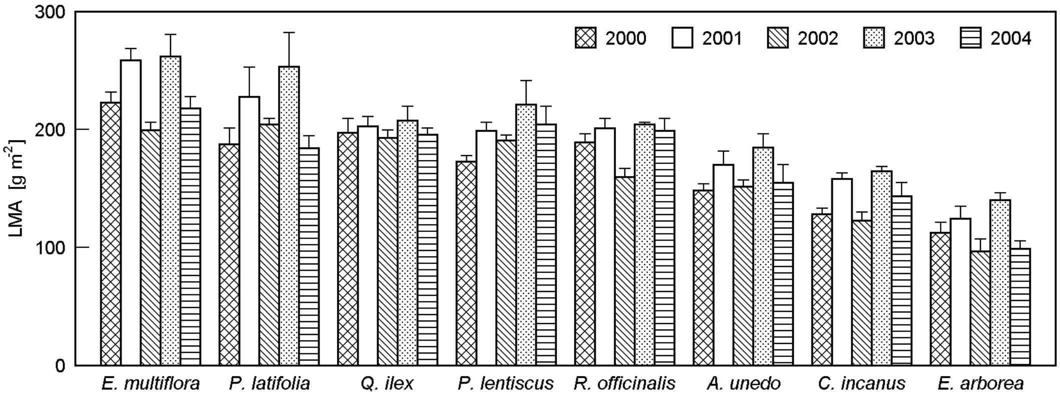

Fig. 3. Leaf mass per area (LMA) trend during the study period (2000–4) of the tested species. Means of twenty determinations with SD.

Comparing LMA values measured in 2003 and 2004 for the considered narrow leaves, a 40 % LMA increase in *E. arborea* was determined by a 20 % DM increase; a 20 % LMA increase in *E. multiflora* was determined by a 12 % LA decrease and a 4 % DM increase. *R. officinalis* showed a decrease of both DM (2 %) and LA (8 %), determining the 3 % LMA increase (Fig. 4).

L showed the same trend as LMA during the study period with the highest values in the year 2003. Among the tested species, *P. latifolia* and *E. multiflora* had the highest L values [µm] (528±9 and 412±17, respectively), followed by *P. lentiscus* (454±30), *A. unedo* (389±19), *R. officinalis* (337±36), *Q. ilex* (317±30), *C. incanus* and *E. arborea* (293±28 and 247±17, respectively) (Fig. 5).

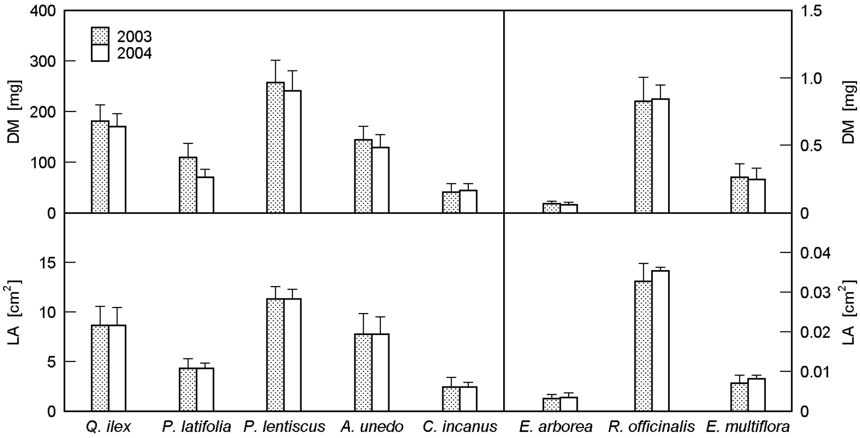

Fig. 4. Leaf dry mass (DM) and leaf area (LA) during the years 2003 and 2004 of the tested species. Means of twenty determinations with SD.

