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Carbon Balance of Mediterranean Evergreen Species

Rosangela Catoni

Tutor : Prof. Loretta Gratani

List of Publications

- I. Gratani, L., Varone, L., **Catoni, R.** Relationships between net photosynthesis and leaf respiration in Mediterranean evergreen species. *Photosynthetica* 46: 567-573, 2008.
 - II. Gratani, L., **Catoni, R.**, Varone, L. *Quercus ilex* L. carbon sequestration capability related to shrub size. *Envir. Monit. Assess.* 178: 383-392, 2011.
 - III. Gratani, L., **Catoni, R.**, Varone, L. Photosynthetic and leaf respiration activity of *Malcolmia littorea* (L.) R. Br. in response to air temperature. *Photosynthetica* 49: 65-74, 2011.
 - IV. Gratani, L., **Catoni, R.**, Pirone, G., Frattaroli, A.R., Varone, L. Physiological and morphological leaf trait variations in two Apennine plant species in response to different altitudes. *Photosynthetica* 50 (1): 15-23, 2012.
 - V. **Catoni, R.**, Gratani, L., Varone, L. Physiological, morphological and anatomical trait variations between winter and summer leaf of *Cistus* species. *Flora* 207: 442-449, 2012.
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Introduction

Leaf photosynthesis and respiration are the two most fundamental plant physiological processes which affect the carbon cycle, on a scale ranging from the leaf to the globe (Cavaleri et al. 2008). Carbon sequestered is the difference between carbon gained by photosynthesis and carbon lost or released by respiration, considering that the overall gain or loss of carbon is usually represented by the net ecosystem productivity (Montagnini and Nair 2004). Accounting for carbon sequestration requires adequate knowledge of variations in the ecosystems carbon exchange with the atmosphere (Pereira et al. 2007) and differences in the photosynthetic capacity among ecosystems contribute to the importance of land cover and use changes on potential carbon sequestration (Metting et al. 2001). Approximately 30–80% of daily carbon assimilated by photosynthesis is respired back into the atmosphere, with 50-70% of whole plant respiration taking place in leaves (Atkin et al. 2007, Ow et al. 2010), whereas roots respiration releases back into the atmosphere from 8 to 52% of the CO₂ assimilated (Lambers et al. 1996). Respiration and photosynthesis are strongly coupled and interdependent in leaves of higher plants (Atkin et al. 2007, Ivanova et al. 2008, Pinheiro and Chaves 2011): whereas respiration relies on photosynthetic substrates, photosynthesis is dependent on respiration for carbon skeletons, ATP required for sucrose synthesis and repair of photosynthetic proteins (Atkin et al. 2007). Moreover, leaf respiration protects the photosynthetic apparatus from photo-inhibitory damage by oxidizing excess photosynthetic reducing equivalents (van Lis and Atteia 2004, Noguchi and Yoshida 2008). The processes of photosynthesis and respiration respond independently and often differently to environmental variations (Turnbull et al. 2001). In particular, the temperature sensitivity of photosynthesis differs from that of respiration (Morison and Morecroft 2006), and hence the ratio between the two processes may be altered following a short-term change in temperature (Loveys et al. 2002, Atkin et al. 2006). Photosynthesis has distinct high and low temperature limits (Larcher 1994, Neuner and Pramsohler 2006). In

particular, the optimum temperature for photosynthesis in C_3 plants rarely exceeds 30°C (Rennenberg et al. 2006, Atkinson et al. 2010), and at temperatures above the optimum, photosynthesis often decreases sharply (Ow et al. 2008). At low temperatures ($5\text{-}10^\circ\text{C}$) there is a rapid inhibition of photosynthesis due to the inhibition of sucrose synthesis (Strand et al. 1999). This leads to an accumulation of phosphorylated intermediates, and a decrease of ATP/ADP ratio (Hurry et al. 2000). Plants of tropical or sub-tropical origin may incur irreversible damage to photosynthesis by temperatures around 10°C , whereas plants from cooler climates may photosynthesize and develop normally at temperatures down to 0°C (Öquist 1983). In the Mediterranean climate, the combination of high irradiance and sub-optimal growth temperature in winter causes a depression of the photosynthetic activity (Larcher 2000, Oliveira and Peñuelas 2002, Varone and Gratani 2007). In the short-term, a change in temperature results in an immediate alteration in respiration rates (Loveys et al. 2003). At low temperatures respiratory flux is probably limited by the maximum rate of the enzyme activity of the respiratory apparatus (i.e. glycolysis, the TCA cycle and mitochondrial electron transport) (Atkin and Tjoelker 2003). The temperature sensitivity of leaf respiration is quantified using the Q_{10} (i.e. the proportional increase in respiration for every 10°C rise in temperature) (Wythers et al. 2005, Armstrong et al. 2006). Tjoelker et al. (2001) synthesize the results of published foliar Q_{10} of respiration rates across a range of plant taxa (grasses, forbs, and woody plants) and across a range of biomes (tropical, temperate, boreal, and arctic biomes) concluding that the respiratory Q_{10} declines linearly with increasing temperature in a consistent manner among a range of taxa and climatic conditions. Variability in Q_{10} values may reflect differences in growth conditions and/ or in the physiological state of the tissues (Atkin et al. 2000, Tjoelker et al. 2001, Loveys et al. 2003). Q_{10} of leaf respiration has been demonstrated to vary between 1.1 and 4.2 (Azcón-Bieto and Osmond 1983, Tjoelker et al. 2001).

Low water availability determines the reduction in plant carbon balance and consequently a limitation of plant growth (Flexas et al. 2006). Under water stress conditions, photosynthesis may decrease up to 100% becoming totally impaired (Gratani and Varone 2004a, Flexas et al. 2005) and the decrease is mostly mediated by stomatal closure (Gratani 1995, Galmés et al. 2007, Gulías et al. 2009).

On the contrary, the impact of water stress on leaf respiration is still far from clear, with reports in literature varying from decreases, to increases, to maintenance in the rates of leaf respiration (Gimeno et al. 2010, Gratani 2007, 2008, 2011a,b). Flexas et al. (2005) attribute this controversy to three possible causes: (i) the use of different species, organs and techniques for respiration studies; (ii) the presence of complex interactions of respiration rates with other environmental factors, and (iii) the presence of a threshold of water stress intensity in which a change in the response of respiration to water stress occurs. Inhibition of leaf respiration under drought has been observed in mature leaves of crops and herbaceous species (Haupt-Herting et al. 2001, Ribas-Carbó et al. 2005, Galmés et al. 2007) while high leaf respiration rates, mainly as the maintenance component, have been observed in drought stressed herbs and shrubs species (Slot et al. 2008, Gratani et al. 2007, 2008, 2011a,b). High demand for respiratory ATP under severe water stress seems to be necessary to compensate for the lower ATP production in the chloroplasts, and may be required to support photosynthesis repair mechanisms (Flexas et al. 2006, Atkin and Macherel 2009), whereas no alterations in leaf respiration under drought are mostly reported in some evergreens perennials (Galmés et al. 2007, Gimeno et al. 2010).

The ratio respiration/photosynthesis can be considered as a simple approach to leaf carbon balance because it indicates the percentage of photosynthate that is respired (Loveys et al. 2002, Galmés et al. 2007, Chu et al. 2011). Moreover, the ratio respiration/photosynthesis is indicative of the capacity of plants to produce new biomass for growing and reproductive structures (Poorter et al 1992, Galmès et al. 2007, Cavaleri et al. 2008, Millar et al. 2011). Drought stress is recognized to be one

of the most important limiting factors of the Mediterranean evergreen species carbon gain (Gratani and Varone 2004a, Galmès et al. 2007, Misson et al. 2010). The overall effects of drought stress on leaf carbon balance depend on the extent to which photosynthesis *versus* respiration is affected (Atkin and Macherel 2009). Although the extent to which respiration/photosynthesis increases under drought stress depends on whether leaf respiration decreases, increases or remains unaltered, overall the most important factor determining how negative a plant's carbon balance becomes under drought stress is the absolute and proportional change in photosynthesis (Flexas et al. 2006, Galmés et al. 2007). Leaf respiration increasing in drought provides several positive roles, since mitochondrial respiration enables survival and rapid recovery of productivity from water-stress conditions (Atkin and Macherel 2009). In spite of the importance of such parameters, only a limited number of studies focus on the respiration/photosynthesis ratio (Dewar et al. 1999, Loveys et al. 2003, Atkin et al. 2007, Gratani et al. 2008, 2011b).

