



Comparative field study of *Quercus ilex* and *Phillyrea latifolia*: photosynthetic response to experimental drought conditions

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Abstract

Quercus ilex and *Phillyrea latifolia* growing in a holm oak forest in Prades mountains (NE Spain) were subjected to experimental drought conditions. Soil water availability was reduced about 15% by plastic strips and funnels that partially excluded rain throughfall and by ditch exclusion of water runoff. Diurnal courses of maximum photochemical efficiency of PSII (Fv/Fm), apparent photosynthetic electron transport rate (ETR), net photosynthetic rate (A), transpiration rate (E) and water use efficiency (WUE) were measured in sunlit and shade leaves of both species during 2 years. Moreover, the responses of photosynthetic rates to PPFD and CO₂ concentrations were also measured. *Q. ilex* experienced lower E rates and higher A rates and WUE than *P. latifolia* throughout the experimental period, but during summer drought these differences disappeared. *Q. ilex* exhibited a less cold sensitive behavior whereas *P. latifolia* showed a more heat–drought resistant behavior. Under severe summer drought conditions none of the two species was able to reach a positive carbon gain. Drought treatment produced a slight decrease in Fv/Fm values of *Q. ilex* plants and a strong decrease in Fv/Fm values of *P. latifolia* only in winter 2000, when drought stress coincided with cold stress. Drought treatment produced also a slight decrease in ETR values of both species. During midday, A and E rates decreased in drought plots in both species associated to lower photochemical efficiencies. In those drought plots, only *P. latifolia* was able to increase WUE by reducing transpiration losses during midday. Both species tended to present higher A rates for a given soil humidity in drought than in control plots. However, whereas *Q. ilex* A rates increased with soil humidity, *P. latifolia* A rates did not increase above 17% soil humidity, showing no water availability response above such threshold. It is very likely that mesic species such as *Q. ilex* lose competitive advantage in the drier environment forecasted for next decades than the more xeric *P. latifolia*.

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1. Introduction

General circulation models predict drier conditions for the Mediterranean basin due to an increase of air temperatures and water deficit

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(Houghton et al., 2001). The increase in water deficit could induce ecophysiological changes in different species affecting their growth and survival (Tenhunen et al., 1987) and, in the long-term, their distribution and abundance (Mitrakos, 1980; Gucci et al., 1999).

In the Mediterranean basin, many publications have described low photosynthetic rates of evergreen species during summer drought due to the stomatal control of water loss by transpiration (Harley et al., 1987; Tenhunen et al., 1990; Filella et al., 1998; Peñuelas et al., 1998; Llusà and Peñuelas, 2000), and low photosynthetic rates (Tretiach et al., 1997; Larcher, 2000) associated to a partial photoinhibition of PSII (Larcher, 2000; Oliveira and Peñuelas, 2000, 2001) during winter cold. However, there are few studies of co-occurring Mediterranean woody species for photoinhibition and photosynthetic rate responses to experimental field drought conditions and for more than a single growing season.

Quercus ilex and *Phillyrea latifolia* are plant species frequently co-occurring in the Mediterranean maquis and in the *Q. ilex* evergreen forests. In particular, *Q. ilex* is widely distributed in the sub-humid areas of the Mediterranean Basin whereas *P. latifolia* in warmer and drier Mediterranean areas (Tretiach, 1993; Lloret and Siscart, 1995; Peñuelas et al., 1998, 2000). We aimed to determine the photosynthetic response of *Q. ilex* and *P. latifolia* to experimental field drought conditions during 2 years in order to elucidate the adaptative strategies of these two species to a changing climate. We expected drought effects on the photosynthetic activity of both species throughout the different seasons, but we also expected a more favorable photosynthetic response of the more drought- and hot-resistant *P. latifolia* during summer drought and a more favorable response of the more mesic- and less cold-sensitive *Q. ilex* during winter.

2. Material and methods

2.1. Study site

The study was carried out in a natural holm oak forest growing at Prades Mountains in North-

Eastern Spain (41°13'N, 0°55'E), on a south-facing slope (25% slope) at 930 m a.s.l. The soil is a stony xerochrept on a bedrock of metamorphic sandstone, and its depth ranges between 35 and 90 cm. The average annual temperature is 12 °C and the annual rainfall 658 mm. Summer drought is pronounced approximately from mid-June to mid-September.

The vegetation of the studied area is a typical machia characterized by 3 or 4-m tall shrubs. This machia is constituted by *Q. ilex* L., *P. latifolia* L., *Arbutus unedo* L., *Erica arborea* L., *Juniperus oxycedrus* L. and *Cistus albidus* L.

2.2. Experimental design

Four (15 × 10 m) plots were randomly distributed in the studied area. Half the plots were subjected to a drought treatment and the other half were control plots. The drought treatment consisted of rain exclusion by suspending PVC strips and funnels at a height of 0.5–0.8 m above the soil. Strips and funnels covered approximately 30% of the total plot surface. Also a 1 m deep ditch was excavated along the entire top edge of the upper part of the treatment plots to intercept runoff water. Water intercepted by strips, funnels, and ditches was conducted outside the plots, below the bottom edge of the plots. Drought treatment was conducted from March 1999 to January 2001.

