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Variations in leaf respiration across different seasons for Mediterranean evergreen species

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Abstract

Leaf respiration (R_L) of evergreen species co-occurring in the Mediterranean maquis developing along the Latium coast was analyzed. The results on the whole showed that the considered evergreen species had the same R_L trend during the year, with the lowest rates [0.83 ± 0.43 μmol(CO_2) m^{-2} s^{-1}, mean value of the considered species] in winter, in response to low air temperatures. Higher R_L were reached in spring [2.44 ± 1.00 μmol(CO_2) m^{-2} s^{-1}, mean value] during the favorable period, and in summer [3.17 ± 0.89 μmol(CO_2) m^{-2} s^{-1}] during drought. The results of the regression analysis showed that 42% of R_L variations depended on mean air temperature and 13% on total monthly rainfall. Among the considered species, *C. incanus*, was characterized by the highest R_L in drought [4.93 ± 0.27 μmol(CO_2) m^{-2} s^{-1}], low leaf water potential at predawn (Ψ_{pd}= –1.08 ± 0.18 MPa) and midday (Ψ_{md} = –2.75 ± 0.11 MPa) and low relative water content at predawn (RWC_{pd} = 80.5 ± 3.4%) and midday (RWC_{md} = 67.1 ± 4.6%). Compared to *C. incanus*, the sclerophyllous species (*Q. ilex*, *P. latifolia*, *P. lentiscus*, *A. unedo*) and the liana (*S. aspera*), had lower R_L [2.72 ± 0.66 μmol(CO_2) m^{-2} s^{-1}, mean value of the considered species], higher RWC_{pd} (91.8 ± 1.8%), RWC_{md} (82.4 ± 3.2%), Ψ_{pd} (–0.65 ± 0.28 MPa) and Ψ_{md} (–2.85 ± 1.20 MPa) in drought. The narrow-leaved species (*E. multiflora*, *R. officinalis*, and *E. arborea*) were in the middle. The coefficients, proportional to the respiration increase for each 10°C rise (Q_{10}), ranging from 1.49 (*E. arborea*) to 1.98 (*A. unedo*) were indicative of the different sensitivities of the considered species to air temperature variation.

Additional key words: drought; leaf respiration; Mediterranean evergreen species; water stress.

Introduction

In Mediterranean-type ecosystems, summer drought is the main environmental constraint limiting plant growth and production (Gulías *et al.* 2002, Galmès *et al.* 2007, Pèrez-Camacho *et al.* 2012). The limitation to plant growth imposed by low water availability is mainly due to reductions of plant carbon balance, which is dependent on the balance between photosynthesis and respiration (Lambers *et al.* 1998, Giffort 2003, Pinheiro and Chaves 2011, Ayub *et al.* 2011). The pattern of respiratory use in recent photoassimilates *vs.* accumulated reserves may change under water-stress conditions in a species-dependent manner. The percentage of daily fixed carbon that is respired is likely to be higher in water-stressed plants due to the fact that drought typically has a greater proportional inhibitory effect on photosynthesis than on respiration (Flexas *et al.* 2006, Atkin and Macherel 2009). Differences in plant species relative to water content (RWC) may account for different respiration responses (Lawlor and Cornic 2002). Nevertheless, to date, the experimental evidences available do not support a clear pattern of respiration in response to water stress (Galmés *et al.* 2007, Crous *et al.* 2011). Moreover, leaf respiration undergoes thermal acclimation when long-term changes in growth temperature occur (Atkin *et al.* 2005, Ow *et al.* 2008a,b, Way and Oren 2010). The extent of temperature acclimation of leaf respiration differs among species, where some species are able to acclimate, and others are not (Loveys *et al.* 2003, Atkin *et al.* 2006, Searle *et al.* 2011, Archontoulis *et al.* 2012). Leaf respiration is very sensitive to short-term air temperature variations (Atkin *et al.* 2005, Crous *et al.* 2011) by the maximum activity of leaf respiration enzymes (Atkin and Tjoelker 2003). Q_{10} describes the short-term sensitivity of leaf respiration to temperature (*i.e.* seconds to hours) (Atkin and Tjoelker 2003, Ow *et al.* 2010) and a larger Q_{10} signifies a larger change in leaf respiration

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Abbreviations: Q_{10} – the coefficient proportional to the respiration increase for each 10°C rise; R – total monthly rainfall; R_L – leaf respiration; RWC_{pd} – relative water content at predawn; RWC_{md} – relative water content at midday; SWC – soil water content; *T* – air temperature; Ψ_{pd} – predawn leaf water potential; Ψ_{md} – midday leaf water potential.

with a 10ºC change in temperature (Bolstad *et al.* 1999, Tjolker *et al.* 2001, Cavaleri *et al.* 2008).