The main object of this research was to analyze leaf carbon balance of the species co-occurring in the Mediterranean maquis developing along the *Latium* coast, in response to water availability and air temperature variations during the year. Among Mediterranean ecosystems, the Mediterranean maquis is largely distributed in areas around the Mediterranean Basin, and its structure is strongly influenced by air temperature and water availability (Vilà and Sardans 1999, Gratani et al. 2003, 2012b). It is dominated by evergreen sclerophyllous species, drought semi-deciduous species, narrow-leaves species and lianas species (Specht 1969, Orshan 1983, Gratani et al. 2003, 2012), which could respond differently to the hypothesized increase of air temperature. Knowledge of shrub structural and physiological traits in favorable as well as in drought conditions can be used to monitor their response to increasing drought stress (Gratani et al. 2012). Among structural traits, leaf area index (LAI) characterizes vegetation structure and function including estimation of plant productivity and canopy cover density (Whittaker and Marks 1975, Kaufmann and

Troendle 1981, Garrigues et al. 2008). LAI constitutes the interface between plants and the atmosphere, and is therefore a key trait for quantifying carbon exchange (Gower and Norman 1991, Gratani et al. 2012). Carbon fluxes between terrestrial ecosystems and atmosphere are strongly controlled by vegetation composition and structure (Pacala et al. 2001, Sun et al. 2010). Variations of the ratio respiration/ photosynthesis may imply change in species structure and productivity in the long term (Haase et al. 2000, Saxe et al. 2001). With regard to the rainfall patterns, there is a common trend among coupled models and projections showing a possible decrease of rainfall for the months April–September in the Mediterranean Basin (Giorgi and Lionello 2008, Lelieveld et al. 2012). How such changes might affect the vulnerability of species and ecosystems is still unknown (Ow et al. 2010). Improving knowledge on processes and factors influencing the respiratory and photosynthetic activity is critical in making accurate models of CO₂ exchange between vegetation and the atmosphere (Armstrong et al. 2006).

Material and Methods

Study area and plant species

The study was carried out under field conditions in the Mediterranean maquis developing along the *Latium* coast (from Fiumicino to Capocotta, 5 m a.s.l., Italy 41°40'N, 12°23'E) in the period December 2009- December 2011. The maquis under study was characterized by the presence of the following species: *Arbutus unedo* L., *Phillyrea latifolia* L., *Pistacia lentiscus* L., *Quercus ilex* L. (typical sclerophyllous species), *Cistus incanus* L. (drought semi-deciduous species), *Erica arborea* L., *Erica multiflora* L., *Rosmarinus officinalis* L. (narrow-leaves species), and *Smilax aspera* L. (liana) (Gratani et al. 2003).

The climate of the area was of the Mediterranean type: the mean minimum air temperature (T_{\min}) of the coldest months (January-February) was 4.2 ± 0.1 °C (mean value \pm SD), the mean maximum air temperature (T_{\max}) of the hottest months (July-August) 30.7 ± 0.2 °C, and the mean yearly air temperature (T_m) 16.2 ± 6.2 °C. Total annual rainfall was 753 mm, most of it occurring in autumn and winter (mean values of the data from Meteorological Station of Roma-Capocotta and Fiumicino-Maccarese, Lazio Regional Agency for Development and Agricultural Innovation; for the years from 2004 to 2011).

The year 2010 was characterized by a T_{\min} of the coldest month (January) of 4.6 ± 3.3 °C, a T_{\max} of the hottest month (July) of 32.2 ± 1.8 °C, and a total rainfall of 963 mm (Fig. 1). In the year 2011 T_{\min} of the coldest month (February) was 3.6 ± 2.2 °C, T_{\max} of the hottest month (August) 30.8 ± 2.4 °C, and total rainfall was 655 mm (Fig. 2).

The species structural traits were analyzed on sixty shrubs randomly distributed in five sub-sample areas (100 m² each) within an area of 1 ha, according to Gratani et al. (2003). Three representative shrubs per each of the considered species were selected in the sample area and morphological and physiological measurements were carried out.

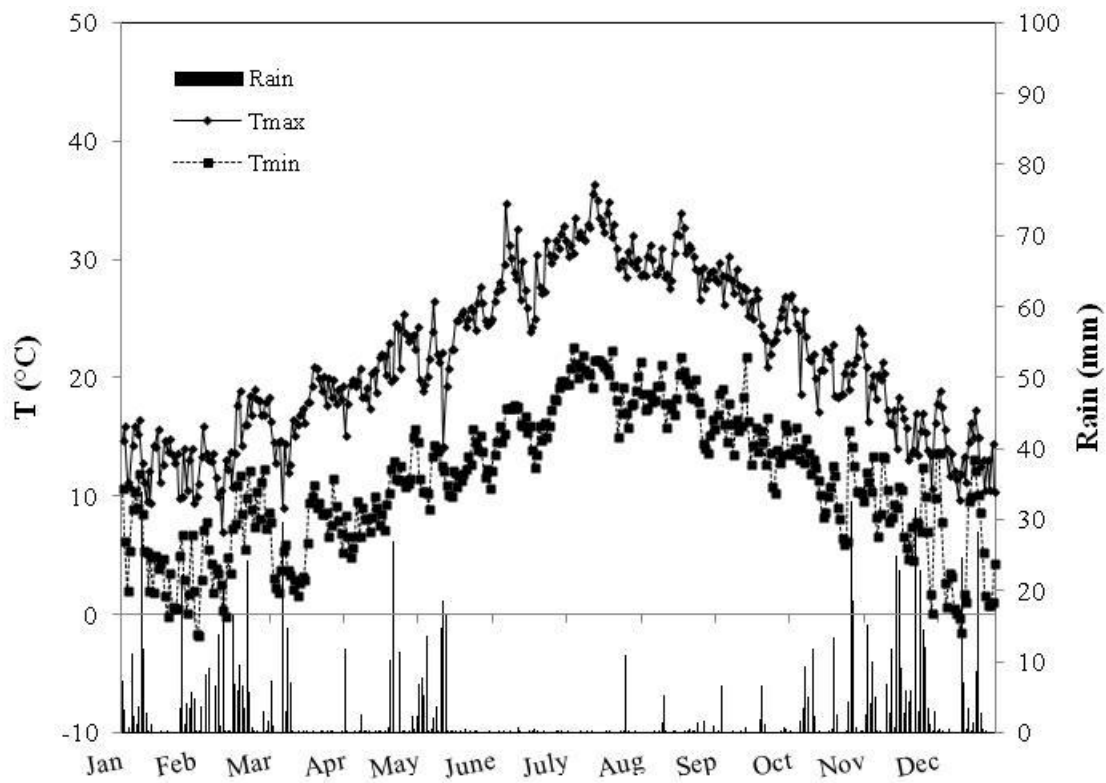


Fig. 1. Trend of daily air temperature and rainfall during the year 2010. R = total daily rainfall; T_{\min} = minimum air temperature; T_{\max} = maximum air temperature (mean values of the data from Lazio Regional Agency for Development and Agricultural Innovation; Metereological Station of Roma-Capocotta and Fiumicino-Maccarese).

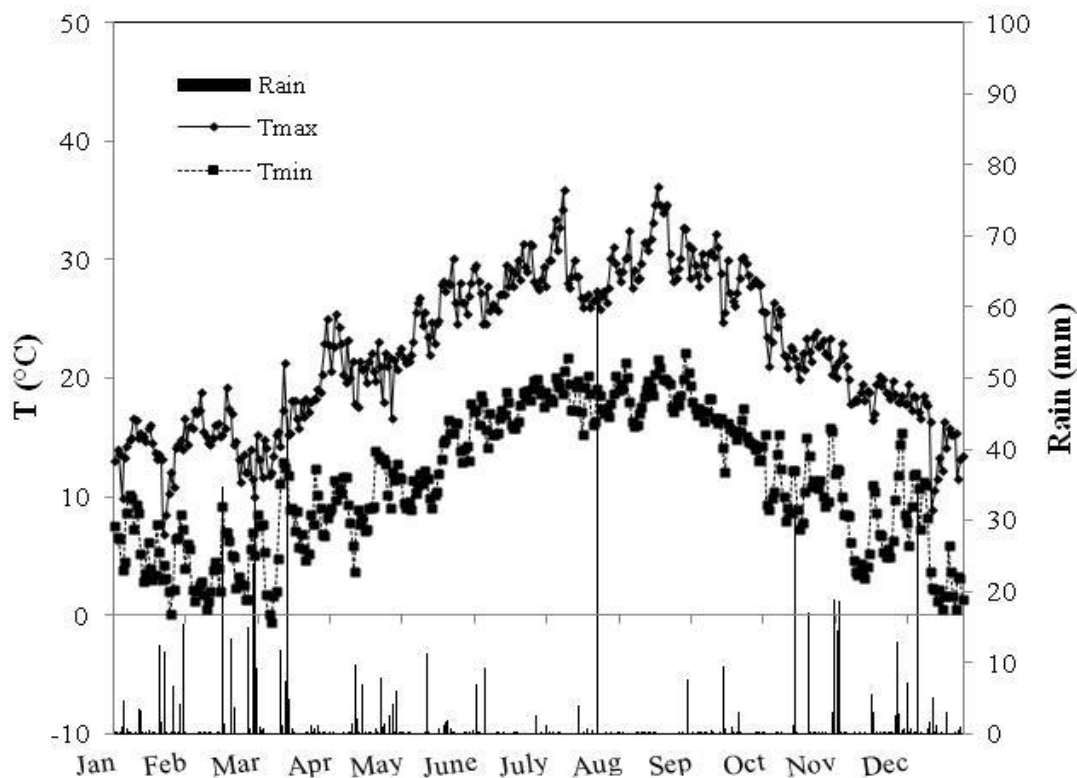


Fig. 2. Trend of daily air temperature and rainfall during the year 2011. R= total daily rainfall; T_{\min} = minimum air temperature; T_{\max} = maximum air temperature (mean values of the data from Lazio Regional Agency for Development and Agricultural Innovation; Metereological Station of Roma-Capocotta and Fiumicino-Maccarese).

