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# Relationship between net photosynthesis and leaf respiration in Mediterranean evergreen species

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## Abstract

The relationship between net photosynthetic ($P_N$) and leaf respiration ($R$) rates of *Quercus ilex*, *Phillyrea latifolia*, *Myrtus communis*, *Arbutus unedo*, and *Cistus incanus* was monitored in the period February 2006 to February 2007. The species investigated had low $R$ and $P_N$ during winter, increasing from March to May, when mean air temperature reached 19.2 °C. During the favourable period, *C. incanus* and *A. unedo* had a higher mean $P_N$ (16.4±2.4 μmol $m^{-2}$ $s^{-1}$) than *P. latifolia*, *Q. ilex*, and *M. communis* (10.0±1.3 μmol $m^{-2}$ $s^{-1}$). The highest $R$ (1.89±0.30 μmol $m^{-2}$ $s^{-1}$, mean of the species), associated to a significant $P_N$ decrease (62 % of the maximum, mean value of the species), was measured in July (mean $R/P_N$ ratio 0.447±0.091). $Q_{10}$, indicating the respiration sensitivity to short-term temperature increase, was in the range 1.49 to 2.21. Global change might modify $R/P_N$ determining differences in dry matter accumulation among the species, and *Q. ilex* and *P. latifolia* might be the most favoured species by their ability to maintain sufficiently higher $P_N$ and lower $R$ during stress periods.

*Additional key words*: *Arbutus*; *Cistus*; *Myrtus*; *Phillyrea*; $Q_{10}$; *Quercus*; seasonal course; temperature.

## Introduction

Respiration is a quantitatively significant component of plant carbon balance, the whole plant respiration rate being positively and strongly related to the whole plant photosynthesis (Amthor 1994, Ryan *et al.* 1997, Cannell and Thornley 2000). Photosynthesis provides the substrate for respiration (Cannell and Thornley 2000), which significantly contributes to plant production, occurring continuously in each organ (Galmés *et al.* 2007). Up to 35 % of the total carbon assimilated may be lost as $CO_2$ by respiration (Atkin and Lambers 1998). Plant respiration varies between species (Reich *et al.* 1992, 1998, Wright *et al.* 2001, Turnbull *et al.* 2003), and leaf respiration accounts for approximately half of the whole plant respiration (Poorter *et al.* 1990). Environmental stress can influence respiration independently of the effects either on growth or photosynthesis by causing damage or metabolic imbalance that require respiratory metabolism (Amthor 1994).

In Mediterranean ecosystems, drought, high irradiance, and high air temperature influence gas exchange for short or long periods during the year (Filella *et al.* 1998). Drought increases leaf respiration rate ($R$) and decreases net photosynthetic rate ($P_N$), and both are responsible for the negative carbon balance over the drought period (Reichstein *et al.* 2002). Mediterranean evergreen species are characterised by lower $P_N$ and $R$ per unit of dry mass than the deciduous ones (Reich *et al.* 1992, Gratani *et al.* 2007). The temperature sensitivity of $P_N$ differs from that of $R$ (Gifford 2003). Temperature is the major determinant of the respiratory activity, and its change in the short-term results in immediate $R$ variations (Armstrong *et al.* 2006). Understanding the effect of environmental changes, in particular of air temperature increase, on plant $R$ is therefore a prerequisite for predicting the impact of global changes on plant functioning and atmospheric $CO_2$ concentration (Ryan 1991, Larigauderie and Körner 1995, Atkin and Tjoelker 2003, Zaragoza-Castells *et al.* 2007).

The main objective of this paper was to analyse the relationship between $P_N$ and R of Mediterranean evergreen species. We hypothesised that the best drought adapted species could maintain lower $R$ allowing sufficient $P_N$ during stress periods. Moreover, we determined $R$ sensitivity to temperature.

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*Abbreviations*: $P_N$ – net photosynthetic rate; PAR – photosynthetically active radiation; $R$ – leaf respiration rate; $T_l$ – leaf temperature; $T_m$ – mean air temperature.