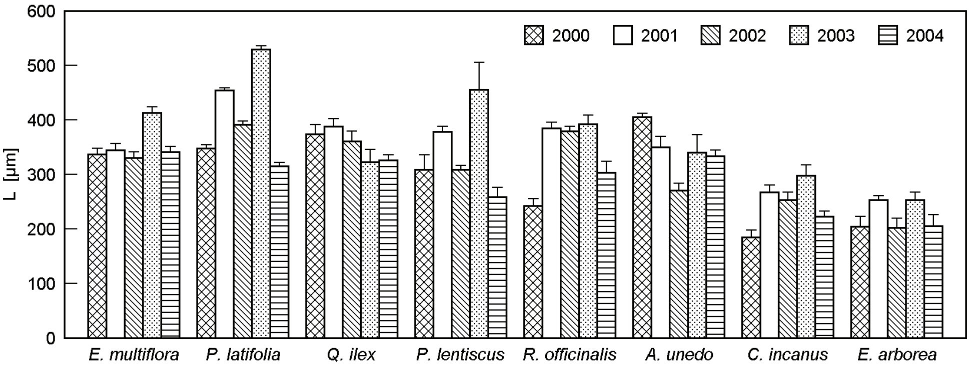

Fig. 5. Leaf thickness (L) trend during the study period (2000–4) of the tested species. Means of twenty determinations with SD.

Leaf life-span: LL varied among the considered species. LL (mean value of the years 2000–2004) of *P. latifolia* was [month] 26±9, *Q. ilex* 21±3, *P. lentiscus* 19±1, *A. unedo* 11±1, *E. arborea* 11±2, *R. officinalis* 9±2, and *E. multiflora* 8±2. *C. incanus* had a LL of 4±1 and 8±2 months (summer and winter leaves, respectively).

During the study period, LL of the considered species was the shortest in the year 2003: *Q. ilex* had a LL [month] of 18±2, *P. latifolia* and *P. lentiscus* 19±1, *A. unedo* and *E. arborea* 10±1; *R. officinalis* 6±2, *E. multiflora* 5±1, and the summer leaves of *C. incanus* 3.5±1.0.

P_N (photosynthetic activity) was measured in 2004. *C. incanus* and *A. unedo* had the highest P_N [µmol(CO$_2$) m^{-2} s^{-1}] (18.3±3.5) in spring (123 mm total rainfall, 22 °C mean maximum air temperature), followed by *Q. ilex*, *P. lentiscus*, and *P. latifolia* (11.1±0.3), *E. arborea* and *E. multiflora* (9.1±0.5), and *R. officinalis* (7.1±0.5) (Fig. 6). The lowest P_N values were found from August 8th to September 15th (30 °C air temperature and 0 mm total rainfall): *R. officinalis* and *C. incanus* showed the greatest P_N decrease (68 % of the maximum, mean value), followed by *E. multiflora* (53 %), *P. lentiscus* and *A. unedo* (49 %, mean), and *Q. ilex*, *P. latifolia* and *E. arborea* (33 %, mean).

Using also data by Gratani and Varone (2004b) for 2003, P_N showed the same trend but a significant decrease in all the tested species with respect to the one measured in the year 2004. In particular: *R. officinalis* and *C. incanus* showed a 91 % P_N decrease, *E. multiflora* and *E. arborea* 80 %, *A. unedo*, *Q. ilex* and *P. lentiscus* 65 %, and *P. latifolia* 58 %.

Table 2. Summary of regression analysis between net photosynthetic rate (P_{N}, y) and leaf mass area (LMA, x), between leaf mass per area (LMA, y) and leaf thickness (L, x), between leaf life-span (LL, y) and leaf mass area (LMA, x), and between leaf mass are (LMA, y) and total rainfall, respectively, during the period of the leaf expansion ($\mathrm{R_{LE}}$, x) for the considered species. The correlations were significant at: $^{*}p \leq 0.05$, $^{**}p \leq 0.01$, and $^{***}p \leq 0.001$.