Shrub structural traits

Measurements of shrub structure were carried out in the period December 2009–December 2010 and included: total height (H, m), defined as the maximum vertical distance from the soil level to the highest point of the shrub; major axis (A, m) and minor axis (a, m, orthogonal to A) of the shrub crown; shrub volume (V, m³), derived from the measured traits (A, a, and H) by assigning a simple geometric solid to the shrub's form, according to Karlik and Winer (2001); leaf area index (LAI, i.e. total leaf area per unit of ground area) of shrubs, measured by the “LAI 2000 Plant Canopy Analyzer” (LI-COR Inc., Lincoln, Nebraska, USA), according to Morales et al. (1996).

Shrub structural traits were used to group the considered shrubs in class sizes. For each shrub, the number of species was counted and shrub density in the sample areas (SD) was calculated as number of shrubs ha⁻¹.

Morphological leaf traits

Measurements of morphological leaf traits were conducted on fully expanded sun leaves for *Q. ilex*, *A. unedo*, *C. incanus*, *P. latifolia*, *P. lentiscus* and *S. aspera* (n = 10 leaves per species for each of the considered shrubs) and needles for *E. arborea*, *E. multiflora* and *R. officinalis* (n= 10 needles per species for each of the considered shrubs), and collected at the end of June 2010.

The following parameters were measured: projected leaf surface area (excluding petiole) (LA, cm²), obtained by the Image Analysis System (Delta-T Devices, UK), and leaf dry mass (DM, mg), determined after drying at 80°C to constant mass. Leaf thickness (L, μm) was measured by leaf sections from five fresh, fully expanded leaves of the selected plants and measured by light microscope. Leaf mass per unit of leaf area (LMA, mg cm⁻²) was calculated by the ratio of leaf DM and LA. Leaf tissue density (LTD, mg cm⁻³) was calculated by the ratio of LMA and total leaf thickness (Wright and Westoby 2002).

Gas exchange

Measurements of gas exchange for the species co-occurring in the shrubs were carried out in the period October 2010- September 2011, using the infrared gas analyzer (ADC LCA4, UK) equipped with a conifer leaf chamber (PLC, Parkinson Leaf Chamber) for *E. arborea*, *E. multiflora* and *R. officinalis*, and with a broad leaf chamber (PLC, Parkinson Leaf Chamber) for *Q. ilex*, *A. unedo*, *C. incanus*, *P. latifolia*, *P. lentiscus* and *S. aspera*.

Measurements were taken on attached fully expanded sun leaves ($n = 3$ in each sampling occasion for *A. unedo*, *C. incanus*, *P. latifolia*, *P. lentiscus*, *Q. ilex*, and *S. aspera*) and on sun apical shoots ($n = 3$ in each sampling occasion for *E. arborea*, *E. multiflora* and *R. officinalis*).

Net photosynthesis (P_N , $\mu\text{mol CO}_2 \text{ m}^{-2}\text{s}^{-1}$), stomatal conductance (g_s , $\text{mol m}^{-2} \text{ s}^{-1}$), transpiration rate (E , $\text{mmol m}^{-2} \text{ s}^{-1}$), leaf temperature (T_l , $^{\circ}\text{C}$) and photosynthetically active radiation (PAR, $\mu\text{mol photons m}^{-2}\text{s}^{-1}$) were measured from 9.00 to 11.00 a.m., under natural conditions on cloud-free days ($\text{PAR} \geq 1,000 \mu\text{mol m}^{-2}\text{s}^{-1}$, saturating level) to ensure that near-maximum daily photosynthetic rates were measured (Reich et al. 1995), periodically, during the study period.

Leaf dark respiration (R_L) measurements were carried out contemporary to net photosynthesis measurements, by darkening the leaf chamber with a black paper, according to Cai et al. (2005), for 30 min prior to each measurement to avoid transient post-illumination bursts of CO_2 releasing (Atkin et al. 1998a, b).

The monthly P_N and R_L rates shown were obtained by averaging the values taken on three days with the same weather conditions in the first week of each month.

The ratio between R_L and P_N was calculated according to Atkin et al. (2007), Galmès et al. (2007) and Chu et al. (2011).

During P_N and R_L measurements air temperature (T_a , $^{\circ}\text{C}$) was monitored by portable thermo-hygrometers (HD 8901, Delta Ohm, Italy).

The coefficient proportional to the respiration increase for each 10°C rise (i.e. Q_{10}) was calculated using T_a measured in the same time of R_L measurements, according to Atkin et al. (2000). Q_{10} was calculated according to Carla et al. (2000) and Armstrong et al. (2006) as :

$$Q_{10} = 10^{(10 \times \text{slope of the regression line})}$$

The slope in the equation was extracted from the regression line between \log_{10} of R_L and T_a .

Statistical analysis

All statistical tests were performed using a statistical software package (*Statistica*, Statsoft, USA). Differences of the means for the considered traits were tested by one-way ANOVA and Tukey test for multiple comparisons. Linear regression analysis was used to evaluate the correlation between LAI and V of the shrubs. All of the investigated species were considered together in a regression analysis between P_N and g_s , R_L and T_m and R_L and R. The relationship between P_N and T_l (photosynthetic thermal window *sensu* Larcher, 1994) was used to calculate leaf temperature ($T_{l\ 100\%}$) determining 100% of the highest P_N , and leaf temperature ($T_{l\ 50\%}$) below or above which P_N dropped below half of its maximum.

A species co-occurrence analysis was performed to identify species pairs that occurred together within single shrubs more or less often than expected by chance irrespective of shrub size. The actual co-occurrences of all species pairs in the real species-per-shrub matrix were checked against the co-occurrence distribution in a set of randomized null matrices to identify the species pairs showing significant deviation, either at the lower part of the distribution (less co-occurrence than expected by chance, or negative species association) or at the upper part of the distribution (higher than random co-occurrence, meaning positive species association), according to Sfenthourakis et al. (2004). The identification of the significant species co-occurrence was carried out with the program COOC (Sfenthourakis et al. 2004), while all randomized matrices were generated with the program 'EcoSim 2004', using the independent swap algorithm to keep species richness within shrubs and the frequency of specie occurrences across shrubs unchanged with respect to the real matrix (Gotelli and Entsminger 2001).

The considered morphological (LMA and LTD) and physiological leaf traits were analyzed by PCA (principal component analysis) on the basis of a matrix of the normalized data. In particular among the physiological traits, P_N and R_L during the

favorable period (April-May), in drought (August) and in winter (December) were considered.

Results

Shrubs structural traits

Shrub density was 1200 ± 500 shrubs ha^{-1} , 17 % of them were constituted by one species and 83 % were multispecies. According to V and LAI, the shrubs were classified in three classes: small (S), medium (M) and large (L) shrubs: V and LAI were $1.4 \pm 0.9 \text{ m}^3$ and 2.0 ± 0.4 , $12.6 \pm 1.5 \text{ m}^3$ and 3.1 ± 0.4 , $35.5 \pm 2.5 \text{ m}^3$ and 3.9 ± 0.1 in S, M and L shrubs, respectively.

The regression analysis showed that 63 % of LAI variance depended on V (Fig. 3). The frequency of occurrence of S, M and L shrubs in the sample areas was 57, 32 and 11 %, respectively. The number of species increased from S to L: S shrubs were constituted by 3 ± 2 species, M by 6 ± 2 species, and L by 6.0 ± 0.4 species. The frequency of mono-species shrubs was 26 and 5% in S and M shrubs, respectively, while L shrubs were always multispecies. *C. incanus* (91 %), *E. multiflora* (71%) and *R. officinalis* (38%) were the most frequent species in S shrubs, while *E. arborea* was always absent. *Q. ilex*, *C. incanus* and *S. aspera* (89%) were the most frequent species in M shrubs, followed by *E. multiflora* (84%), *A. unedo* (68%), *P. latifolia* (58%), *R. officinalis* (42%), *E. arborea* and *P. lentiscus* (16%). *A. unedo*, *P. latifolia* and *Q. ilex* were always present in all L shrubs, followed by *C. incanus* and *S. aspera* (86%), *E. multiflora* (71%), *E. arborea* and *P. lentiscus* (29%) and *R. officinalis* (14%). Sixty percent of the mono-species shrubs were constituted by *C. incanus*, 30% by *R. officinalis* and 10% by *Q. ilex*.