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## Materials and methods

**Study site and plants**: Experiments were carried out in the period February 2006 to February 2007 on *Quercus ilex* L., *Phillyrea latifolia* L., *Myrtus communis* L., *Arbutus unedo* L., and *Cistus incanus* L. growing in open air at the Botanical Garden of Rome (41°53′53″N, 12°28′46″E; 53 m a.s.l.). During the study period the selected shrubs were not watered and they received only natural rain.

The study area climate was of Mediterranean type, and most of the total annual rainfall (653 mm) occurred in autumn and winter. The minimum mean air temperature ($T_m$) of the coldest month (January) was 5.2 °C, the maximum $T_m$ of the hottest month (July) 30.9 °C, and the yearly $T_m$ was 16.9 °C. Dry period (May to August) was characterized by 79.7 mm of the total rainfall (data from the Collegio Romano Meteorological Station, for 1995−2006). During the study period the minimum $T_m$ of the coldest month (January 2007) was 3.2 °C, the maximum $T_m$ of the hottest month (July 2006) 32.6 °C, and the total rainfall 600 mm (data from the Collegio Romano Meteorological Station, for February 2006−February 2007).

**$CO_2$ exchange** was measured using an infrared gas analyser (*ADC LCA4*, UK) equipped with a leaf chamber (*PLC*, Parkinson Leaf Chamber). For each species we considered four shrubs. Measurements were made on fully expanded sun leaves (three leaves per shrubs per each sampling day), according to Whitehead *et al.* (2004). $P_N$, photosynthetically active radiation (PAR), leaf temperature ($T_l$), and $R$ were monitored in four comparable days, each month in the period February 2006 to February 2007. Measurements were carried out in the morning, from 08:00 to 12:00 (one measure each hour) to ensure that maximum daily rates were measured (Gratani *et al.* 2000, Varone and Gratani 2007). Only the maximum $P_N$ and $R$ values were used. Measurements were carried out under natural conditions, on cloud-free days (saturating PAR ≥800 µmol $m^{-2}$ $s^{-1}$) (Reich *et al.* 1995).

On each sampling day, $R$ was measured after $P_N$ (on the same leaves) as $CO_2$ efflux, darkening leaf chamber by a black paper, according to Cai *et al.* (2005) for 30 min prior to each measurement, to avoid transient post-irradiation bursts of $CO_2$ release (Atkin *et al.* 1998a,b). $R$ and $P_N$ represented the means of the maximum values of the four days' measurements per month.

**$Q_{10}$**, a coefficient proportional to respiration increasing for each 10 °C rise (Atkin *et al.* 2000), was calculated according to Carla *et al.* (2000) and Armstrong *et al.* (2006) as $Q_{10} = 10^{(10\times\text{slope of regression line})}$. The slope in this equation was extracted from the regression line between $\log_{10}$ of $R$ and air $T_m$. $T_m$ averaged for 2 d (measurement day and the day preceding it) was used to calculate $Q_{10}$ according to Atkin *et al.* (2000).

**Statistical analysis** was carried out by one-way ANOVA ($p$=0.05) to test significant differences in $P_N$, $R$, and $Q_{10}$ during the study period; mean values were compared by Tukey's test HSD. In order to meet the requirement of normality and homogeneity of variances, data were $\log_{10}$ transformed when necessary. Moreover, regression analysis was carried out to examine the correlations between $P_N$ and $R$, $P_N$ and $T_l$, and between $R$ and $T_l$.

## Results

**$P_N$** peaked in May ($T_m$ 19.2 °C). *C. incanus* and *A. unedo* had the highest $P_N$ (16.4±2.4 µmol $m^{-2}$ $s^{-1}$, mean value), followed by *Q. ilex* and *P. latifolia* (11.2±1.1 µmol $m^{-2}$ $s^{-1}$, mean value), and *M. communis* (7.7±0.20 µmol $m^{-2}$ $s^{-1}$) (Fig. 1). The species had a significant ($p$<0.05) $P_N$ decrease in July ($T_{max}$ 32.6 °C; total rainfall of the month 7.8 mm), *P. latifolia* having the lowest decrease (44 %) and *C. incanus* the highest one (76 %). All the species recovered ($P_N$ was 62 % of the maximum, mean value) after the first rainfall at the middle of September (163.8 mm total rainfall from September 11th to 30th; $T_m$ 21.1 °C). Low $P_N$ was monitored in February 2006 ($T_m$ 8.8 °C), ranging from 2.5±0.2 µmol $m^{-2}$ $s^{-1}$ in *M. communis* to 6.0±0.4 µmol $m^{-2}$ $s^{-1}$ in *Q. ilex*.