Temperature, photosynthetic active radiation, air humidity, and precipitation were monitored each half-hour by an automatic Meteorological station installed in a gap between the plots. Soil moisture was measured every 2 weeks throughout the experiment by time domain reflectometry (Tektronix 1502C, Beaverton, OR, USA) (Zegelin et al., 1989). Three stainless steel cylindrical rods, 25 cm long, were permanently fully driven into the soil at four randomly selected places in each plot. The time domain reflectometer was connected to the ends of the rods in each measurement.

2.3. Chlorophyll fluorescence and gas exchange measurements

Chlorophyll fluorescence and gas exchange were measured during 2–6 consecutive days in the study

period (one for each season of the year during 2 years). Sunlit leaves (from the upper layer of the canopy) and shade leaves (from the lower layers of the canopy) were measured under clear-sky conditions.

The maximum photochemical efficiency of PSII (F_v/F_m) and the apparent photosynthetic electron transport rate (ETR) were measured with a PAM-2000 fluorometer (Walz, Effeltrich, Germany). ETR was estimated as

$$\text{ETR} = \Delta F/F'_m \times \text{PPFD} \times 0.84 \times 0.5$$

where $\Delta F/F'_m$ (actual photochemical efficiency of PSII) was calculated according to Genty et al. (1989), 0.84 is the coefficient of absorption of the leaves, and 0.5 is the fraction of electron involved in the photoexcitation produced by one quanta, since two photosystems are involved. Chlorophyll fluorescence was measured on five current-year leaves of each one of two plants per species and canopy position ($5 \times 2 \times 2 \times 2 = 40$ leaves) in each plot twice a day: morning (08:00–10:00 h, solar time) and midday (11:00–13:00 h, solar time). The maximum PSII photochemical efficiencies (F_v/F_m) were measured after keeping leaves in the dark for at least 25 min.

Net photosynthetic rate (A), transpiration rate (E) and stomatal conductance (g_s) were measured with a portable gas exchange system ADC LCA4, with a PLC4B chamber (ADC Inc., Hoddesdon, Hertfordshire, UK). Water use efficiency (WUE) was calculated as A/E in μmol fixed CO_2 per mmol transpired H_2O , and Vapor Pressure Deficit (VPD) was calculated from air temperature and relative humidity. One current-year leaf of two different plants per species and canopy position ($1 \times 2 \times 2 \times 2 = 8$ leaves) in each plot were measured two times a day: morning (08:00–10:00 h, solar time) and midday (11:00–13:00 h, solar time). A, E, and g_s values were expressed on a projected leaf area basis measured with a Li-Cor 3100 Area Meter (Li-Cor Inc., Nebraska, USA).

As complementary measurements, net photosynthetic rate (A) response curves to PPFD and CO_2 were conducted with a portable gas exchange system CIRAS2 (PP Systems, Hitchin, Hertfordshire, UK) during 4 consecutive days in autumn 2001. Four *Q. ilex* and four *P. latifolia* individuals

were selected. One sunlit leaf per plant was used for the CO_2 response curves, and one sunlit leaf and one shade leaf per plant were used for the PPFD response curves.

In one terminal twig of two different plants per species in each plot, leaf water potential before dawn was determined using a Scholander pressure chamber (PMS, Corvallis, OR, USA). Leaf water potential was measured on several dates (at least once every season) between February 1999 and November 2000.

2.4. Statistical analyses

Repeated measurements analysis of variance (ANOVA) was conducted with soil moisture values in each plot as dependent variable and treatment as independent factor. Overall ANOVAs were conducted with the mean values of F_v/F_m , ETR, A, E and WUE in each plot as dependent variables and with species, treatment, season, time of the day and canopy position as independent factors. Moreover, in each season, canopy position, and time of the day, differences of the mean of the above-mentioned variables between control and drought plants were tested in each species by ANOVA with treatment as the independent factor.

Non-linear regression analyses were also conducted to examine the PPFD and CO_2 response curves. Analyses of covariance (ANCOVA) were used to test the differences of these relationships between control and drought plants in both species, and between sunlit and shade leaves. Other ANCOVAs were conducted to test the differences in the relationships A–soil moisture, leaf water potential, A–VPD, and A– g_s between control and drought plants in both species. When necessary (for CO_2 and soil moisture), variables were log transformed to reach the normality assumptions of the ANCOVAs. For Michaelis–Menten type relationships, only the linear unsaturated part of the curves was analyzed with ANCOVAs. The saturated values were analyzed with ANOVAs or *t*-tests.

All analyses were performed with the SUPERANOVA software package (Abacus Concepts Inc.,

1991) and the STATVIEW software package (Abacus Concepts Inc., 1998).

3. Results

The climate of the area studied is of Mediterranean type; the mean annual temperature during the study period was 12.3 °C, and mean total rainfall 668 mm (Fig. 1). Soil moisture showed variations during the study period (Fig. 1); the lowest values (about 15%) were reached in both summers and in early autumn 2000, the maximum values (about 35%) were present in spring and autumn–winter 2001, following the rainfall distribution. On average, control plots had 15% higher soil moisture than drought plots.

Both species exhibited lower Fv/Fm values in sunlit than in shade leaves, the differences being larger in winter (Fig. 2). On few occasions control plants had significantly higher Fv/Fm values than drought ones (Fig. 2), but only in winter 2000 there was an overall drought effect on sunlit leaves when both species and both times of the day were considered all together ($P < 0.01$), this effect being larger in *P. latifolia* (Fig. 2). Moreover, sunlit leaf Fv/Fm was higher in *Q. ilex* than in *P. latifolia*. ETR values were higher in spring periods than in the other periods, and in *Q. ilex* higher than in *P. latifolia* during all the experimental period (data not shown).