The analysis of the species co-occurrences identified 12 pairs of species out of the 36 possible ones that occurred together more (or less) often than expected by chance within single shrubs. This result means that the Mediterranean shrubs were not assembled at random from the available species pool - (two-tailed test, $p < 0.05$, 999 randomizations). Among them the species pairs showing significant negative association were: *A. unedo* – *E. multiflora*; *A. unedo* – *R. officinalis*; *E. arborea* – *E. multiflora*; *E. multiflora* – *P. lentiscus*; *E. multiflora* – *S. aspera*; *P. latifolia* – *R.*

officinalis. The species pairs showing significant positive association were: *A. unedo* – *P. latifolia*; *A. unedo* – *P. lentiscus*; *A. unedo* – *Q. ilex*; *A. unedo* – *S. aspera*; *P. latifolia* – *P. lentiscus*; *Q. ilex* – *S. aspera*.

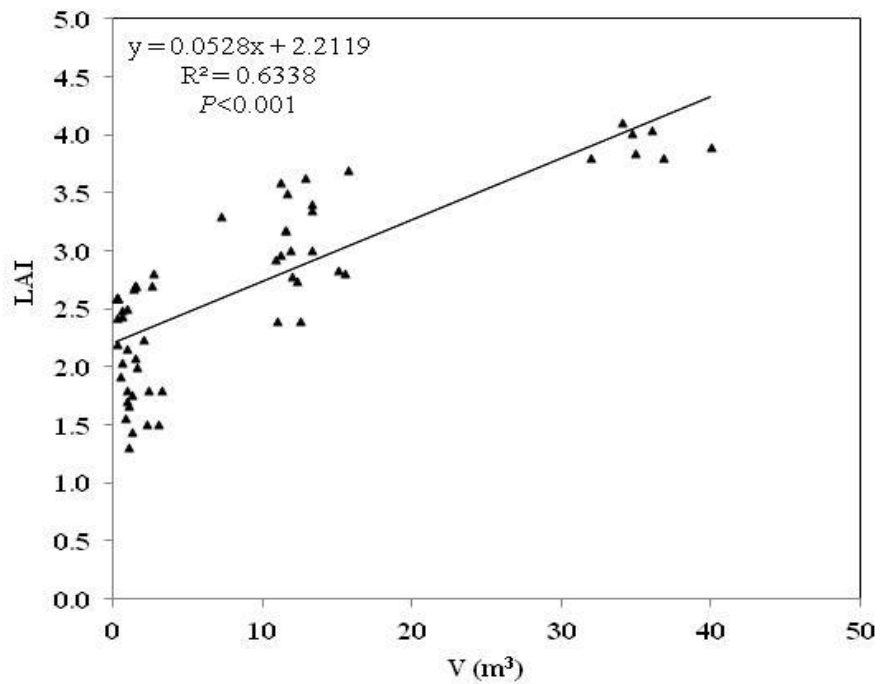


Fig. 3. Regression analysis between leaf area index (LAI) and volume (V) for the considered shrubs. Regression equation, determination's coefficient (R^2) and p -level are shown.

Morphological leaf traits

Morphological leaf traits of the considered species are shown in table 1. Among the considered species, *P. latifolia* had the highest L (400 ± 22 μm) and *E. arborea* the lowest one (246 ± 29 μm), *P. lentiscus* showed the highest DM (249 ± 30 mg) and the narrow-leaved species (*R.officinalis*, *E.arborea* and *E.multiflora*) the lowest one (4.9 ± 6.2 mg, mean value). *S. aspera* showed the highest LA (14.8 ± 0.8 cm^2) and the narrow-leaved species the lowest one (0.2 ± 0.3 cm^2 , mean value).

LMA ranged from 12.4 ± 1.1 mg cm^{-2} (*E. arborea*) to 25.9 ± 1.7 mg cm^{-2} (*E. multiflora*), and LTD from 355 ± 18 mg cm^{-3} (*S. aspera*) to 756 ± 24 mg cm^{-3} (*E. multiflora*).

Table 1. Leaf surface area (LA), leaf dry mass (DM), leaf thickness (L), leaf mass per unit of leaf area (LMA) and leaf tissue density (LTD) of the considered species. Mean values (\pm SD) are shown ($n= 30$). Inter-specific differences were tested by Tukey test for multiply comparison; mean values with the same letter are not significantly different ($p<0.05$).

Species	LA	DM	L	LMA	LTD
	cm ²	mg	μ m	mg cm ⁻²	mg cm ⁻³
<i>A.unedo</i>	9.8 \pm 0.7c	157 \pm 10d	378 \pm 27cd	15.8 \pm 0.6c	419 \pm 7b
<i>C.incanus</i>	2.8 \pm 0.7b	42 \pm 9b	258 \pm 29a	15.1 \pm 0.7bc	580 \pm 10e
<i>E. arborea</i>	0.03 \pm 0.02a	0.58 \pm 0.08a	246 \pm 29a	12.4 \pm 1.1a	504 \pm 16c
<i>E. multiflora</i>	0.06 \pm 0.03a	2.2 \pm 1.0a	343 \pm 32bc	25.9 \pm 1.7f	756 \pm 24g
<i>P.latifolia</i>	3.7 \pm 0.3b	75 \pm 9c	400 \pm 22d	20.1 \pm 1.2de	515 \pm 18c
<i>P.lentiscus</i>	13.1 \pm 1.4d	249 \pm 30f	345 \pm 29bc	18.9 \pm 1.0d	548 \pm 22d
<i>Q.ilex</i>	9.8 \pm 0.7c	200 \pm 29e	329 \pm 41b	20.4 \pm 1.1e	622 \pm 19f
<i>R.officinalis</i>	0.58 \pm 0.09a	12 \pm 1a	347 \pm 59bc	20.2 \pm 0.6de	580 \pm 24e
<i>S.aspera</i>	14.8 \pm 0.8e	205 \pm 33e	395 \pm 34d	13.9 \pm 0.8ab	355 \pm 18a

Gas exchange

Trends of P_N during the study period for all the considered species are shown in figure 4. During the study period, all the considered species reached the highest P_N rates in spring (April –May) when T_m was $17.0 \pm 2.3^\circ\text{C}$. Among them, *C. incanus* showed the highest rates ($20.0 \pm 0.6 \mu\text{mol m}^{-2} \text{s}^{-1}$) and *E. multiflora* and *R. officinalis* the lowest ones ($7.4 \pm 0.4 \mu\text{mol m}^{-2} \text{s}^{-1}$, mean value). The lowest P_N rates were monitored in summer and in winter. In particular, during summer, the lowest rates were reached in August when T_{max} was $30.8 \pm 0.8^\circ\text{C}$. On an average, P_N decreased 73 % (mean value of the considered species) compared to the maximum in spring, and *S. aspera* had the highest decrease (89 %) and *P. latifolia* the lowest one (57%).

During winter, the lowest P_N rates were measured in December ($T_{\text{min}} = 5.3 \pm 1.4^\circ\text{C}$) and, on an average, P_N decreased 48 % compared to the maximum (mean value of the considered species), *C. incanus* showing the highest decrease (59 %) and *Q. ilex* the lowest one (28 %).

The mean yearly P_N was the highest in *C. incanus* ($11.5 \pm 5.2 \mu\text{mol CO}_2 \text{ m}^{-2} \text{s}^{-1}$) and the lowest in *E. multiflora* and *R. officinalis* ($5.1 \pm 0.2 \mu\text{mol CO}_2 \text{ m}^{-2} \text{s}^{-1}$, mean value). The g_s trend followed that of the P_N , as underlined by the regression analysis between the two variables ($r = 0.89$), with the highest rates in spring ($0.126 \pm 0.054 \text{ mol m}^{-2} \text{s}^{-1}$, mean value in April-May of the considered species). In particular, among the considered species, *C. incanus* had the highest g_s rates ($0.244 \pm 0.049 \text{ mol m}^{-2} \text{s}^{-1}$). In August, g_s decreased, on an average, 76 % (mean value of the considered species) compared to the spring value, and *S. aspera* showed the highest decrease (89 %). In December g_s decreased, on an average, 53 % and *Q. ilex* showed the lowest decrease (30 %).