**Leaf *R* was** high in May; *C. incanus* and *A. unedo* had the highest $R$ (2.57±0.01 and 1.56±0.03 µmol $m^{-2}$ $s^{-1}$, respectively), followed by *Q. ilex* and *P. latifolia* (1.52±0.01 µmol $m^{-2}$ $s^{-1}$, mean value), and *M. communis* (1.47±0.04 µmol $m^{-2}$ $s^{-1}$) (Fig. 1). The species showed the highest $R$ in July, ranging from 1.55±0.05 µmol $m^{-2}$ $s^{-1}$ in *P. latifolia* to 3.09±0.02 µmol $m^{-2}$ $s^{-1}$ in *C. incanus*, and decreased by 34 % (mean value) in September. The lowest $R$ (77 % decrease from the maximum) was found in winter, *C. incanus* having the highest value (0.84±0.05 µmol $m^{-2}$ $s^{-1}$) and *P. latifolia* the lowest one (0.14±0.06 µmol $m^{-2}$ $s^{-1}$).

The $R/P_N$ peaked during drought (0.447±0.091, mean value), and the lowest values were monitored in winter (0.113±0.011, mean value). The mean $R/P_N$ value of the study period was the highest in *M. communis*, *C. incanus*, and *A. unedo* (0.216±0.080, mean value) and the lowest one in *P. latifolia* (0.123±0.020) (Fig. 2).

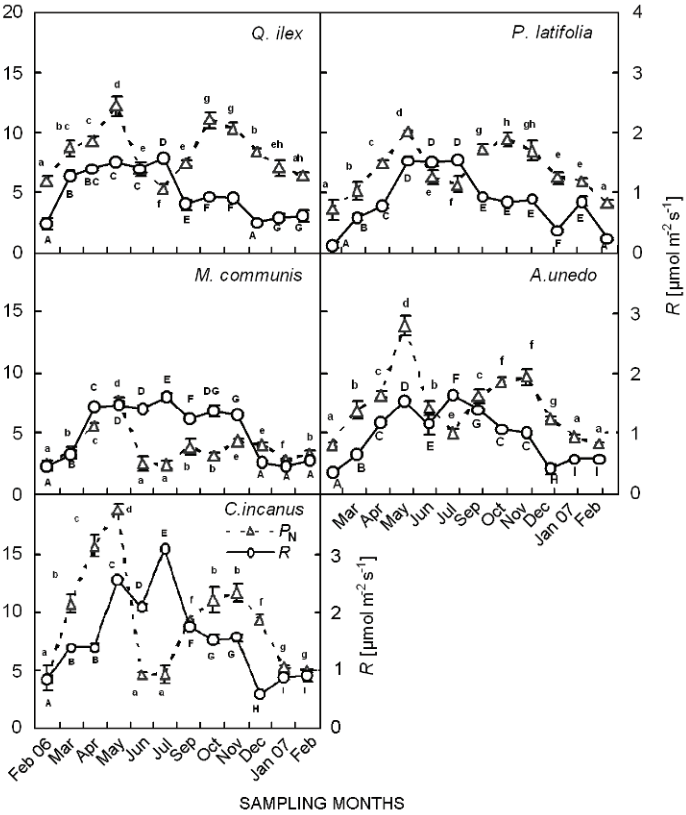

Fig. 1. Trends of net photosynthetic ($P_N$) and leaf respiration ($R$) rates during the study period. Means±S.E. of four sampling days in each month ($n$ = 48). For each measured variable monthly mean value with the same letters is not significantly different (ANOVA, $p$>0.05).