Both species showed negative A values in summer (August) 1999 (after a long drought period, Fig. 1), but not in summer 2000 (Fig. 3) surely because measurements were conducted earlier in summer 2000 (July) when water availability was not yet very low, especially in that year 2000 which had rains in late spring (Fig. 1). In October 2000 during midday, A values were higher in control plots than in drought ones in *Q. ilex* ($P < 0.05$), but not in *P. latifolia* (Fig. 3).

The relationships between A and CO₂, and A and PPFD showed higher A rates for *Q. ilex* both in sunlit and shade leaves than for *P. latifolia*

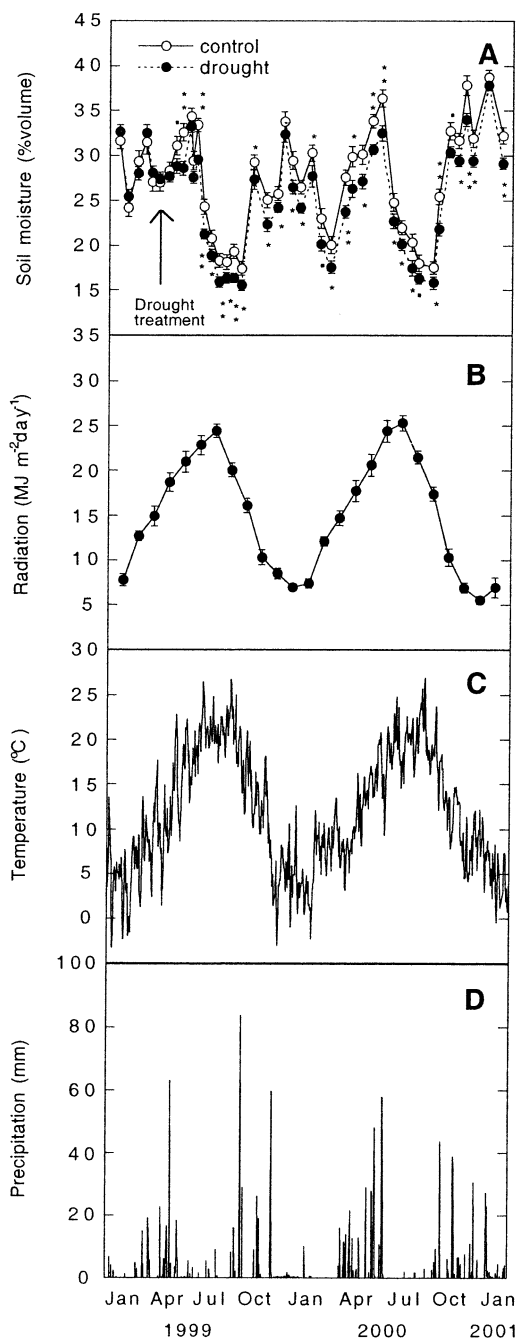


Fig. 1 (Continued)

Fig. 1. Seasonal course of soil moisture (0.25 m depth) (A), mean daily values of radiation (B), mean monthly temperature (C), and precipitation (D) at the study site. Vertical bars indicate standard errors of the mean ($n = 2$ plot averages of four to eight TDR measurements per plot in A and $n = 28$ –31 days in B). Drought significant effect on soil moisture is also indicated (repeated measures ANOVA).

(Figs. 4 and 5). A rates decreased due to the drought treatment in both A–CO₂ ($P = 0.036$) and A–PPFD relationships ($P = 0.004$ and $P < 0.0001$ in the unsaturated and saturated parts of the curves, respectively) only in sunlit leaves of *P. latifolia*. Shade leaves of both species showed lower A rates in control plants than in drought ones ($P = 0.021$ and $P = 0.006$ in the saturated parts of the curves in *Q. ilex* and *P. latifolia*, respectively) (Fig. 5).

Q. ilex reached maximum A rates at lower temperatures than *P. latifolia* (Fig. 6). There were no significant differences between control and drought plants, but in *Q. ilex*, the maximum A rates were reached at higher temperature under the drought treatment (12.5 and 16.5 °C in control and drought plots, respectively), whereas in *P. latifolia* maximum A rates were reached at similar temperatures in the two treatments (22.1 and 21.2 °C in control and drought plots, respectively). On the other hand, A rates reached values near 0 when T was between 34.8 and 36.5 °C, without significant differences between the two species and the two treatments (Fig. 6).

There was an increase in net photosynthetic rates with increasing soil water availability in *Q. ilex* but not in *P. latifolia* (Fig. 7). In drought plots, both species had higher A values for a given soil moisture in the lower range of soil moistures but only *Q. ilex* kept this trait in the higher range of soil moisture (Fig. 7). A rates were very dependent on leaf water potential (which was strongly correlated with soil moisture), and very low values of both A and water potential were reached during summer 1999 (Fig. 7). A–VPD relationships showed higher slopes in *Q. ilex* than in *P. latifolia*, but no differences were found between control and drought plots (Fig. 8). A–g_s relationships had also higher slopes in *Q. ilex* than in *P. latifolia*, and in *P. latifolia*, drought plants had higher slopes than control plants ($P = 0.020$) (Fig. 8).