The results of the regression analysis showed a significant ($p < 0.01$) correlation between P_N and T_1 for all the considered species (Fig. 5); in particular, the highest P_N rates (100 %) were monitored when T_1 was in the range of $21.4\text{--}25.1^\circ\text{C}$. Significant differences among the considered species were found in T_1 that caused P_N to decrease

below half of its maximum. In particular, P_N dropped below half of the maximum rate when T_l was over 33.3 °C and under 13.0 °C for *C. incanus*, *E. multiflora*, *R. officinalis* and *S. aspera*, and over 36.2 °C and under 10.8°C for *A. unedo*, *E. arborea*, *P. latifolia*, *P. lentiscus* and *Q. ilex*.

The considered species had the same R_L trend during the study period (Fig. 6). The lowest R_L rates were monitored in December ($0.83 \pm 0.43 \mu\text{mol m}^{-2} \text{s}^{-1}$, mean value of the considered species), and *C. incanus* had the highest rates ($1.82 \pm 0.19 \mu\text{mol m}^{-2} \text{s}^{-1}$). R_L increased from February to April-May, ($2.44 \pm 1.00 \mu\text{mol m}^{-2} \text{s}^{-1}$, mean value of the considered species), *C. incanus* having the highest rates ($4.56 \pm 0.22 \mu\text{mol m}^{-2} \text{s}^{-1}$). The highest R_L rates were reached in August ($3.21 \pm 0.90 \mu\text{mol m}^{-2} \text{s}^{-1}$, mean value of the considered species) and *C. incanus* had the significantly ($p \leq 0.05$) highest rates ($4.93 \pm 0.31 \mu\text{mol m}^{-2} \text{s}^{-1}$) and *S. aspera* the lowest ones ($1.90 \pm 0.52 \mu\text{mol m}^{-2} \text{s}^{-1}$).

C. incanus showed the highest mean yearly R_L ($3.59 \pm 1.11 \mu\text{mol m}^{-2} \text{s}^{-1}$) and *A. unedo* the lowest one ($1.19 \pm 0.58 \mu\text{mol m}^{-2} \text{s}^{-1}$).

During the year, the ratio R_L/P_N was the highest in August (1.44 ± 0.93 , mean value of the considered species) and the lowest in December (0.16 ± 0.09 , mean value of the considered species). The ratio R_L/P_N ranged from 0.16 (*A. unedo*, mean yearly value) to 0.71 (*R. officinalis*, mean yearly value).

Q_{10} of the considered species was 1.72 ± 0.18 (mean value): *A. unedo* had the highest value (1.98 ± 0.10), followed by *P. latifolia* and *P. lentiscus* (1.88 ± 0.03 , mean value), *E. multiflora* and *R. officinalis* (1.77 ± 0.05 , mean value), *C. incanus* and *S. aspera* (1.58 ± 0.01 , mean value), *Q. ilex* (1.55 ± 0.06) and *E. arborea* (1.49 ± 0.06) (Tab. 2).

The results of the regression analysis between R_L and T_m , and between R_L and R, showed that 39% of R_L variation depends on T_m and 11% on R (Fig. 7).

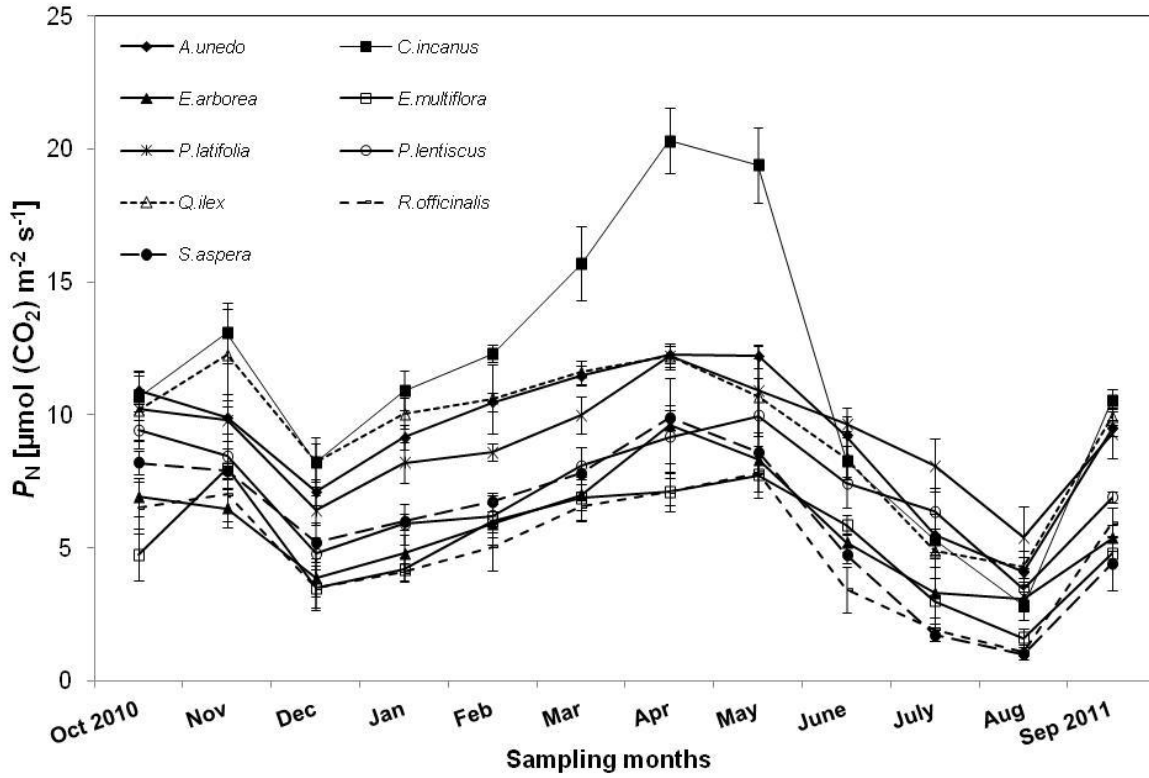


Fig. 4. Seasonal course of the net photosynthetic rates (P_N) during the study period, for the considered species. Each point is the mean value of three sampling days per months ($n = 27$). Mean values (\pm SD) are shown.

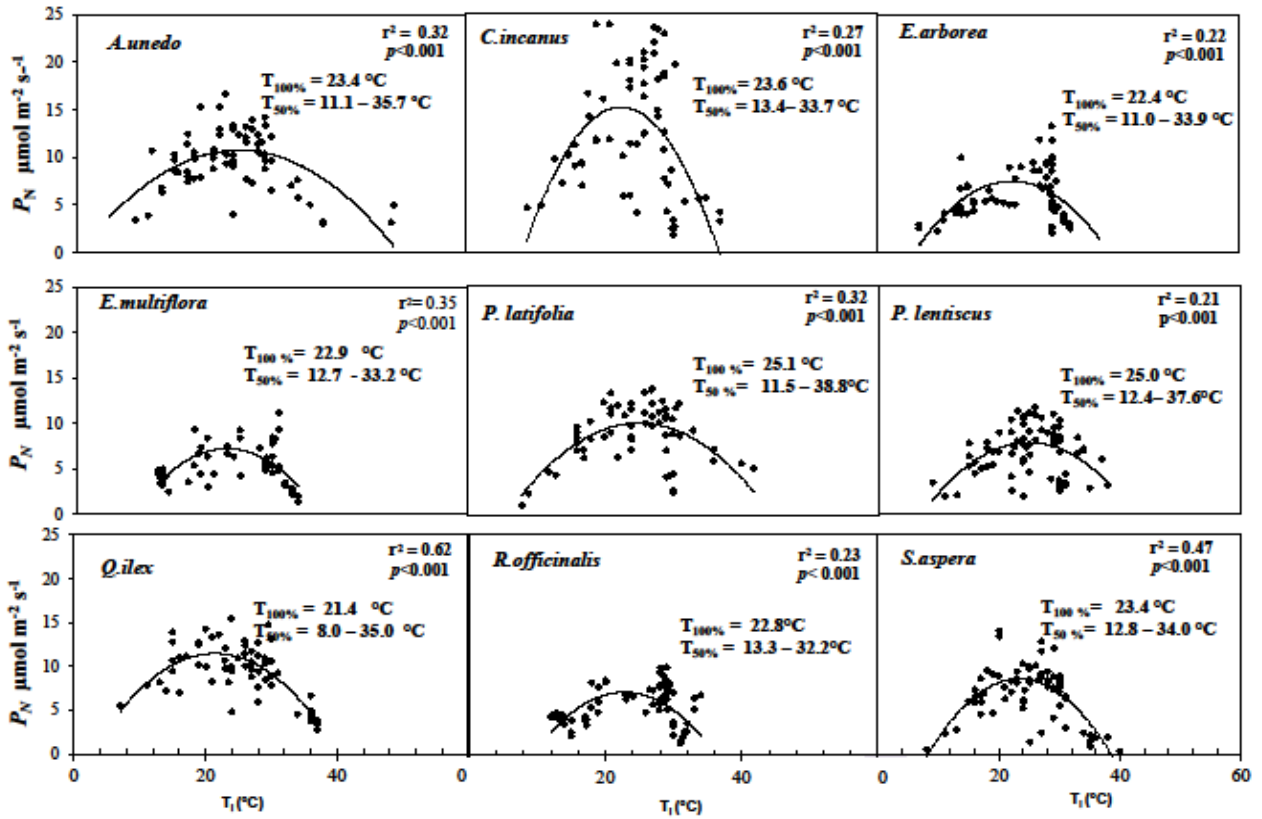


Fig. 5. Correlation analysis between net photosynthetic rates (P_N) and leaf temperature (T_l) of the considered species during the study period. T_{100} = leaf enabling 100% of high photosynthetic rates, $T_{50\%}$ = leaf temperature enabling 50% of high photosynthetic rates.