Species	Correlation	*R*
Q. ilex	$P_{\mathrm{N}} = 0.53\,\mathrm{LMA}^2 - 19.55\,\mathrm{LMA} + 187.9$	0.72^{*}
	$\mathrm{LMA} = 0.0008\,\mathrm{L}^2 - 0.5532\,\mathrm{L} + 116.3400$	0.88^{***}
	$\mathrm{LL} = 4.030\,\mathrm{LMA} - 70.280$	0.73^{**}
	$\mathrm{LMA} = 0.0005\,\mathrm{R}^2_{\mathrm{LE}} - 0.0700\,\mathrm{R_{LE}} + 21.2700$	0.74^{**}
P. latifolia	$P_{\mathrm{N}} = -0.66\,\mathrm{LMA}^2 + 2.37\,\mathrm{LMA} - 11.0$	0.69^{*}
	$\mathrm{LMA} = 6\,\mathrm{E} - 05\,\mathrm{L}^2 - 0.0207\,\mathrm{L} + 19.4060$	0.96^{***}
	$\mathrm{LL} = 1.564\,\mathrm{LMA} - 19.170$	0.70^{**}
	$\mathrm{LMA} = 0.0047\,\mathrm{R}^2_{\mathrm{LE}} - 0.4440\,\mathrm{R_{LE}} + 25.7900$	0.96^{**}
P. lentiscus	$P_{\mathrm{N}} = 0.11\,\mathrm{LMA}^2 - 3.91\,\mathrm{LMA} + 42.60$	0.68^{*}
	$\mathrm{LMA} = 0.0003\,\mathrm{L}^2 - 0.1865\,\mathrm{L} + 49.6360$	0.85^{**}
	$\mathrm{LL} = 1.502\,\mathrm{LMA} - 19.200$	0.60^{*}
	$\mathrm{LMA} = 0.0006\,\mathrm{R}^2_{\mathrm{LE}} - 0.1310\,\mathrm{R_{LE}} + 21.9700$	0.65^{*}
A. unedo	$P_{\mathrm{N}} = 0.14\,\mathrm{LMA}^2 - 3.56\,\mathrm{LMA} + 30.67$	0.75^{**}
	$\mathrm{LMA} = 0.0002\,\mathrm{L}^2 - 0.0874\,\mathrm{L} + 26.7900$	0.66^{*}
	$\mathrm{LL} = 0.718\,\mathrm{LMA} - 5.130$	0.62^{*}
	$\mathrm{LMA} = 0.0004\,\mathrm{R}^2_{\mathrm{LE}} - 0.0870\,\mathrm{R_{LE}} + 18.2100$	0.70^{**}
C. incanus	$P_{\mathrm{N}} = 0.006\,\mathrm{LMA}^2 - 1.450\,\mathrm{LMA} + 31.000$	0.73^{*}
	$\mathrm{LMA} = 0.0004\,\mathrm{L}^2 - 0.1392\,\mathrm{L} + 25.9700$	0.78^{*}
	$\mathrm{LL} = 0.172\,\mathrm{LMA} - 1.190$	0.59^{*}
	$\mathrm{LMA} = 0.0005\,\mathrm{R}^2_{\mathrm{LE}} - 0.1140\,\mathrm{R_{LE}} + 17.0600$	0.73^{*}
E. arborea	$P_{\mathrm{N}} = -1.05\,\mathrm{LMA}^2 + 16.44\,\mathrm{LMA} - 54.20$	0.82^{**}
	$\mathrm{LMA} = 0.0014\,\mathrm{L}^2 - 0.6635\,\mathrm{L} - 68.0650$	0.90^{***}
	$\mathrm{LL} = 1.321\,\mathrm{LMA} - 6.780$	0.82^{**}
	$\mathrm{LMA} = 0.0008\,\mathrm{R}^2_{\mathrm{LE}} - 0.118\,\mathrm{R_{LE}} + 14.37$	0.97^{***}
E. multiflora	$P_{\mathrm{N}} = -0.06\,\mathrm{LMA}^2 + 1.84\,\mathrm{LMA} - 4.76$	0.68^{*}
	$\mathrm{LMA} = 0.0042\,\mathrm{L}^2 - 3.2043\,\mathrm{L} - 578.1200$	0.90^{***}
	$\mathrm{LL} = 0.340\,\mathrm{LMA} - 1.270$	0.61^{*}
	$\mathrm{LMA} = -7\,\mathrm{E} - 05\,\mathrm{R}^2_{\mathrm{LE}} - 0.06\,\mathrm{R_{LE}} + 26.06$	0.88^{*}
R. officinalis	$P_{\mathrm{N}} = -0.06\,\mathrm{LMA}^2 + 1.14\,\mathrm{LMA} + 3.48$	0.69^{*}
	$\mathrm{LMA} = -0.0006\,\mathrm{L}^2 - 0.3987\,\mathrm{L} - 50.2700$	0.96^{***}
	$\mathrm{LL} = 0.461\,\mathrm{LMA} - 1.950$	0.66^{*}
	$\mathrm{LMA} = -0.0008\,\mathrm{R}^2_{\mathrm{LE}} - 0.0300\,\mathrm{R_{LE}} + 19.9900$	0.76^{*}