Sunlit leaves had higher transpiration than shade leaves in both species, and on average slightly higher in *P. latifolia* than in *Q. ilex* (Fig. 9). In the different seasons there were no significant differences between control and drought plants, but when all seasons were considered,

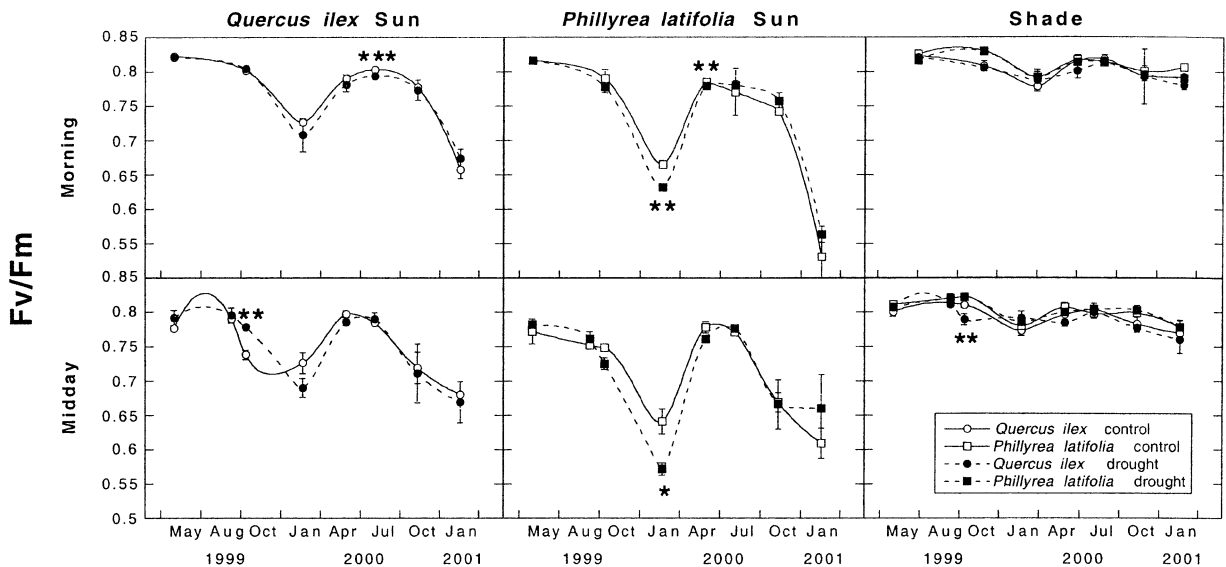


Fig. 2. Seasonal course of maximum photochemical efficiency (Fv/Fm) in the morning and the midday in sunlit and shade leaves of *Q. ilex* and *P. latifolia* during the experimental period. Error bars indicate standard error of the mean ($n = 2$ plot averages of ten measurements per plot). * $P < 0.1$, ** $P < 0.05$, *** $P < 0.01$ statistical significance of the difference between drought and control treatment (ANOVA) for the signaled species.

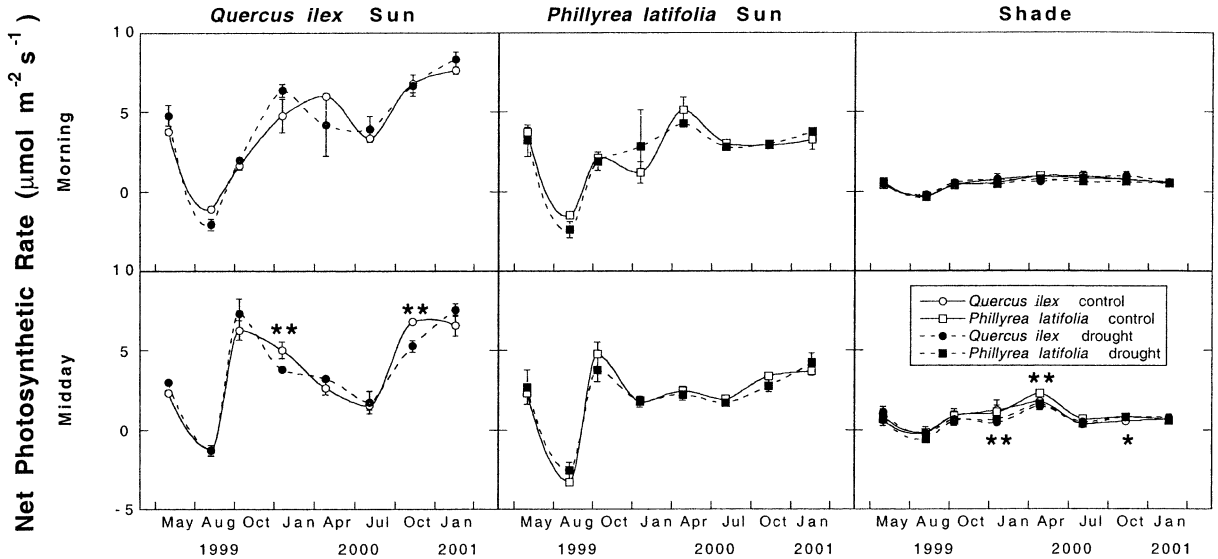


Fig. 3. Seasonal course of net photosynthetic rates during the morning and midday in sunlit and shade leaves of *Q. ilex* and *P. latifolia* during the experimental period. Error bars indicate standard error of the mean ($n = 2$ plots and two measurement per plot). * $P < 0.1$, ** $P < 0.05$, *** $P < 0.01$ statistical significance of the difference between drought and control treatment (ANOVA) for the signaled species.

sunlit leaves of *P. latifolia* showed higher E rates in control plots than in drought ones during midday ($P = 0.005$).