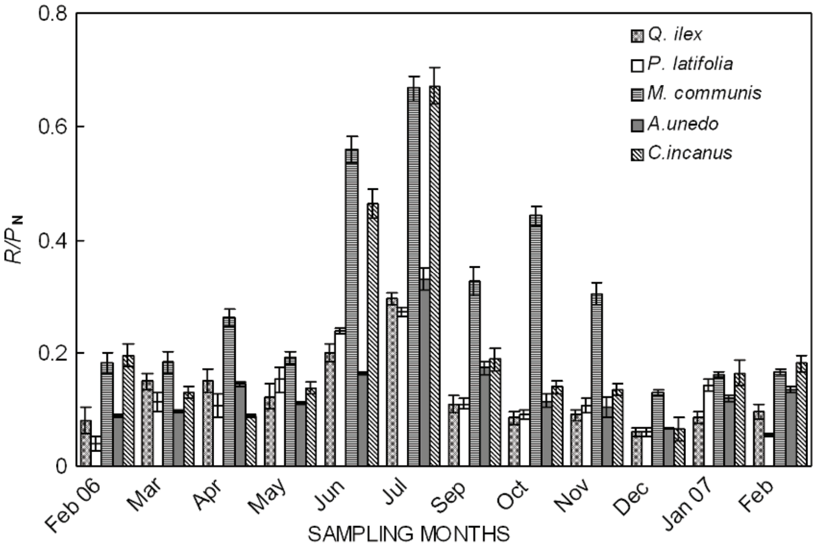

Fig. 2. Ratio between leaf respiration and net photosynthesis ($R/P_N$) rates during the study period. Means±S.E. of four sampling days in each month ($n$ = 48).

Table 1. $Q_{10}$ values. Means±S.E. with the same letters are not significantly different (ANOVA, $p$>0.05).

| Species | $Q_{10}$ |
|---|---|
| *Q. ilex* | 1.49±0.10a |
| *P. latifolia* | 2.21±0.20b |
| *M. communis* | 1.85±0.11c |
| *A. unedo* | 1.88±0.10c |
| *C. incanus* | 1.82±0.10c |

Table 2. Regression analysis between monthly mean net photosynthetic ($P_N$) and leaf respiration ($R$) rates during the study period ($n$ = 12). $^*p\leq0.05$; $^{**}p\leq0.001$.

| Species | Regression equation | *r* |
|---|---|---|
| *Q. ilex* | $P_N = -9.2\,R^2 + 20.0\,R - 1.1$ | $0.52^*$ |
| *P. latifolia* | $P_N = -4.6\,R^2 + 10.6\,R + 2.1$ | $0.73^{**}$ |
| *M. communis* | $P_N = -2.4\,R^2 + 5.8\,R + 0.8$ | $0.50^*$ |
| *A. unedo* | $P_N = -4.8\,R^2 + 13.1\,R - 0.0$ | $0.64^*$ |
| *C. incanus* | $P_N = -3.3\,R^2 + 13.1\,R - 1.6$ | $0.51^*$ |