Studies examining the combination of water limitation and high air temperature effects on leaf respiration are scarcer than those analyzing photosynthesis (Lawlor and Cornic 2002, Rennenberg *et al.* 2006, Atkin and Macherel 2009) and the lack of knowledge is even greater when referring to Mediterranean species (Galmés *et al.* 2007). Recent climate projections include a decline in rainfall by more than 20% during spring and summer, combined with a larger evaporative demand due to warmer air temperatures for the Mediterranean Basin (Giorgi 2006, Rowel and Jones 2006, Giorgi and Lionello 2008, Lelieveld *et al.* 2012). Over the last century, temperatures in the Mediterranean Basin have already shown warming trends (Peñuelas and Boada 2003, Tsanis *et al.* 2011, Gimeno *et al.* 2012). Increasing air temperature by exceeding the optimal temperature for carbon gain may have the potential to alter plant functioning (Centritto *et al.* 2011). In particular, the increased air temperature might result in a sustained imbalance between respiration and photosynthesis (King *et al.* 2006, Gratani *et al.* 2008, Keith *et al.* 2012), because high temperatures associated to water stress decrease the photochemical efficiency in the Mediterranean species (Valladares and Pearcy 1997, Gratani and Ghia 2002, Llorens *et al.* 2003, Ogaya *et al.* 2011). Understanding leaf respiration variations in response to air temperature and water stress is of paramount importance in consideration to global change, because the efflux of CO_2 from plant respiratory processes is a critical and uncertain component of plant, ecosystem, and global carbon budget (King *et al.* 2006, Houghton 2007, Searle and Turnbull 2011).

The main objective of this study was to analyze daytime dark respiration variations in evergreen species co-occurring in the Mediterranean maquis. While photosynthesis is limited temporally (*i.e.* to daytime hours), leaf respiration occurs continuously both in the light and in the darkness (Atkin *et al.* 2000a, Galmès *et al.* 2007). Night-time and daytime dark respiration rates can be considered statistically indistinguishable (Zaragosa-Castells *et al.* 2008, Lusk *et al.* 2011). Since Mediterranean evergreen species may have different climatic constraints, each species will likely respond differently to climate change (Llorens *et al.* 2003). We hypothesized that leaf dark respiration variations during the year could differ among semideciduous species, sclerophyllous species, narrow-leaved species, and liana by their different sensitivities to high air temperature and water stress. Improving knowledge in leaf respiration is important in understanding the capability of the considered evergreen species to withstand the hypothesized air temperature increases, taking into account that leaf respiration affects plant survival under water stress conditions (Pinheiro and Chaves 2011).

Materials and methods

Study area and plant species: The study was carried out under field condition in the Mediterranean maquis developing along the Latium coast (Capocotta, Italy, 5 m a.s.l., 41°40′23′′N; 12°23′38′′E) (Gratani and Crescente 1997), in the period October 2010–September 2011. A representative sample area of 1,200 m^2 was selected, and the following species were considered: *Arbutus unedo* L., *Cistus incanus* L., *Erica arborea* L., *Erica multiflora* L., *Phillyrea latifolia* L., *Pistacia lentiscus* L., *Quercus ilex* L., *Rosmarinus officinalis* L., and *Smilax aspera* L. Three representative shrubs per each of the considered species were selected in the sample area.

The climate of the area was of Mediterranean type. The average minimum air temperature (T_{min}) of the coldest month (January) was 5.2 ±1.7°C and the average maximum air temperature (T_{max}) of the hottest months (July–August) was 30.8 ± 0.2°C. The mean yearly air temperature was 16.8 ± 6.5°C (T_m). Total annual rainfall was 694 mm. During the study period, T_{min} of the coldest month (February) was 4.2 ± 1.6°C and T_{max} of the hottest month (August) was 31.4 ± 1.3°C. Total rainfall (R) of the study period was 816 mm. The monthly trend of T_{max}, T_{min}, and R during the study period are shown in Fig. 1. (Data were obtained from the Collegio Romano Meteorological Station, located 33 km from the study area, for the years 1995–2011).

Leaf respiration: Leaf dark respiration (R_L) was measured using an infrared gas analyzer *ADC LCA4* (*ADC Bioscientific Ltd.,* Hoddesdon, UK) equipped with a conifer leaf chamber *(PLC, Parkinson Leaf Chamber*) for *E. arborea*, *E. multiflora*, and *R. officinalis* measurements, and a broad leaf chamber (*PLC, Parkinson Leaf Chamber*) for *A. unedo*, *C. incanus*, *P. latifolia*, *P. lentiscus, Q. ilex,* and *S. aspera* measurements.