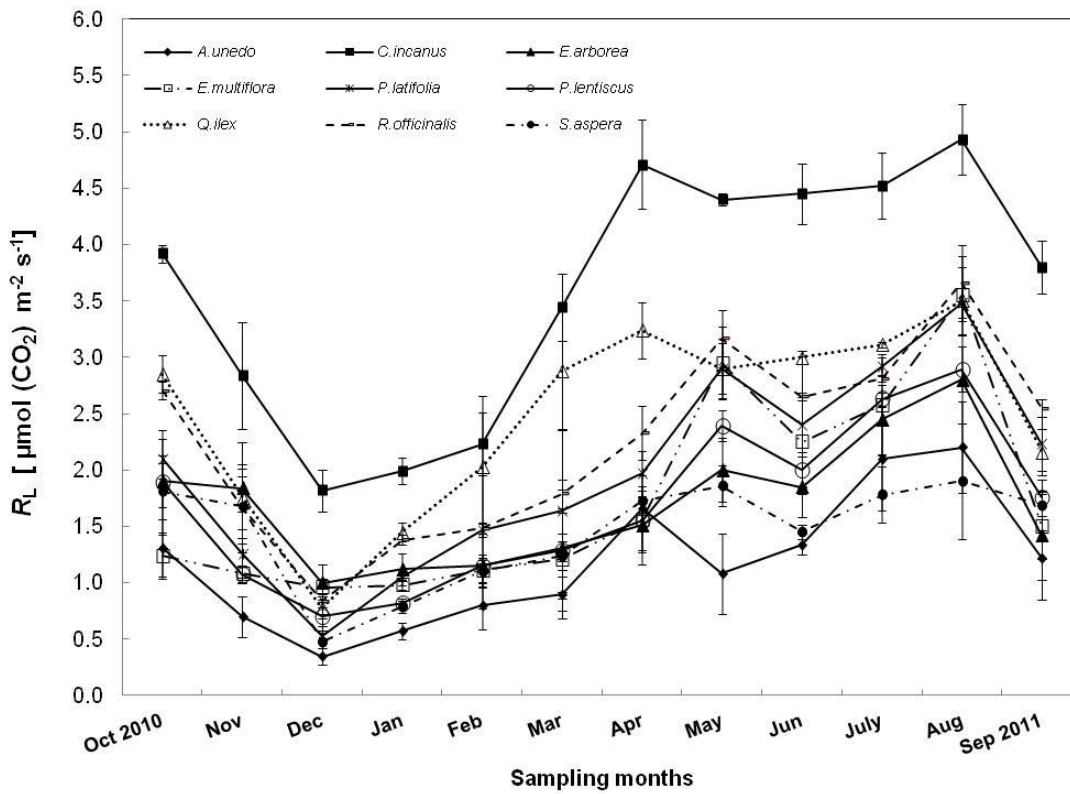


Fig. 6. Seasonal course of leaf dark respiration (R_L), during the study period, for the considered species. Each point is the mean value of three sampling days per months ($n = 27$). Mean values (\pm SD) are shown.

Table 2.

Q₁₀ values. Mean values (\pm SD) are shown. Mean values with the same letter-are not significantly different (Tukey test, $p>0.05$)

Species	Q ₁₀
<i>A.unedo</i>	1.98 \pm 0.10d
<i>C.incanus</i>	1.57 \pm 0.08ab
<i>E.arborea</i>	1.49 \pm 0.06a
<i>E.multiflora</i>	1.80 \pm 0.07cd
<i>P.latifolia</i>	1.90 \pm 0.10cd
<i>P.lentiscus</i>	1.86 \pm 0.13cd
<i>Q.ilex</i>	1.55 \pm 0.06ab
<i>R.officinalis</i>	1.73 \pm 0.05bc
<i>S.aspera</i>	1.58 \pm 0.09ab

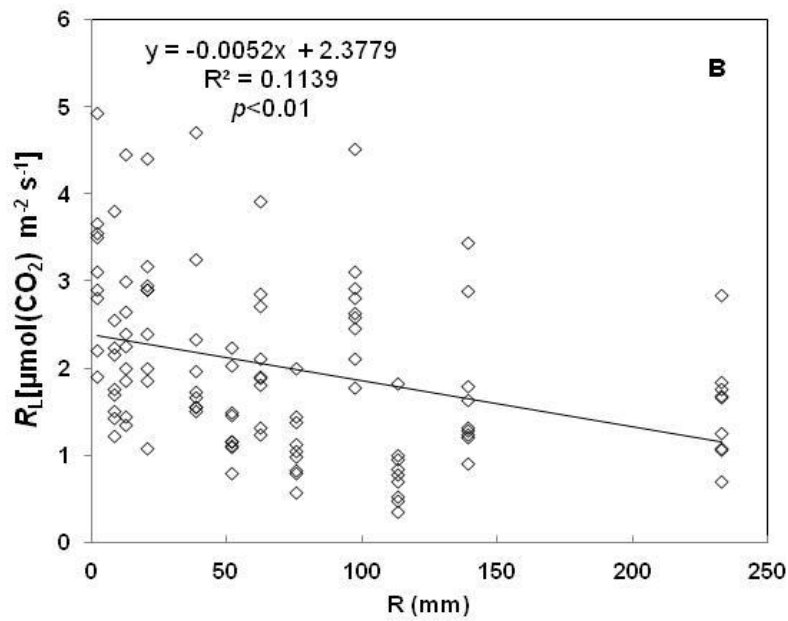
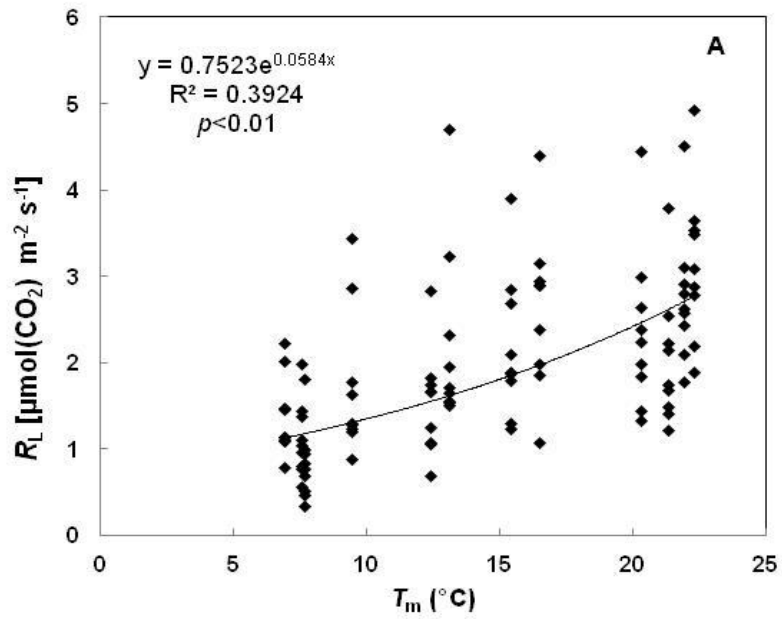


Fig. 7. Regression analysis between leaf respiration (R_L) and mean monthly air temperature (T_m) (A), and between R_L and total monthly rainfall (R) (B). Regression equation, determination's coefficient (R^2) and p -level are shown.

Principal component analysis

The PCA highlighted a non-linear gradient among the considered species with respect to the considered traits, with the first two principal components accounting for 75 % of the total variance (Fig. 8). The first component explained 43 % of the total variance and it was correlated to P_N and R_L during the favorable period ($r = 0.77$ and 0.95 , respectively), R_L in August ($r = 0.90$) and in December ($r = 0.84$). The second component explained 32 % of the total variance, and it was correlated to LMA ($r = 0.79$) and LTD ($r = 0.87$). Along the first component, *C. incanus* showed the highest values and *S. aspera* the lowest ones, while *E. multiflora*, *E. arborea*, *R. officinalis*, *Q. ilex*, *P. latifolia* and *P. lentiscus* were in the middle. *A. unedo* was closer to *S. aspera*. Along the second component *E. multiflora* and *R. officinalis* had the highest values and *A. unedo* the lowest ones, *C. incanus*, *P. latifolia*, *P. lentiscus*, *E. arborea* and *Q. ilex* were in the middle, while *S. aspera* was closer to *A. unedo*.