WUE was slightly higher in sunlit leaves than in shade ones, and higher in *Q. ilex* than in *P. latifolia* (3.77 and $2.02 \mu\text{mol CO}_2 \text{ mol}^{-1} \text{ H}_2\text{O}$,

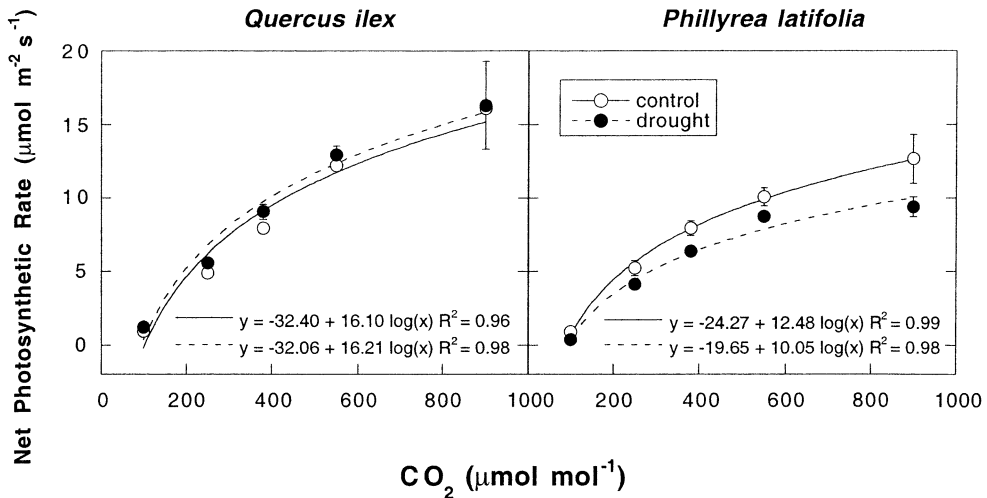


Fig. 4. Responses of PPFD-saturated photosynthetic rates to different CO_2 concentrations in sunlit leaves of *Q. ilex* and *P. latifolia* in control and drought plots. Each point is the mean of the measurements at the same CO_2 concentration in all response curves ($n = 4$) (these response curves were measured in Autumn 2001).

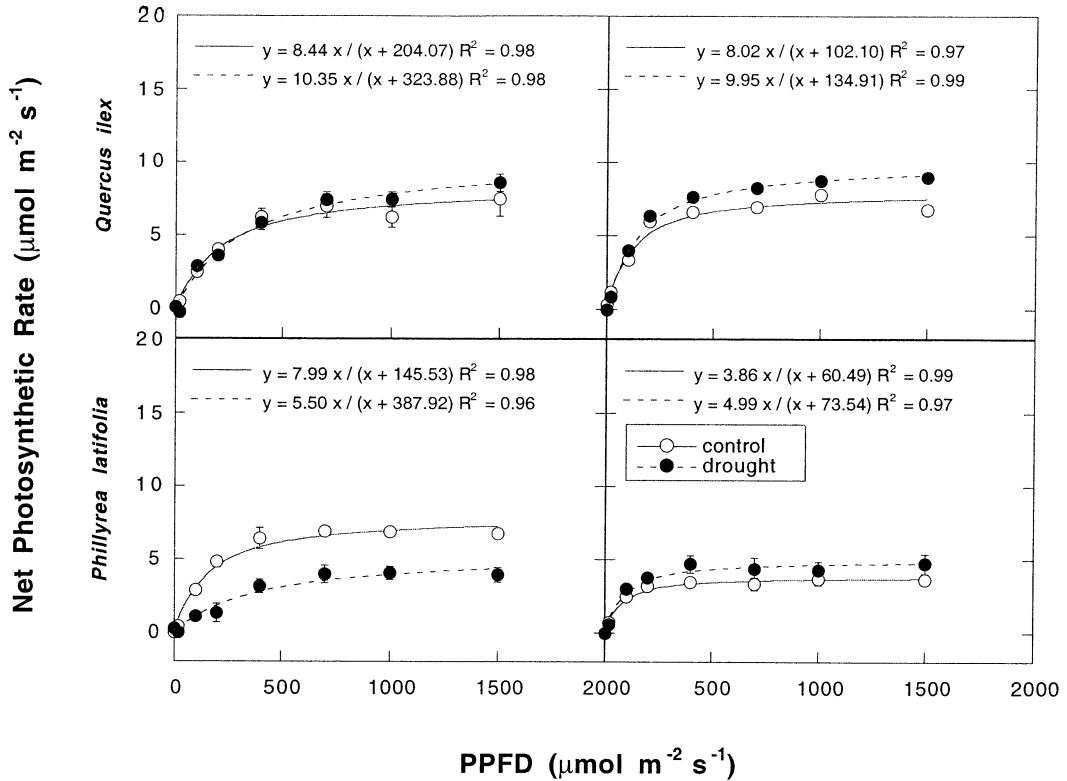


Fig. 5. Responses of CO_2 -saturated photosynthetic rates to different PPFD fluxes in sunlit and shade leaves of *Q. ilex* and *P. latifolia* in control and drought plots. Each point is the mean of the measurements at the same PPFD in all response curves ($n = 4$) (these response curves were measured in Autumn 2001).