R_L measurements were carried out on intact, fully expanded, sun leaves of *A. unedo*, *C. incanus*, *P. latifolia*, *P. lentiscus*, *Q. ilex*, and *S. aspera* and on current-year needles in sun apical shoots of *E. arborea*, *E. multiflora*, and *R. officinalis*. Three leaves (in broad-leaved species) and three apical shoots (in narrow-leaved species) from each of the considered shrubs were used in each sampling occasion.

Measurements were carried out daily, from 09.00 to 11.00 h (Lusk *et al.* 2011), 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). During R_L measurements, air temperature (*T*, °C) was monitored by portable thermo-hygrometers (*HD 8901, Delta Ohm,* Italy). The monthly R_L rates shown were obtained by averaging the values taken on three following days with the same weather conditions in the first week for each month.

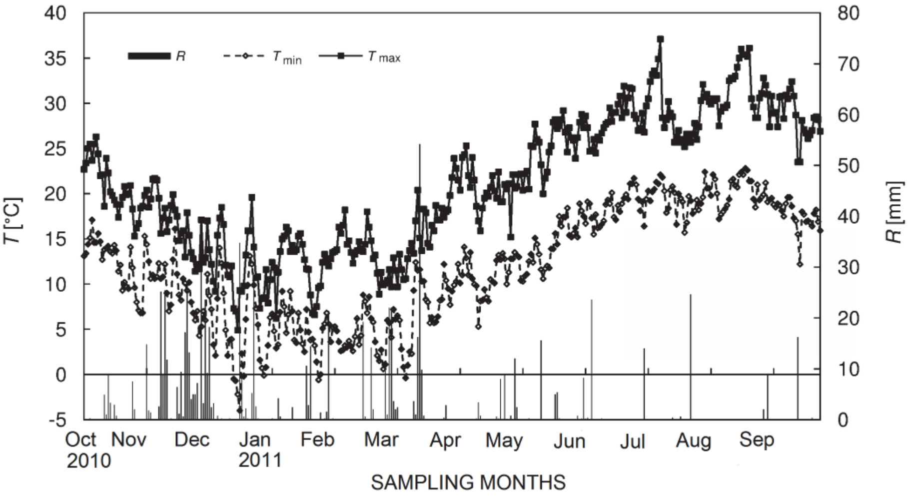

Fig. 1. Trends of air temperature and rainfall during the study period (October 2010–September 2011). R – total monthly rainfall: T_{min} – minimum air temperature; T_{max} – maximum air temperature (data of the Collegio Romano Metereological Station, Rome).

Q_{10}: The coefficient proportional to the respiration increase for each 10°C rise (*i.e.*, Q_{10}) was calculated using T measured in the same time of R_L measurements, according to Atkin *et al.* (2000b). In particular, 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.

Leaf water status: Ψ_{pd} and Ψ_{md} were measured on leaves of *A. unedo*, *C. incanus*, *P. latifolia*, *P. lentiscus*, *Q. ilex*, and *S. aspera* and on shoots of *E. arborea*, *E. multiflora*, *R. officinalis* (five leaves and five apical shoots per species and per each sampling occasion).

Ψ measurements were carried out using a portable pressure chamber (*SKPM 1400, Skye Instruments,* UK).

RWC_{pd} and RWC_{md} were calculated at the same time and on the same leaves used for Ψ measurements as: RWC = (FM – DM)/(TM – DM) × 100, where FM was the leaf fresh mass, DM the leaf mass after drying at 90°C until constant mass was reached, and TM the leaf mass after rehydration until saturation for 48 h at 5°C in the darkness (Bacelar *et al.* 2007). Ψ and RWC measurements were carried out in April and May (during the favorable period) and in August (during drought), simultaneously with R_L measurements, according to Gratani *et al*. (2011).

Soil water content (SWC) was measured by soil samples taken at a depth of 30 cm, after drying at 105°C until constant mass was reached (Rundel and Jarrel 1989).

Soil samples were collected in April, May, and August (three samples in each month), in the same days of Ψ and RWC measurements.

Statistics: All statistical tests were performed using a statistical software package (*Statistica*, *Statsoft*, USA). The differences in physiological leaf traits were determined by the analysis of variance (*ANOVA*) and *Tukey*'s test for multiple comparisons.

Regression analysis was carried out to examine the correlations between R_L and T, and between R_L and R.

Results

Leaf respiration: All the considered species had the same R_L trend during the year, with the lowest rates [0.83 ± 0.43 μmol(CO_2) m^{-2} s^{-1}, mean value] in December, *C. incanus* having significantly ($p \leq 0.05$) the highest R_L rates [1.82 ± 0.19 μmol(CO_2) m^{-2} s^{-1}] (Fig. 2).