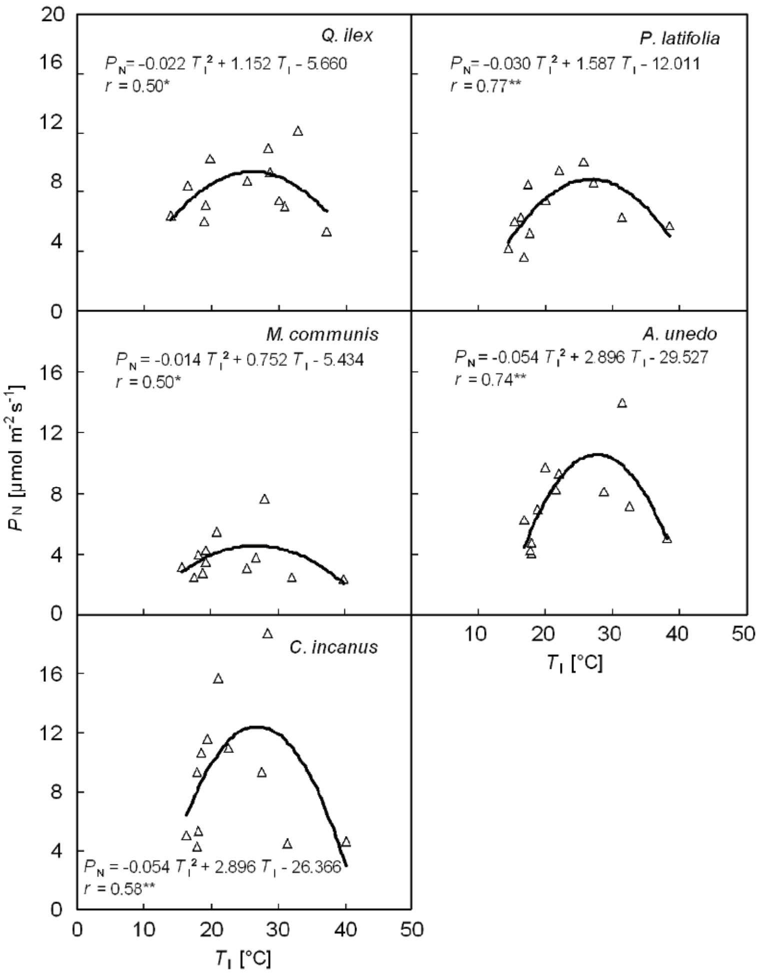

Fig. 3. Regression analysis between net photosynthetic rate ($P_N$) and leaf temperature ($T_l$) during the study period. Regression equations and correlation coefficients (*r*) are shown. Monthly mean values ($n = 12$). $^*p \leq 0.05$; $^{**}p \leq 0.001$.

**$Q_{10}$** values indicated that the respiration sensitivity to short-term air temperature increase was in the range 1.49 to 2.21, *P. latifolia* having the highest one (Table 1). The regression analysis showed that, on an average, 58 % of $P_N$ variation depended on *R* in the species (Table 2).

Both $P_N$ and *R* were significantly ($p<0.05$) correlated to $T_l$, and the best fit explaining $P_N$-$T_l$ correlation was a polynomial line (Fig. 3); moreover, *R* increased exponentially with $T_l$ (Fig. 4).

## Discussion

Drought is one of the most important limiting factors of Mediterranean carbon gain, as it induces stomata closure lowering gas diffusion between the mesophyll and the surrounding atmosphere (García-Plazaola and Becerril 2000), particularly when water stress is associated to higher air temperatures and irradiance (Peñuelas *et al.* 1998, Gratani and Bombelli 2000, Pesoli *et al.* 2003).

Amthor (1989, 2000) supports a positive relationship between photosynthesis and saccharide contents in leaves; a higher content of saccharides leads to an increased amount of energy available for respiration. Nevertheless, the mechanism is not entirely dependent on the substrate supply, and it may also be driven by the demand for respiratory products. Environmental stresses limit photosynthesis and saccharide production; low saccharide contents reduce respiratory capability and repress growth as a result of an inhibition of photosynthesis and subsequent down-regulation of metabolism in response to saccharide depletion (Amthor 1994).

The analysis of the data sets underlines the significant correlations between *R* and $P_N$, and between the two leaf variables and $T_l$. In particular, the relationship between *R* and $P_N$ underlines the economic carbon budget optimisation at the plant's level, according to Rouhi *et al.* (2007). Relatively high *R* (1.72±0.21 µmol $m^{-2}$ $s^{-1}$, mean value of the species) associated to the highest $P_N$ (12.6±1.9 µmol $m^{-2}$ $s^{-1}$, mean value) underline the high metabolic activity under favourable conditions ($T_m$ 19.2 °C), associated to a high water availability allowing biomass accumulation (Gratani *et al.* 2000). Under favourable conditions leaves take up roughly three to five times as much $CO_2$ as they lose by dissimilatory process