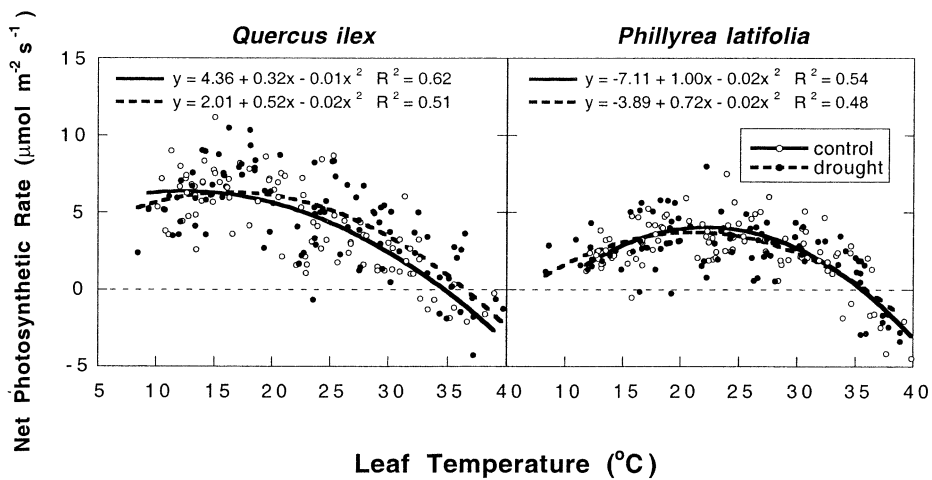


Fig. 6. Relationships between net photosynthetic rates and leaf temperature. All measurements were made in sunlit leaves of *Q. ilex* and *P. latifolia* and correspond to both morning and midday values of the overall experimental period ($n = 192$).

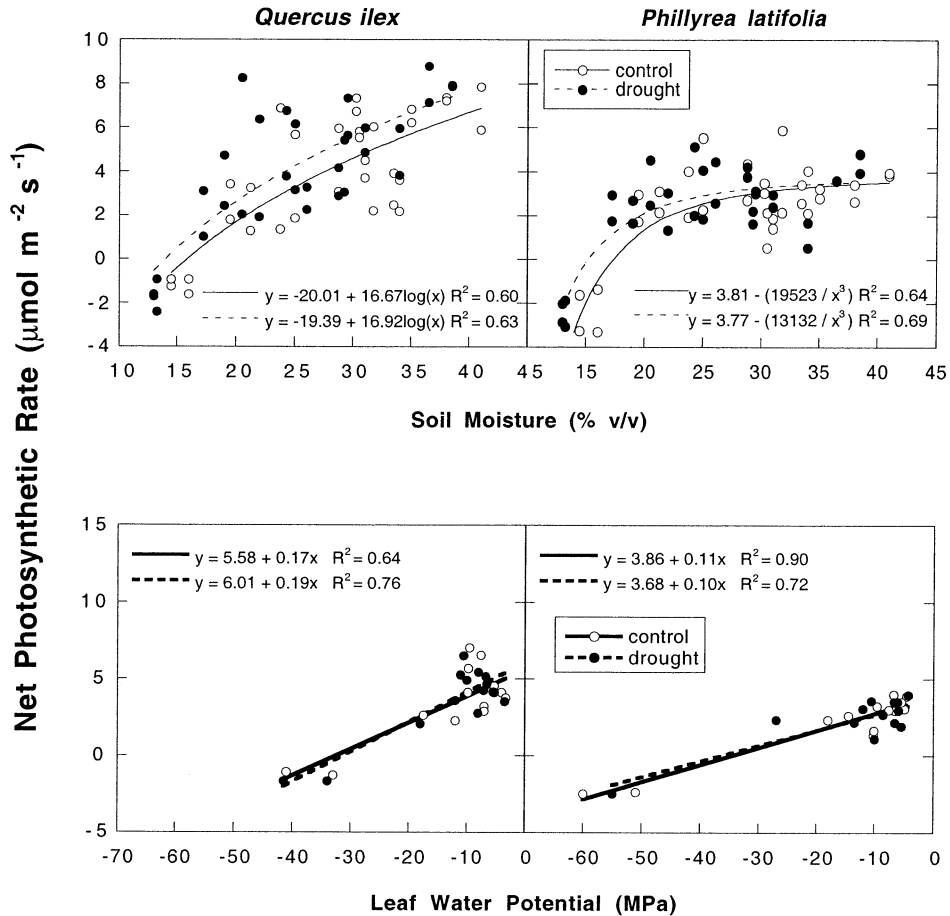


Fig. 7. Relationships between net photosynthetic rates and soil moisture and leaf water potential. All measurements were made in sunlit leaves of *Q. ilex* and *P. latifolia* and correspond to both morning and midday values of the overall experimental period ($n = 64$ in soil moisture relationships and $n = 28$ in leaf water potential relationships).

respectively, for the overall studied period). In sunlit leaves during the morning, this difference between species was statistically significant ($P = 0.044$). In sunlit leaves and during midday, drought treatment exerted an opposite effect on the WUE of the two species in some dates such as January 2001 ($P = 0.040$), when *Q. ilex* showed higher WUE in control plots whereas *P. latifolia* experimented higher WUE in drought plots (data not shown).