R_L increased in February reaching higher rates in April–May, [2.44 ± 1.00 μmol(CO_2) m^{-2} s^{-1}, mean value of the considered species], *C. incanus* having the highest rates [4.56 ± 0.22 μmol(CO_2) m^{-2} s^{-1}].

R_L decreased, on an average by 15% in June compared with the maximum in spring and peaking in August [3.17 ± 0.89 μmol(CO_2) m^{-2} s^{-1}, mean value of the considered species]; *C. incanus* had significantly ($p \leq 0.05$) the highest rates [4.93 ± 0.27 μmol(CO_2) m^{-2} s^{-1}] and *S. aspera* the lowest ones [1.90 ± 0.52 μmol(CO_2) m^{-2} s^{-1}]. In September, R_L decreased, on an average, 36% compared with the August rates.

The mean yearly R_L was the highest in *C. incanus* [3.59 ± 1.11 μmol(CO_2) m^{-2} s^{-1}] and the lowest in *A. unedo* [1.19 ± 0.58 μmol(CO_2) m^{-2} s^{-1}].

There was a significant ($p<0.01$) positive correlation between R_L and T, 42% of R_L variations being explained by T. Moreover, there was a significant negative ($p<0.01$) correlation between R_L and R, 13% of R_L variations depended on R (Fig. 3).

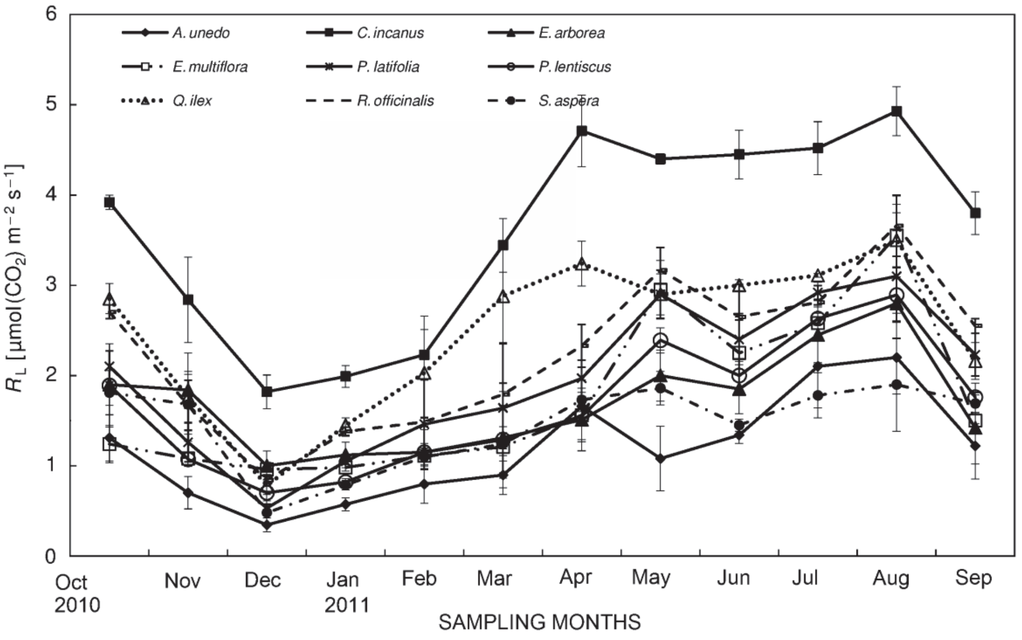

Fig. 2. Trends of leaf respiration (R_L) of the considered species during the study period. Each point is the mean value of three sampling days per months (n = 27). Mean values (± SD) are shown.