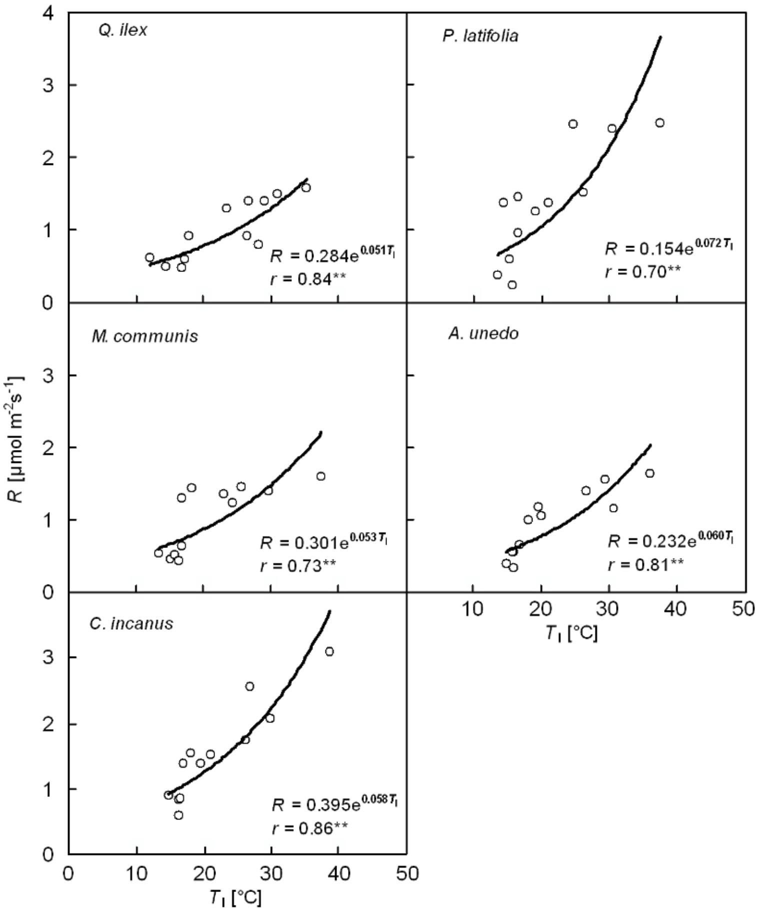

Fig. 4. Regression analysis between leaf respiration rate ($R$) and leaf temperature ($T_l$), during the study period. Regression equations and correlation coefficients ($r$) are shown. Monthly means ($n$ = 12). $^{**}p\leq0.001$.

during the same period of time (Larcher 2003). Nevertheless, the higher $R$ of *C. incanus* and *A. unedo* than in the other species during the favourable period may be justified by the lost of most of their leaves—up to 90 % of the total plant leaves (Gratani and Bombelli 2001), thus demanding for more respiratory products which are necessary to produce new leaves before the beginning of the drought period. The sclerophyllous species, on the contrary, lose only a part of their older leaves (up to 40 %) in spring (Gratani and Crescente 1997) and require lower $R$.

The highest $R$ associated to a significant $P_N$ decrease (62 % of the maximum, mean of the species) was measured during drought ($R/P_N$ ratio 0.447±0.091, mean value), when biomass allocation was not favoured (Gratani *et al*. 2000, Gratani and Varone 2004), and the stored material was mobilized in response to the plant's requirements for maintenance, according to Butler and Landsberg (1981); thus, $P_N$ decrease in drought was not paralleled by $R$ decrease. The whole plant maintenance respiration decline during drought is the result of an overall slowing of the metabolic activity (McCree 1986, Amthor 1994).

Global change may modify the ratio $R/P_N$ determining differences in the total-season dry matter accumulation, and favouring the typical sclerophyllous species than the semi-deciduous ones, which are able to maintain sufficiently higher $P_N$ and lower $R$ during the stress period. $Q_{10}$ of the species was 1.49−2.21, and among them *P. latifolia* showed the highest respiration sensitivity to air temperature ($Q_{10}$ 2.21), suggesting that it will be able to adjust the stored material immobilization according to air temperature increase. On the contrary, the cumulative carbon assimilation available for *C. incanus* and *A. unedo* growth may be drastically reduced at increased drought, attested also by the highest $R/P_N$ during the year. *M. communis* might be considered in an intermediate position between the sclerophyllous and semi-deciduous species.

Temperature-mediated changes in $P_N$ and $R$ are now accepted as important components of the biosphere's response to global change (Schimel 1995); thus, quantification of dry matter accumulation capability of Mediterranean evergreen species in response to $T_m$ is important as they cover large areas in the world, and in particular in the Mediterranean Basin, with a potential effect on global carbon budget.

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