4. Discussion

The maximum photochemical efficiency of PSII (F_v/F_m) exhibited lower values in the colder seasons in agreement with several recent studies of Mediterranean plants (Larcher, 2000; Oliveira and Peñuelas, 2000, 2001). The results were also in agreement with other reports showing higher photosynthetic activity of *Q. ilex* than *P. latifolia* during winter (Tretiach, 1993) and of *P. latifolia*

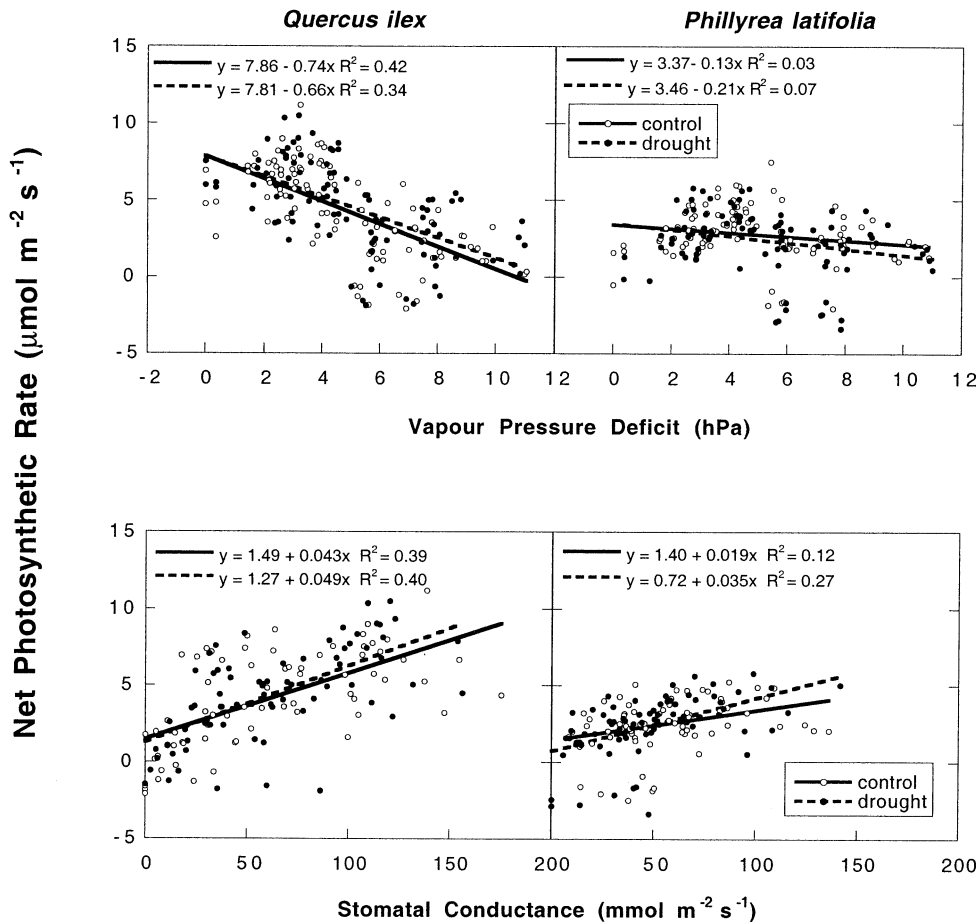


Fig. 8. Relationships between net photosynthetic rates and VPD and stomatal conductance. All measurements were made in sunlit leaves of *Q. ilex* and *P. latifolia* and correspond to both morning and midday values of the overall experimental period ($n = 192$ in VPD relationships and $n = 146$ in stomatal conductance relationships).

than *Q. ilex* during summer drought (Tretiaich, 1993; Peñuelas et al., 1998). Drought treatment strongly decreased F_v/F_m values of *P. latifolia* during winter 2000, when drought stress coincided with cold stress, while in *Q. ilex*, drought also decreased F_v/F_m values more than one occasion during the study period. These differences indicated a higher resistance of *P. latifolia* to drought. ETR values were higher in *Q. ilex* than in *P. latifolia*, as a result of its higher actual photochemical efficiencies of PSII ($\Delta F/F'_m$). In sunlit leaves, ETR values were higher during spring, when water availability was higher, in agreement

with previous literature results (Valladares and Pearcy, 2002).

In both species A rates were higher in the morning than in the midday, especially in summer, when a strong stomatal closure occurred (Mooney et al., 1975; Tenhunen et al., 1980; Lange et al., 1982; Martínez-Ferri et al., 2000; Llusà and Peñuelas, 2000). During late summer 1999 soil moisture was very low. Under the severe drought conditions of that summer none of the two species was able to reach a positive carbon gain, even in the morning. Higher photorespiration rates as a consequence of drought (Wingler et al., 1999) or