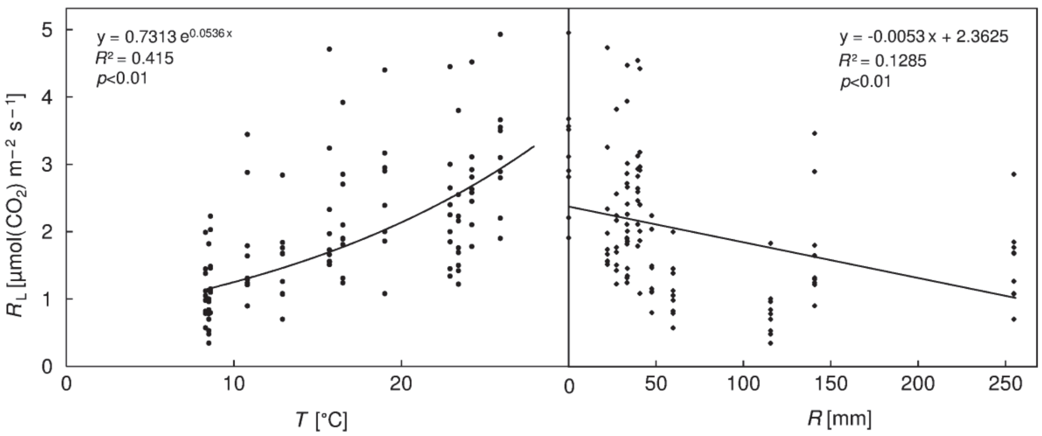

Fig. 3. Regression analysis between leaf respiration (R_L) and mean monthly air temperature (T), and between R_L and total monthly rainfall (R). Regression equation, determination's coefficient (R^2) and p-level are shown.

Table 1. Q_{10} values. Means values (± SD) are shown. Mean values with *the same letters* are not significantly different (*ANOVA*, p>0.05).

Species	Q_{10}
A. unedo	1.98 ± 0.11^{ade}
C. incanus	1.57 ± 0.10^{bc}
E. arborea	1.49 ± 0.06^{c}
E. multiflora	1.80 ± 0.06^{de}
P. latifolia	1.90 ± 0.14^{e}
P. lentiscus	1.86 ± 0.12^{ade}
Q. ilex	1.55 ± 0.09^{bc}
R. officinalis	1.73 ± 0.05^{bde}
S. aspera	1.58 ± 0.09^{bc}

Q_{10} of the considered species was 1.72 ± 0.18 (mean value): *A. unedo* had the highest value (1.98 ± 0.11), 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 ± 0.09) and *E. arborea* (1.49 ± 0.06) (Table 1).

Leaf water status: The highest Ψ_{pd} and Ψ_{md} were measured in the favorable period (April-May) (–0.12 ± 0.03 and –2.09 ± 0.75 MPa, respectively, mean values of the considered species), *A. unedo* and *E. multiflora* having the highest Ψ_{pd} (–0.09 ± 0.01 MPa, mean value) and *R. officinalis* the lowest one (–0.18 ± 0.01 MPa); *P. lentiscus* showed the highest Ψ_{md} (–0.37 ± 0.08 MPa)

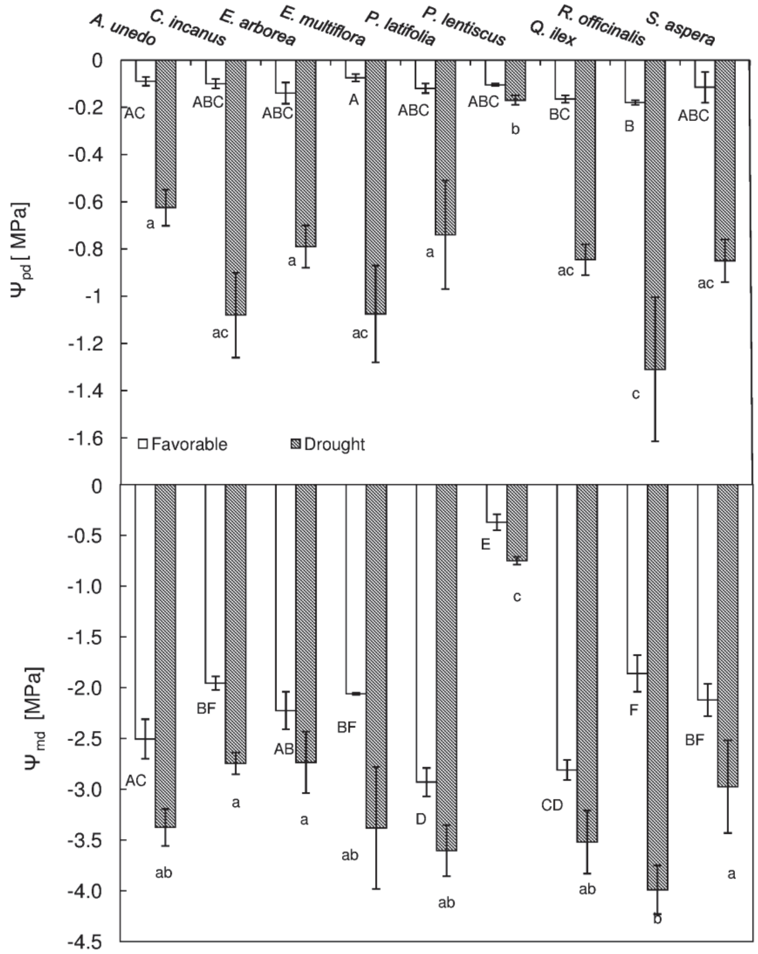

Fig. 4. Leaf water potential at predawn (Ψ_{pd}) and midday (Ψ_{md}) of the considered species in the favorable period (April–May) and in drought (August) (n = 30 in the favorable period and 15 in drought). Capital and lowercase letters indicate the inter-specific differences during the favorable and drought period, respectively. The means with *the same letters* are not significantly different (*ANOVA*, $p \geq 0.05$). Mean values (± SD) are shown.

