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BRIEF COMMUNICATION

Environmental induced variations in leaf dark respiration and net photosynthesis of *Quercus ilex* L.

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Abstract

The relationships between dark respiration rate (R_D) and net photosynthetic rate (P_N) in *Quercus ilex* L. shrubs growing at the Botanical Garden in Rome were analysed. Correlation analysis of the data sets collected in the year 2006 confirmed the dependence among the considered leaf traits, in particular, R_D was significantly ($p<0.05$) correlated with P_N ($r = 0.40$). R_D and P_N increased from March to May [1.40±0.10 and 10.1±1.8 μmol(CO_2) m^{-2} s^{-1} mean values of the period, respectively], when air temperature was in the range 14.8–25.2 °C, underlining the highest metabolic activity in the period of the maximum vegetative activity that favoured biomass accumulation. On the contrary, the highest R_D [1.60±0.02 μmol(CO_2) m^{-2} s^{-1}], associated to the lowest P_N rates (44 % of the maximum) and carbon use efficiency (CUE) in July underlined the mobilization of stored material during drought stress by a higher air temperature (32.7 °C).

Additional key words: carbon use efficiency; leaf temperature; seasonal course.

Plant respiration is of comparable importance to photosynthesis as a determinant of plant production (Harris *et al.* 1975, Pearcy *et al.* 1987, Amthor 1989, Ryan *et al.* 1997) being linked to processes such as growth, allocation, and nitrogen uptake (Cannell and Thornley 2000). Photosynthesis and respiration are strongly coupled because photosynthesis provides the substrate for respiration (Cannell and Thornley 2000) and because of this the photosynthesis/respiration ratio is stable over a long time (Charles-Edwards 1982, Dewar *et al.* 1998). Moreover, respiration responds to air temperature (T_a) (Amthor 1984, Reich *et al.* 1996); dark respiration rate (R_D) increases exponentially with air temperature in the short time, but there is a compensatory adjustment (acclimation) over the long time (few days, weeks, or months) (Atkin and Tjoelker 2003, Loveys *et al.* 2003, Atkin *et al.* 2005). At very high temperatures, biochemical reactions take place so rapidly that substrates and metabolites (*e.g.* ADP) cannot keep up with the high turnover rate of substance and energy, thus the R_D soon drops (Larcher 2003). The link between air temperature and respiration suggests that global change could influence the magnitude of the respiration response. Thus, under-standing relationships between leaf R_D and other leaf traits may help to predict physiological adjustments of plant species under new environmental conditions (Xu and Griffin 2006).

R_D of not-senescent fully expanded leaves reflects "maintenance" respiration (McCree 1970) more than respiratory costs associated with the conversion of reserve materials into new structure ("growth" respiration) (Wright *et al.* 2006). Mediterranean evergreen species are characterised by lower rates of photosynthetic carbon gain and R_D per unit dry mass than deciduous species (Reich *et al.* 1992). Villar *et al.* (1995) underline that the effect of inhibitory irradiance on respiration is not very strong in leaves of evergreen species depending on leaf longevity and irradiance. Whole-plant maintenance respiration generally declines during water stress as a result of an overall slowing of metabolic activity (McCree 1986, Amthor 1994); nevertheless, Nogué *et al.* (2001) underline a lower dark respiration sensibility to water stress than photosynthesis (90 and 40 % decreasing, respectively) in *Rosmarinus officinalis*.

The objective of this research was to investigate relationships between R_D and net photosynthetic rate (P_N)

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Abbreviations: CUE – carbon use efficiency; P_G – gross photosynthetic rate; P_N – net photosynthetic rate; PAR – photosynthetically active radiation; R_D – dark respiration rate; T_a – air temperature; T_{leaf} – leaf temperature.

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in *Quercus ilex* L. and their dependence on temperature. Measurements were carried out in the period February 2006 to February 2007. P_N, photosynthetically active radiation (PAR), leaf temperature (T_{leaf}), and R_D were monitored on 10 *Q. ilex* shrubs (1.5 m height) growing at the Botanical Garden of Rome (41°53′53″N, 12°28′46″E; 53 m a.s.l.). Gas exchange was measured using an infrared gas analyser (*ADC LCA4*, UK) equipped with a leaf chamber (*PLC*, Parkinson Leaf Chamber). R_D was determined as CO_2 efflux, darkening leaf chamber by a black paper (Shirke 2001, Cai *et al.* 2005). During gas exchange measurements, air temperature (T_a) was measured by a thermohygrometer (*HD8901*, *Delta Ohm*, I). Moreover, carbon use efficiency (CUE) was calculated by the ratio of P_N and gross photosynthesis (P_G) according to Choudhury (2001). P_G was calculated as the sum of the average values of P_N, photorespiration, and R_D, and based on the assumption that respiration rates (excluding photorespiration) were similar in the light and in the dark (Van Iersel 2003). Photorespiration was evaluated considering that under natural conditions C_3 plants immediately lose about 20 % of the photosynthetically acquired CO_2 in the form of photorespiratory CO_2 (Larcher 2003). The highest P_N values (Fig. 1) were monitored in spring [12.2±0.8 μmol(CO_2) m^{-2} s^{-1}, T_a = 25.2 °C], decreasing by 56 % during drought (July, T_a = 32.7 °C, 0.8 mm total rainfall of 15 d before measurement).

The significant ($p<0.001$) polynomial relationship between P_N and T_{leaf} ($r = 0.72$) indicated that the favourable leaf temperature enabling the highest photosynthetic rates (90 to 100 %) was in the range 16.6 to 27.7 °C dropping over 50 % when T_{leaf} was under 9.7 and over 34.6 °C, respectively (Table 1).