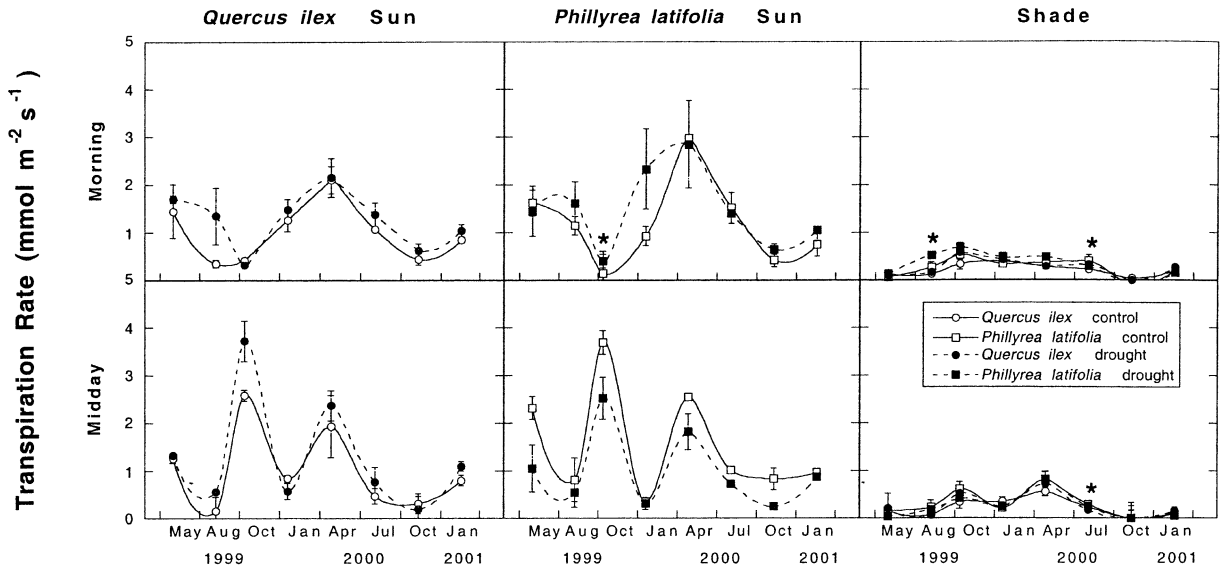


Fig. 9. Seasonal course of transpiration rates during the morning and midday in sunlit and shade leaves of *Q. ilex* and *P. latifolia* during the experimental period. Error bars indicate standard error of the mean ($n = 4$ plots and one measurement per plot). * $P < 0.1$, ** $P < 0.05$, *** $P < 0.01$ statistical significance of the difference between drought and control treatment (ANOVA) for the signaled species.

high temperatures (Peñuelas and Llusà, 2002) might have greatly contributed to such negative net photosynthetic rates. Transpiration rates also decreased in the midday of the hotter seasons, but WUE was similar in morning and in midday because stomatal closure reduced proportionally both A and E rates. During most of the experimental period, *P. latifolia* experienced lower A rates, higher E rates and consequently lower WUE values than *Q. ilex*. However, during the summer drought *P. latifolia* reached similar, or even higher A rates and WUE than *Q. ilex* in agreement with previous results of Peñuelas et al. (1998) and Filella et al. (1998). On the other hand, only *P. latifolia* was able to reduce significantly its E rates (about 33%) and to increase its WUE (about 56%) in sunlit leaves during midday under drought treatment, precisely when water availability was the lowest.

Both species developed different physiological responses to the drought treatment. *Q. ilex* showed an increase in the temperature of maximum A rates and in the temperature at which A rates reached values near 0, while *P. latifolia* incremented the slope in A - g_s relationship. In

drought plots, both species tended to present higher net photosynthetic rates for a same soil humidity than in control plots, indicating a quick and incipient acclimation to continuous lower water availability. However, *Q. ilex* increased A rates with soil moisture whereas *P. latifolia* reached A rates saturation at low soil moisture of 17% (v/v). *Q. ilex* showed a greater water availability dependence and a greater water availability response than *P. latifolia*. In the same way, *Q. ilex* showed higher slopes in the relationships between A rates and leaf water potential, VPD, and stomatal conductance than *P. latifolia*.

P. latifolia exhibited lower A rates in the CO_2 and PPFD response curves conducted in the sunlit leaves of the drought plots than in the control ones. These response curves were conducted in late autumn, when temperatures are cold and *P. latifolia* shows a great photoinhibition, especially under drought treatment. *Q. ilex* in the drought plots did not experience either A or E reduction in the response curves, and seemed to conserve less water than *P. latifolia*. Surprisingly, in PPFD curves, A rates of shade leaves were slightly higher in drought plots than in control ones in both

species. Other studies showed, on the contrary greater A decrease in shade plants than in sunlit plants during a drought period (Valladares and Pearcy, 2002). We studied sunlit and shade leaves in the same plant, and it seemed that shade leaves, under drought conditions, experimented an increase in A rates to compensate the A decrease of sunlit leaves. In natural conditions shade leaves received very low radiation and their A rates are low in both control and drought plots, so carbon gain at whole plant level seems to be more dependent on sunlit leaves than on shade ones.

In the marked seasonality of Mediterranean climate conditions, drought has strongly influenced evolution and plant life (Pereira and Chaves, 1995). Predicted water stress in the Mediterranean Basin (Houghton et al., 2001) may be associated with physiological and phenological responses in plant species (Peñuelas and Filella, 2001; Peñuelas et al., 2002), but different species can develop different responses to these climatic changes. It is likely that more drought- and heat-resistant species such as *P. latifolia* will tolerate the increase of temperature and dry conditions better than more mesic less cold-sensitive species such as *Q. ilex*. These physiological responses could be followed by changes in carbon acquisition of Mediterranean forests (Reichstein et al., 2002), and in a long term, by changes in species distribution conferred by the different capacity of different species to survive under the new climatic constraints.

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