and *P. latifolia* the lowest one (–2.93 ± 0.14 MPa) (Fig. 4). Ψ_{pd} and Ψ_{md} of the considered species significantly decreased in August, *P. lentiscus* showing the highest values (–0.17 ± 0.02 and –0.75 ± 0.04 MPa, respectively) and *R. officinalis* the lowest ones (–1.31 ± 0.31 and –3.99 ± 0.24 MPa, respectively).

RWC_{pd} and RWC_{md} followed the same Ψ_{pd} and Ψ_{md} trend during the study period, with the highest values in April–May (94.8 ± 1.6 and 82.2 ± 4.8%, mean values, respectively) (Fig. 5). RWC_{pd} and RWC_{md} significantly decreased in August, *S. aspera* having the highest values (93.8 ± 1.1 and 87.4 ± 1.6%, respectively) and *R. officinalis* the lowest ones (78.0 ± 0.5 and 59.6 ± 3.4%, respectively).

Soil water content: The highest SWC values were measured in April–May (6.1 ± 0.4%, mean value), decreasing by 84% in August. (Table 2).

Discussion

The results show that the co-occurring evergreen species have the same R_L trend during the year. In particular, high R_L rates [2.44 ± 1.00 μmol(CO_2) m^{-2} s^{-1}, mean value of the considered species] are reached in April–May, when soil water availability (6.1 ± 0.4% SWC) and T_m(14.2–21.3°C) favor vegetative activity (Gratani *et al.* 2008) sustained also by the high RWC_{pd} and RWC_{md} (94.8 ± 1.6 and 82.2 ± 4.8 %, respectively, mean values of the considered species). The regression analysis underlines that most of the R_L variations depended on air temperature (42%) and only partially on R (13%), according to the results of Wright *et al.* (2006) underlining that air temperature is the most important environmental variable significantly related to R_L. Our finding of a negative correlation between R_L and R is consistent with the evolutionary trend that led to higher respiratory rates in species from lower than from higher rainfall sites (Wright *et al.* 2006). In spring, the energy generated through R_L is used for producing new leaves and for the maintenance of the oldest ones, according to Amthor (1986) and Laureano *et al.* (2008).

Low water availability represents the main environmental constraint for plant growth and productivity worldwide, and when coupled with rising temperatures, it influences strongly the flux of carbon assimilated by plants through photosynthesis or released by