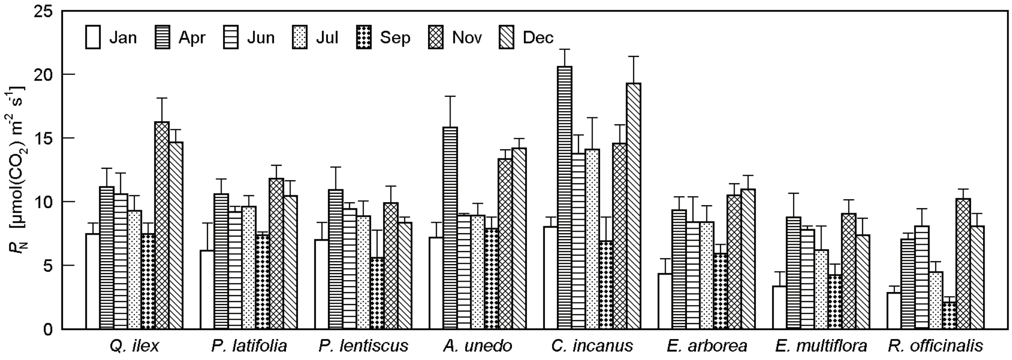

Fig. 6. Monthly trends of net photosynthetic rate (P_{N}) during the year 2004 of the tested species. Means of ten determinations with SD.

Statistics: The correlation analysis (Table 2), using also data from Gratani and Crescente (1997), Crescente (1998), Gratani and Bombelli (1999, 2001), Gratani and Ghia (2002), and Gratani and Varone (2004 a,b) indicated that LMA was significantly ($p \leq 0.05$) correlated with P_{N} ($r \geq 0.68$), L ($r \geq 0.66$), and LL ($r \geq 0.59$).

Table 3. Results of multiple regression analysis using leaf mass per area (LMA) as dependent variable and total rainfall during the period of leaf expansion (R_{LE}), total yearly rainfall (R_{tot}), maximum air temperature during the period of leaf expansion (T_{max}), and minimum air temperature during the period of leaf expansion (T_{min}) or leaf dry mass (DM), leaf area (LA), leaf thickness (L), leaf life span (LL), and net photosynthetic rate (P_N) as independent variables. Multiple R value, intercept value, un-standardized (β coefficient), standardized (B coefficient) regression coefficients, and significance levels of those coefficients (*p*-level) are shown.

Independent variable		R_{LE}		DM	LA	L	LL	P_N
Multiple R value	0.32		0.79					
Intercept	19.20		10.40					
β regression coefficient		–0.32		0.75	–0.69	0.47	0.14	–0.15
B regression coefficient		–0.05		0.04	–0.63	0.02	0.08	0.14
p-level		0.01		0.000004	0.008000	0.000040	0.140000	0.110000

The polynomial negative correlation between LMA and rainfall (Table 2) underlined the influence of rainfall, in particular, during the period of leaf expansion (from May to the end of July) (Gratani and Crescente 1997, Gratani and Ghia 2002). The narrow-leaf species had a higher correlation coefficient ($r \geq 0.76$) than the broad-leaved ones ($r \geq 0.65$).

The multiple regression analysis was carried out using also data from Gratani and Crescente (1997), Crescente (1998), Gratani and Bombelli (1999, 2001), Gratani and Ghia (2002), Gratani and Varone (2004a,b) throughout the years 1991–2004, considering LMA as dependent variable and climatic parameters (R_{LE}, R_{Tot}, T_{max}, T_{min}) as independent variables; total rainfall during the period of leaf expansion was the most significant ($p \leq 0.05$) variable negatively correlated with LMA (β = –0.32) (Table 3).

A multiple regression analysis was carried out employing LMA as dependent variable and morphological, anatomical, phenological, and physiological leaf traits as independent variables. L, DM, and LA were the variables most significantly ($p \leq 0.05$) correlated with LMA (Table 3).