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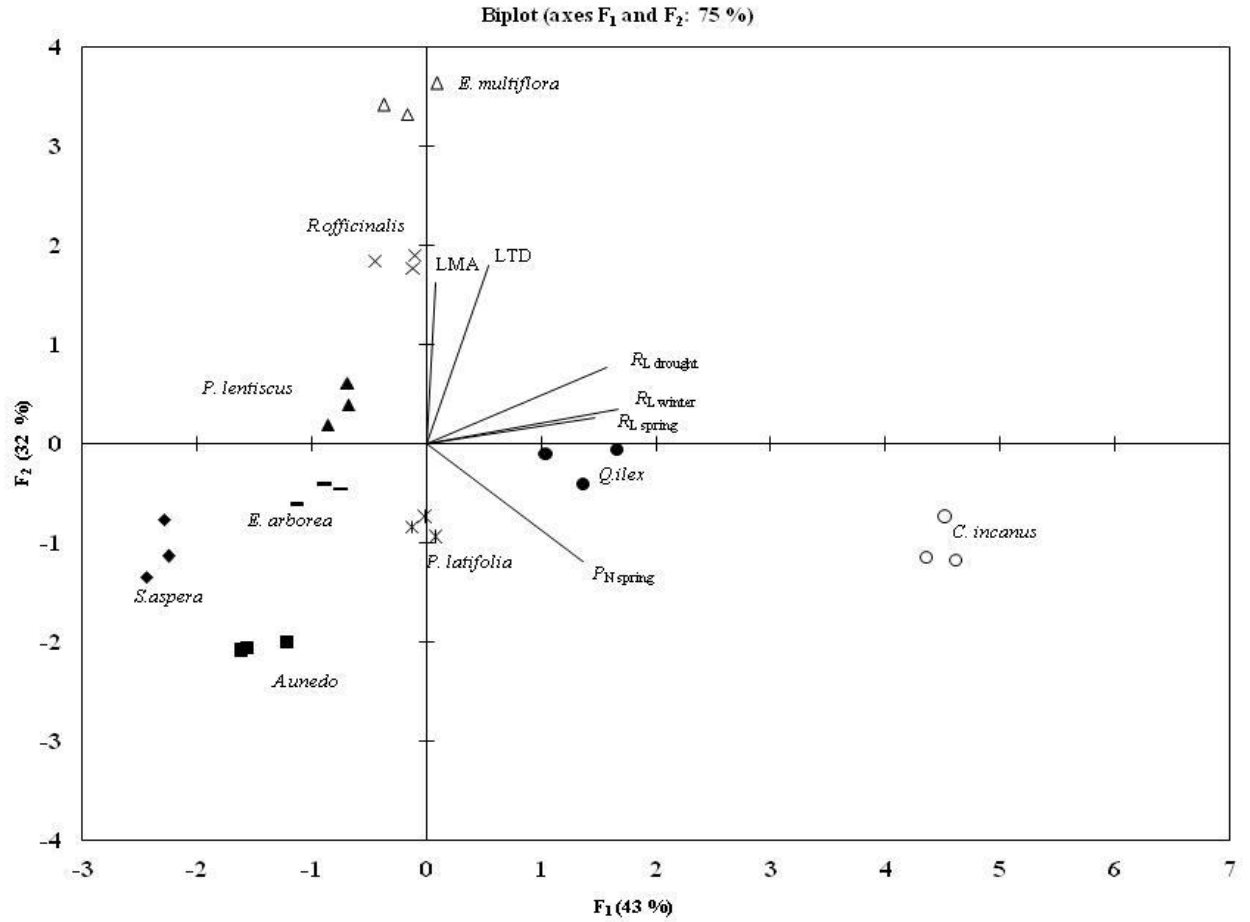


Fig. 8. Principal component analysis (PCA) carried out using leaf morphological traits (LMA and LTD) and leaf physiological traits (P_N and R_L) measured in spring, drought and winter. Component 1, accounting for 43% of the total variance, was significantly related to P_N and R_L during spring, R_L in drought and in winter. Component 2, accounting for 32 % of the total variance, was significantly related to LMA and LTD.

Discussion

The Mediterranean maquis developing along the *Latium* coast (Italy) is characterized by shrubs of different size; small shrubs are the most frequent (57%), followed by medium (32%) and large shrubs (11 %). The number of species increased from S to L shrubs showing different associations among them, which depend on their size, as underlined by the analysis of co-occurrence. Moreover, competition for light may contribute to plant species association, according to Vilà (1997). The results underline a significant correlation between LAI and V of shrubs, 63 % of LAI variations being explained by V. Accordingly, species characterized by a small size (i.e. low V and LAI) co-occur rarely with species characterized by a large size, because large plants can shade and reduce the growth of small plants, as suggested by Weiner (1990). In particular, the negative co-occurrence of *E. multiflora* and *R. officinalis* with *A. unedo*, *E. arborea*, *P. latifolia* and *P. lentiscus* may be explained by their need to grow in full sun. In fact, *E. multiflora* and *R. officinalis* develop exclusively in shrublands while they are absent in Mediterranean evergreen forests where total irradiance is decreased by 94 % with respect to open space (Gratani 1997, Gratani et al. 2006). *C. incanus* does not form preferential pairs with the others species as attested by its presence in all shrub sizes (90 %), and its contribution to 60 % of the mono-species shrubs. *C. incanus* always occupies a position outside the different shrub size (L, M and S) since it is a *helifilous* species (Gratani and Amadori 1991, Civeyrel et al. 2011). On the contrary, the co-occurrence of *S. aspera* with *A. unedo* and *Q. ilex* can be explained by the species ability to grow in full sun as well as in shade, as suggested by Sack et al. (2003). Moreover, *S. aspera* is a non-self-supporting plant species that gains advantage by directing biomass into extension growth and stem length rather than stem stiffness (Niklas 1994, Isnard et al. 2003). *S. aspera* naturally grows in the understory of the Mediterranean evergreen forests and it is a component of shrublands (Gratani 1997).

With regards to the physiological behaviors, the results underline a similar trend among the considered species during the study period. In particular, the highest P_N rates in April–May ($10.9 \pm 3.7 \mu\text{mol m}^{-2} \text{s}^{-1}$, mean value of the considered species) can be related to the high R_L rates ($2.44 \pm 1.00 \mu\text{mol m}^{-2} \text{s}^{-1}$, mean value) that provide ATP, reducing equivalents, and carbon skeletons necessary for biosynthetic reactions (Atkin et al. 2000), and determining a relatively low R_L/P_N ratio (0.23 ± 0.08 , mean value). The high P_N rates may lead to biomass accumulation and growth (Gratani and Crescente 2000). The highest P_N rates of the considered species, when T_m is $17.0 \pm 2.3^\circ\text{C}$ is in agreement with other species in temperate climates (in the range of $15\text{--}30^\circ\text{C}$, Atwell et al. 1999, Larcher 2004, Atkinson et al. 2010). In this period, the high R_L seems to be necessary in providing energy used for producing new leaves (Gratani et al. 2008) and maintenance of the oldest ones, according to the results of Amthor (1986) and Laureano et al. (2008). During the favorable period, among the considered species, *E. multiflora* and *R. officinalis* show the highest R_L/P_N ratio (0.34 ± 0.04 , mean value), justified by the relatively high R_L rates and the lowest P_N . This latter can be related to their high LMA (25.9 ± 1.7 and $20.2 \pm 0.6 \text{ mg cm}^{-2}$, respectively) and LTD values (756 ± 24 and $580 \pm 24 \text{ mg cm}^{-3}$, respectively), according to Peña-Rojas et al. (2005) underlining that high LMA values occur at the expense of a lower photosynthetic potential. Thus, LMA represents a trade-off between photochemical efficiency and photo-protection (Camarero et al. 2012). *C. incanus* the drought semi-deciduous shrub, has a relatively high R_L/P_N of 0.23 ± 0.01 due to the highest P_N and R_L values. The large light-capture area developed per leaf mass (i.e. low LMA, $15.1 \pm 0.7 \text{ mg cm}^{-2}$, Gratani and Bombelli 2001) and the low LTD value ($580 \pm 10 \text{ mg cm}^{-3}$), which determines the shorter diffusion pathway from stomata to chloroplast (Parkhurst 1994, Gratani and Varone 2004a), thus increasing the capacity of this species to assimilate CO_2 (Gratani and Varone 2004a). Moreover, the high photosynthetic rates of *C. incanus* justifies its large vegetative regeneration capability, emphasizing its ecological role in the first reconstitution stages of the Mediterranean maquis after fire

(Gratani and Amadori 1991). *C. incanus*, like other pioneer species, has high R_L rates (Bazzaz and Pickett 1980, Chazdon et al. 1996) which may be a result also of the loss of most of its leaves (winter leaves) in spring-beginning of summer, thus demanding more respiratory products necessary to produce new leaves (summer leaves) (Gratani et al. 2008, Catoni et al. 2012).