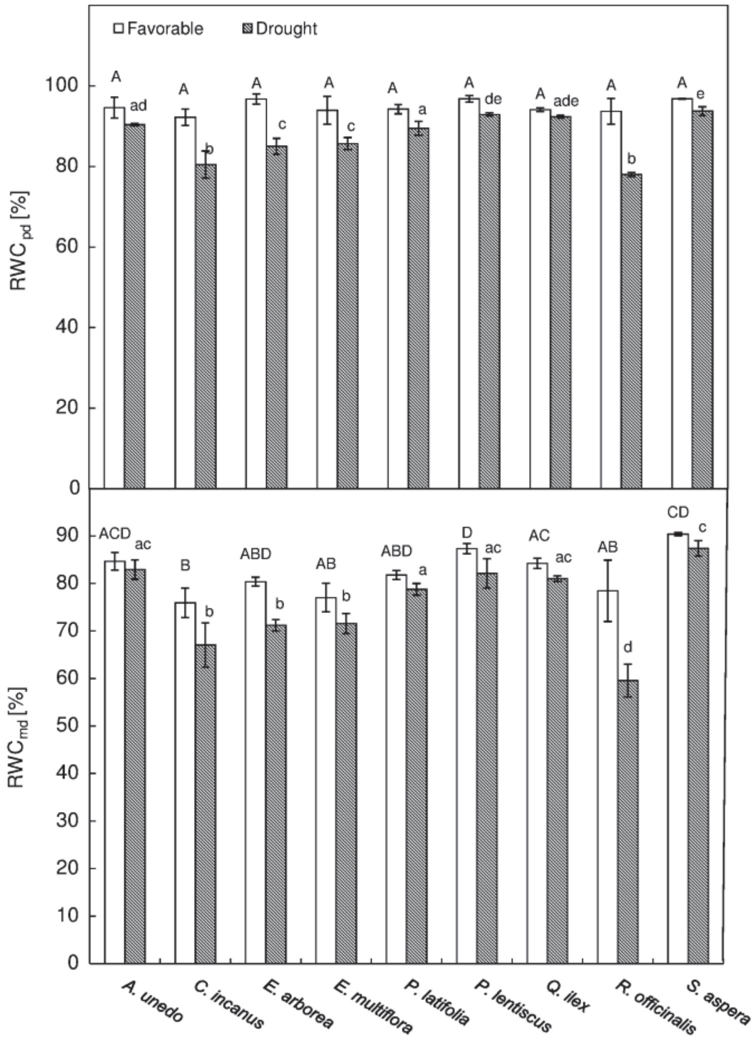

Fig. 5. Relative water content at predawn (RWC$_{pd}$) and at midday (RWC$_{md}$) of the considered species in the favorable period (April–May) and in drought (August) (n = 30 in the favorable period and 15 in drought). *Capital* and *lowercase letters* indicate the interspecific differences during the favorable and drought period, respectively. The means with *the same letters* are not significantly different (*ANOVA*, $p \geq 0.05$). Mean values (± SD) are shown.

Table 2. Values of soil water content (SWC) in April, May and August. Means values (± SD) are shown. Mean values with *the same letters* are not significantly different (*ANOVA*, $p > 0.05$).

Month	SWC [%]
April	5.8 ± 0.3^a
May	6.3 ± 0.4^a
August	1.0 ± 0.1^b

mitochondrial respiration (Way and Oren 2010). In drought, plants develop strategies such as closing stomata to avoid water loss and maintaining a high solute gradient, which requires high energy resulting in potentially higher R_L rates (Chu *et al.* 2011). Warren *et al.* (2011) showed that the decreased stomatal conductance reduces the latent heat loss and thereby increases leaf temperatures, both reducing photosynthesis and increasing respiration, which could further exacerbate impacts of the direct effects of g_s on assimilation. Thus, severe water stress could result in an increased demand for respiratory energy to deal with increased maintenance costs and/or a requirement for oxidation of excess cellular redox equivalents (Atkin and Macherel 2009). In August, when air temperature increased (T_{max} = 31.4 ± 1.3°C) and water availability decreased (SWC = 1.0 ± 0.1%; R = 0 mm), R_L rates of the considered species increase, on an average, 35% compared with the spring rates. At high RWC with large photosynthesis, R_L is a small proportion of it, but at severe stress the progressive decrease in RWC reduces photosynthesis and CO_2 is released from R_L activity (Lawlor and Cornic 2002). In this period, RWC$_{pd}$ and RWC$_{md}$ of the considered species decrease on an average, 7 and 8%, respectively, from the spring values, and leaf water potential had the lowest values (–0.83 ± 0.32 and –3.01 ± 0.94 MPa, respectively, Ψ_{pd} and Ψ_{md}). Moreover, a higher demand for respiratory ATP under severe water stress is required to support photosynthetic repair mechanisms (Atkin and Macherel 2009). Higher respiration rates, mainly as the maintenance component underline acclimation mechanisms to drought (Gratani *et al.* 2007, Slot *et al.* 2008).

In September, R_L rates decrease by 36% compared to August measurements, in response to the favorable air temperature (T_m = 23.2 ± 1.3°C; T_{max} = 28.8 ± 1.1°C). The lowest R_L rates are measured in December, when air temperature is the lowest (T_m = 8.5 ± 2.8°C and T_{min} = 5.0 ± 3.6°C), suggesting a limitation of the enzyme activity of the respiratory apparatus (Atkin and Tjoelker 2003). The Q_{10} of the considered species (1.72 ± 0.18, mean value) is in the range of the Mediterranean species (Larcher 1983), and it is lower compared to different vegetation types (*e.g.* 2.14 and 2.56 for tropical and arctic biomes, respectively, Tjolker *et al.* 2001).