Discussion

The analysis of correlation among the considered leaf traits for the evergreen broad-leaf and narrow-leaf species of the Mediterranean maquis, developing along the Latium coast, indicated that LMA variations were tightly associated with LL variation. Understanding the basis for leaf life-span and LMA relationships is of significant interest because both traits are pivotal in the carbon-fixation strategy (Wright and Westoby 2002).

In the study period, *C. incanus* and *A. unedo* were characterised by a short LL and LMA. This reflects a larger PAR-capture area per leaf mass, and a shorter diffusion path from stomata to chloroplasts (Gratani and Varone 2004a) determining a higher photosynthetic capacity per unit leaf area [18.3±3.5 μmol(CO_2) m^{-2} s^{-1}] in the favourable period. On the contrary, *Q. ilex, P. latifolia,* and *P. lentiscus,* the typical sclerophyllous species, were characterised by a longer LL and higher LMA determining lower P_N in the favourable period. Nevertheless, they were characterised by a higher drought resistance, set forth by the low P_N reduction during drought (38 % mean value), according to our earlier results (Gratani and Varone 2004b).

The narrow-leaf species had a short LL associated either with low or high LMA, and a low photosynthetic capacity in the favourable period. *E. arborea* and *R. officinalis* have a low drought resistance (53 % P_N reduction), according to the results of Gratani and Varone (2004a,b).

Considering the variability of the Mediterranean climate at Castelporziano from 1991 to 2004, the LMA trend may be defined using also data collected for the evergreen broadleaf species from Gratani and Crescente (1997), Crescente (1998), Gratani and Ghia (2002), and Gratani and Bombelli (1999, 2001). LMA (mean value for the period 1991–9) is [g m^{-2}] 195±12 for *Q. ilex*, 177±37 for *P. latifolia*, 174±26 for *P. lentiscus*, 151±27 for *A. unedo*, and 127±29 for *C. incanus* when the average total rainfall during the period of leaf expansion (from May to July) is 82.5 mm; on an average LMA increases by 13 % in these species in the period 2000–4, in response to a 19 % decrease of rainfall, and LMA has the highest values (13 % increase with respect to the mean value for the study period) in the year 2003 (characterised by a 95 % decrease of rainfall).

The considered narrow-leaf species, *E. multiflora*, *R. officinalis*, and *E. arborea* had a mean LMA of 233±27, 192±19, and 115±17 g m^{-2}, respectively (2000–4). In 2003 LMA of these species increased by 13, 7, and 22 % of the mean value, respectively.

The multiple regression analysis underlined that total rainfall during the period of leaf expansion was the most significant ($p \leq 0.05$) climatic variable negatively correlated with LMA (β = –0.32).

Moreover, the results underline that LMA variation in the considered species is significantly associated with DM and LA variations, which is confirmed also by the multiple regression analysis (β = 0.75 and –0.69 for DM and LA, respectively). Nevertheless, the considered species are characterised by an unequal variation of these two leaf traits. On an average, the LMA increase is mainly due to DM increase in *Q. ilex, P. latifolia*, *P. lentiscus*, and *E. arborea*, while it is mainly due to LA decrease in *C. incanus, R. officinalis*, and *E. multiflora* and in *A. unedo* both DM and LA contribute to the LMA increase.

High LMA values improve drought resistance, also according to the results of Abril and Hanano (1998), Castro-Díez *et al*. (1998), Gratani and Bombelli (1999), Werner *et al*. (1999), Gratani and Ghia (2002), and Gratani and Varone (2004a). *Q. ilex* and *P. latifolia* have the highest LMA values and they show the best adaptation capacity to drought. *C. incanus* and *R. officinalis* are the species which suffer the most from severe drought, the first because of its low LMA and the second because of its low tolerance to high air temperature (Gratani and Varone 2004b); it loses *ca.* 50 % of its leaves after a severe drought period (Gratani and Varone 2004a). The results underline that LMA increases in response to the decreasing rainfall. LMA is a good indicator of the capacity of Mediterranean evergreen species to respond to the hypothesized total annual rainfall decrease and air temperature increase in the Mediterranean Basin.

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