R_D showed the highest rates in the period March to July [1.50±0.08 μmol(CO_2) m^{-2} s^{-1}, mean value of the period] (Fig. 1) when air temperature was in the range 16.6–32.7 °C decreasing by 67 % from December to February (T_a in the range 15.6–9.8 °C). R_D was significantly correlated with T_{leaf} ($r = 0.88$, $p<0.001$) and P_N ($r = 0.40$, $p<0.05$). During the study period there were no significant variations of CUE [0.52±0.02 mol(CO_2) mol^{-1}(CO_2), yearly mean value], nevertheless a 13 % significant CUE decrease was observed in July (Fig. 1). CUE was significantly ($p<0.001$) and inversely correlated to R_D ($r = -0.74$) (Table 1).

These results underline the correlation among the considered physiological traits in *Q. ilex*: R_D and P_N increased from March to May up to T_a of 25.2 °C. Under

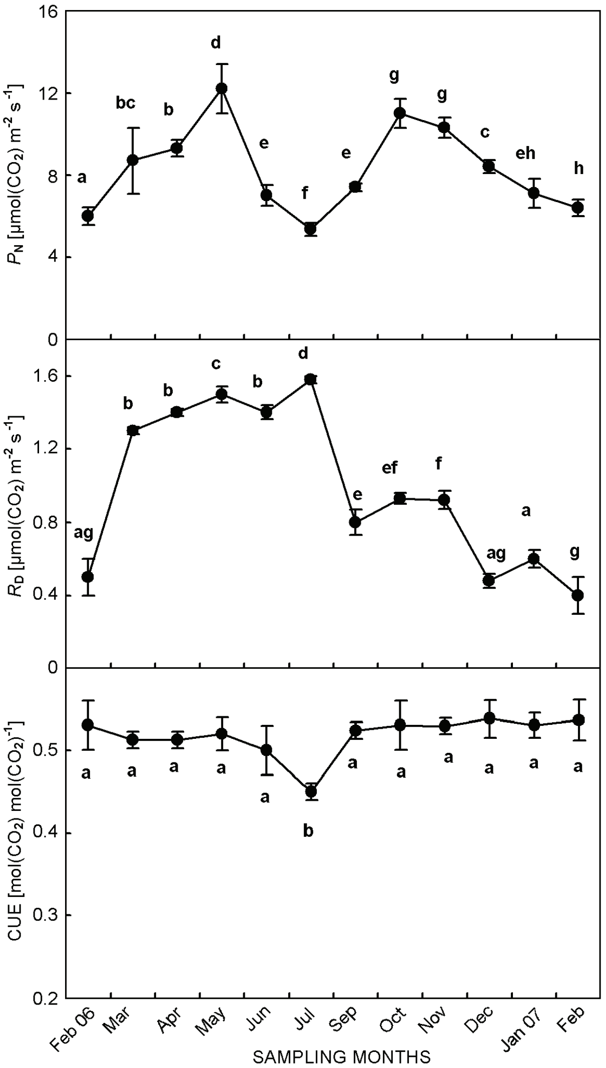

Fig. 1. Net photosynthetic rate (P_N), dark respiration rate (R_D), and carbon use efficiency (CUE) trend of *Q. ilex* during the study period. Standard error is shown. Monthly mean values with the same letters are not significantly different (ANOVA, $p>0.05$).

Table 1. Summary of regression analysis between net photosynthetic rate (P_N) and leaf temperature (T_{leaf}), between dark respiration rate (R_D) and T_{leaf}, between R_D and P_N, and between R_D and carbon use efficiency (CUE). Regression equations and correlation coefficients (r) are shown. The correlations are significant at $^{*}p<0.005$ and $^{**}p<0.001$. For the correlation between P_N and T_{leaf} (photosynthetic thermal window, *sensu* Larcher 1994), T_{leaf} enabling 100–90 % ($T_{100\text{-}90}$) and 100–50 % ($T_{100\text{-}50}$) of the maximum P_N is shown.

Regression equation	r	$T_{100\text{-}90}$	$T_{100\text{-}50}$
$P_N = -0.0312T_{leaf}^2 + 1.3008\,T_{leaf} - 5.589$	0.72^{**}	16.6–27.7 °C	9.7–34.6 °C
$R_D = 0.2256\,e^{0.0592T_{leaf}}$	0.88^{**}		
$R_D = 0.0312\,P_N^2 - 0.4862\,P_N + 2.7471$	0.40^{*}		
$R_D = -3.331\,\text{CUE} + 7.8905$	-0.74^{**}		

favourable conditions, leaves of C_3 plants take up roughly three to five times as much CO_2 as they lose by dissimilatory processes during the same period of time (Larcher 2003). The high R_D associated to the highest P_N underline the high metabolic activity in the period of maximum vegetative activity, favouring biomass accumulation. R_D variations at different times of the year may be attributed to the acclimation of the respiring biomass to temperature and to varying amounts of respiring tissues (Linder and Troeng 1981).

The highest R_D associated to the lowest P_N (44 % of the maximum) is observed in July, during drought stress, when biomass allocation is not allowed and stored material is mobilized in response to the plant's requirements for material growth and maintenance, according to Butler and Landsberg (1981). Thus, P_N decreasing in drought is not paralleled with R_D in *Q. ilex*, by the different role of these two physiological leaf traits.

Moreover, the cumulative carbon assimilation available for plant growth during summer may be drastically reduced, due to a lower conversion efficiency of photosynthetic primary products into the final dry mass; this is confirmed by CUE trend, an index describing how efficiently saccharides are converted into structural dry matter, according to Van Iersel (2001). A significant CUE decrease (13 %) is observed in July, and it may be related to the mobilization of stored material by the highest R_D.

These results underlin that global change, and in particular air temperature increase might modify the ratio P_N/R_D determining differences in the total dry matter accumulation.

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