Although the species show a similar R_L trend during the year, some differences can be underlined, particularly in drought, considering that under field conditions respiration rates are also a function of a plant physiological history, and are subject to acclimation or adaptation, or both (Amthor 1984, 1989, Atkin *et al.* 2000b, Turnbull *et al.* 2001). Among the considered species, *C. incanus* (the drought semideciduous species) is characterized by the highest R_L rates in spring [4.56 ± 0.22 μmol(CO_2) m^{-2} s^{-1}] justified by the highest photosynthetic activity compared to the other considered species (Gratani and Varone 2004a) and the loss of most of its leaves (winter leaves), when new ones (summer leaves) are produced (Gratani and Bombelli 2001). The increased R_L in drought (8% higher than spring value) might be necessary to provide energy due to the drastic decrease of the *C. incanus* photosynthetic activity (Gratani and Varone 2004a), which was justified by its lower RWC_{pd}, RWC_{md} (80.5 ± 3.4 and 67.0 ± 4.6%, respectively), Ψ_{pd} and Ψ_{md} (–1.08 ± 0.29 and –2.75 ± 0.15 MPa, respectively). These parameters are considered among the most reliable for quantifying plant water-stress response (Siddique *et al.* 2000). Compared to *C. incanus*, the sclerophyllous species (*Q. ilex* and *P. latifolia, A. unedo* and *P. lentiscus*) showed a lower R_L [2.92 ± 0.54 μmol(CO_2) m^{-2} s^{-1}] and a higher leaf water status in drought (Ψ_{pd} = –0.60 ± 0.30 MPa, Ψ_{md} = –2.81 ± 1.38 MPa, RWC_{pd} = 91.3 ± 1.6% and RWC_{md} = 81.2 ± 1.8%, mean value), which may be related to their deeper-root apparatus (Vilagrosa *et al.* 1997, Gratani *et al.* 2000, Vilagrosa 2002, Filella and Peñuelas 2003, Lloret *et al.* 2004) and high leaf consistency (*i.e.*, high LMA, Gratani and Varone 2006) allowing drought resistance. In particular, *A. unedo* has a higher R_L increase in drought (61%) with respect to the other sclerophyllous species, which can be related to its higher sensitivity to air temperature (Gratani and Ghia 2002), also attested by the higher Q_{10} value (1.98 ± 0.11). The lowest R_L increase of *S. aspera* in drought (6%), with respect to the other considered species, is indicative of its large capability to sustain water stress (Alessio *et al.* 2004), also attested by its water status (RWC_{pd} = 93.8 ± 1.1% and RWC_{md} = 87.4 ± 1.6%). Moreover, *S. aspera* naturally develops in the understory of the Mediterranean evergreen forests (Gratani 1997) through its ability to grow in sun as well as in shade conditions (Sack *et al.* 2003). As underlined by Lusk and Reich (2000), variation in R_L has been widely proposed as a component of both adaptation and acclimation to light availability and it has been argued that plants adapted to low light should have lower carbon losses *via* R_L than those not so adapted. R_L trend of the narrow-leaved species (*E. multiflora*, *R. officinalis*, and *E. arborea*) during drought [3.34 ± 0.47 μmol(CO_2) m^{-2} s^{-1}, mean value] is between the semideciduous and the sclerophyllous species. Nevertheless, among them, the lowest R_L of *E. arborea* in drought may be related to its low sensitivity to air temperature (Q_{10} = 1.49 ± 0.06). The higher RWC_{pd} and RWC_{md} in drought can be explained by *E. arborea* ability to access water from those parts of the soil profile which are subjected to narrow change in water availability. The high LMA resulting in a higher leaf compactness improves drought resistance (Gratani and Varone 2004b).

In conclusion, R_L varies in the considered Mediterranean evergreen species according to climatic factors and in particular to air temperature. The high R_L rates are monitored in spring, when air temperature is favorable to allow new biomass production, and in drought, when air temperature increase and water availability is low. Changes in respiration in response to drought were smaller as compared to the largest decrease in photosynthesis; therefore, as carbon uptake becomes more limited under water scarcity, respiration increases proportionally leading to increased leaf intercellular CO_2 and these altering plant carbon balance (Lawlor and Tezara 2009, Pinheiro and Chaves 2011). The hypothesized increase of air temperature could modify R_L of the considered co-occurring species limiting carbon acquisition with a consequent decrease in biomass production. Consequently, the modified carbon acquisition can determine in the long-term changes in species composition and vegetation type (Box and Choi 2000, Gratani and Varone 2004b), because not all species will be able to withstand the same type and intensity of environmental stress. In particular, the sclerophyllous species and *E. arborea* might have a competitive advantage, relative to the other species, by their ability to maintain lower R_L in drought and favoring carbon assimilation. Moreover, variations in respiration of the species constituting the Mediterranean maquis can influence atmospheric CO_2 concentration considering that 30–70% of CO_2 fixed per day by photosynthesis is released back into the atmosphere by respiration. Thus, plant respiration represents an important factor in the global carbon (C) cycle (Cox 2001). Several land-surface climate models (Cox 2001) assume that plant *R* increases exponentially with rising temperature with a constant Q_{10} of 2.0 (*i.e. R* doubles for every 10°C increase in temperature) (Crous *et al.* 2011). Vulnerability of components of the C cycle refers to the risk of accelerated carbon release from a pool due to climate change and the resulting positive feedback of increasing atmospheric carbon dioxide concentration (Field and Raupach 2004, Cias *et al.* 2005, Keith *et al.* 2012).

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