The typical sclerophyllous species (*P. latifolia*, *P. lentiscus* and *Q. ilex*) and *E. arborea* have a high R_L/P_N of 0.22 ± 0.05 (mean value) in spring, justified by a relatively high P_N and R_L , which underlines high metabolic activity under the favorable conditions (Gratani et al. 2008). In the same period, *S. aspera* shows a relatively low R_L/P_N value (0.20 ± 0.03), due to relatively high P_N rates and low R_L rates. *A. unedo* shows the lowest R_L/P_N (0.11 ± 0.03) due to the low R_L rates associated with a relatively high P_N rates.

With regards to carbon balance during drought, the R_L/P_N ratio shows variations among the considered species in relation to their different sensitivity to drought of both photosynthesis and respiration. The highest R_L/P_N ratio in response to drought (2.77 ± 0.79 , mean value) in *E. multiflora* and *R. officinalis*, is due to the high R_L increase (45 %) justified by their sensitivity to air temperature, as confirmed by Q_{10} value (1.77 ± 0.05 , mean value) and by the significantly high P_N decrease (82 %), as underlined by the thermal window analysis showing that P_N drops below half of its maximum when T_1 is above 32.7 °C (mean value of the two species). Moreover, the short *E. multiflora* and *R. officinalis* root system accesses water from the superficial soil profile that is subjected to large changes in water content (Aubert 1978, Correia and Catarino 1994, Vilà and Lloret 2000, Gratani and Varone 2004b), resulting in a lower capacity to adjust the photosynthetic rates in drought. In contrast, *A. unedo* shows the lowest R_L/P_N ratio in August (0.54 ± 0.05) as compared to the other species. *A. unedo* is functionally adapted to cope with the summer drought by its large stomata control (Gratani and Ghia 2002), combined with a broad temperature range for biomass accumulation ($T_{1\ 50\%} = 11.1-35.7$ °C) which allows the maintenance of sufficient P_N rates during drought. Moreover, the

adaptive strategy of *A. unedo* seems to be due to the high LA ($9.8 \pm 0.7 \text{ cm}^2$) increasing the capacity of light interception and to the steeper leaf inclination (Gratani and Ghia 2002) which is a prevention mechanism against a potential photo-inhibition of water-stressed leaves during drought, according to Ludlow and Björkman (1984), Werner et al. (1999) and Neuner et al. (1999) for alpine rock species. Consequently, the lowest R_L/P_N ratio is justified by a 66 % P_N decrease and a 61 % R_L increase, this latter being justified by the highest Q_{10} value (1.98 ± 0.10). *S. aspera* shows a relatively high R_L/P_N ratio (1.88 ± 0.05) due to the significantly highest P_N decrease (89 %) in August, related to its low LMA and LTD values ($13.9 \pm 0.8 \text{ mg cm}^{-2}$ and $355 \pm 18 \text{ mg cm}^{-3}$, respectively), associated to the lowest R_L rates ($1.90 \pm 0.52 \text{ } \mu\text{mol m}^{-2} \text{ s}^{-1}$). This latter can be related to *S. aspera* shade-tolerance (Sack et al. 2003), because plants adapted to low irradiance have lower carbon losses via R_L than those not adapted, as underlined by Lusk and Reich (2000). *C. incanus* shows a high R_L/P_N ratio (1.75 ± 0.13) in August, that is relates to a high P_N rates decrease (86 %) and the highest R_L rates ($4.93 \pm 0.31 \text{ } \mu\text{mol m}^{-2} \text{ s}^{-1}$). The high P_N rates decrease is justified by the fact that this species is characterized by a low LMA and a shallow, markedly planar root system (Amato and Sarnataro 2001).

The others considered species (*E. arborea*, *P. latifolia*, *P. lentiscus* and *Q. ilex*) show an intermediate value of R_L/P_N ratio (0.81 ± 0.09 , mean value), due to their low P_N decrease in drought (62%) and their high R_L rates ($3.17 \pm 0.37 \text{ } \mu\text{mol m}^{-2} \text{ s}^{-1}$, mean value), the first also related to the large and deep root system (Aubert 1978, Peñuelas et al. 1998, Green et al. 2005) favoring biomass accumulation (Gratani and Varone 2004a).

The result of the photosynthetic thermal window of these species underline that P_N drops below half of its maximum when T_l is above $36.3 \text{ } ^\circ\text{C}$ (mean value). Water availability is the most important factor affecting photosynthetic activity of Mediterranean species (Llorens et al. 2003); Gratani and Varone (2004a) underline that the relatively high water potential and relative water content in *Q. ilex*, *P. latifolia*, *P. lentiscus* and *E. arborea* improve drought tolerance. Moreover, the high LMA and LTD values ($18.0 \pm 3.7 \text{ mg cm}^{-2}$ and $547 \pm 53 \text{ mg cm}^{-3}$, mean value, respectively) of these species contribute to drought

tolerance (Gratani and Varone 2006). The maintenance of high R_L values associated to a P_N decrease is related to the mobilization of the stored material in response to the plant's requirements for growth and maintenance (Butler and Lansberg 1981), underlining the positive role of R_L during drought stress. The high R_L rates during drought is further confirmed by the exponential relationship between R_L and T_m and the negative linear regression between R_L and R .

Winter stress represents an additional limitation to Mediterranean plant production (Larcher 2000) by the limitation of the enzyme activity of the respiratory apparatus (Atkin and Tjoelker 2003). The considered species have the lowest R_L/P_N ratio (0.16 ± 0.09 , mean value) in winter justified by a 48 % P_N decrease than the maximum (mean value of the considered species in December) and the lowest R_L value ($0.83 \pm 0.43 \mu\text{mol m}^{-2} \text{s}^{-1}$, mean value).

Among the considered species, *Q. ilex* is the most cold-tolerant species underlined by the lowest P_N decrease in December (28 %), according to the results of Oliveira and Peñuelas (2004) and Varone and Gratani (2007). This result is confirmed by the analysis of the photosynthetic thermal window showing that P_N drops below half of its maximum when T_l is lower than 8.0 °C. Moreover, the low R_L rates ($0.78 \pm 0.10 \mu\text{mol m}^{-2} \text{s}^{-1}$) in *Q. ilex* determines a low R_L/P_N ratio (0.09 ± 0.04).

On the contrary, *C. incanus* seems to be the most cold-susceptible species by its highest P_N decrease (59 %) in December, that is associated with the highest R_L rates ($1.82 \pm 0.19 \mu\text{mol m}^{-2} \text{s}^{-1}$) determining a higher R_L/P_N ratio (0.22 ± 0.03).

The PCA summarizes the above considerations, showing a different physiological and morphological gradient among the considered species. In particular, *C. incanus* having the highest mean yearly P_N and R_L rates and relatively low LMA and LTD values is furthest from the other species emphasizing its drought semi-deciduous *habitus*. Another group is formed by *E. multiflora* and *R. officinalis* and is characterized by the highest LMA and LTD, higher R_L rates in the favorable, drought and winter periods, and the lowest P_N rates in the favorable period. The group formed by *E. arborea*, *P.*

lentiscus, *P. latifolia* and *Q. ilex* is in the middle. *A. unedo* and *S. aspera* are close to this group despite the lower R_L rates in the favorable period, during drought and in winter as compared to the others species, and the relatively low LMA and LTD values. On the whole the results show the response of the considered species to the stress factors typical of the Mediterranean climate; in particular, the carbon balance over the year ranges from 0.16 ± 0.09 (in winter) through 0.23 ± 0.08 (in spring) to 1.44 ± 0.93 (in summer), and it is indicative of the different sensitivity of both R_L and P_N to water availability and air temperature changes during the year. Moreover, the results support the different potential role of leaf morphological traits that deal with climatic stress in Mediterranean evergreen species as well as for others species in limited growth conditions, according to Larcher (2003) and Aryal and Neuner (2010). In fact, the xeromorphic leaves of the Mediterranean evergreen species, attested by a reduced leaf area, high leaf thickness (i.e. high LMA) and leaf density (i.e. high LTD) favor carbon gain profits over transpiration losses during drought (Turner 1994, Rotondi et al. 2003). Moreover, the high cost of construction in these leaf types (Gratani and Varone 2004a, 2006) justifies the relatively high R_L value, compared to other species (i.e. deciduous species, Mitchell et al. 1999, Turnbull et al. 2005, Ow et al. 2010), reflecting metabolic expenditure of photosynthate in the leaf structure (Mitchell et al. 1999, Wright et al. 2004).

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