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Spatio-temporal dynamics of chlorophyll fluorescence in a semi-arid Mediterranean shrubland

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Abstract

We examined the spatio-temporal variations of chlorophyll fluorescence on a semi-arid Mediterranean shrubland in SE Spain during the 1998–1999 period. We performed the study on three species (*Quercus coccifera*, *Pistacia lentiscus* and *Pinus halepensis*) in two sites with contrasted slope aspect (north/south) located within a small distance from each other. Our main objectives were to assess the effect of slope aspect on the chlorophyll fluorescence features of these species, and to evaluate how this effect is influenced by temporal variations in climatic conditions. The results showed the presence of consistent higher values of maximum efficiency of photosystem II (F_v:F_m) in the north-facing slope at both predawn and midday throughout the study period, but with differences in patterns between the different species. For all species, midday values of F_v:F_m were considerably lower than predawn ones at the south-facing slope throughout 1999. For all species, and over the course of the day, the increase and subsequent decrease in radiation was closely followed by a pronounced decrease and subsequent increase of effective quantum yield of photosystem II, but it was less pronounced in the north-facing slope. Our results show how small-scale spatial differences in climate associated with slope aspect cause pronounced differences on the chlorophyll fluorescence features of shrubs. These differences could have important consequences for carbon assimilation and storage and for vegetation dynamics in Mediterranean semi-arid shrublands.

Keywords: Chlorophyll fluorescence; Heterogeneity; Photochemical efficiency; *Pinus halepensis*; *Pistacia lentiscus*; *Quercus coccifera*; Semi-arid; Slope aspect

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1. Introduction

In semi-arid environments, vegetation establishment and development is strongly limited by low levels of soil moisture and harsh climatic conditions (Veenendaal et al., 1996; Keya, 1997). In these areas, both soil moisture and climatic conditions typically show a strong degree of spatial heterogeneity at several scales (Breshears et al., 1998; Bellot et al., 1999; Domingo et al., 2000; Gómez-Plaza et al., 2001). One of the factors that may strongly influence these variables in semi-arid areas is slope aspect. North-facing slopes typically receive lower solar radiation flux density than south-facing ones, which, in turn, results in lower evapo-transpiration rates and lower daily maximal temperatures during water stress periods in the former (Galicia et al., 1999; Coops et al., 2000). Climatic differences between north- and south-facing slopes, even at small spatial scales, affect soil moisture (Gómez-Plaza et al., 2001), but also other soil properties like temperature, nutrient content and aggregation processes (Klemmedson and Wienhold, 1992; Kutiel, 1992). These changes ultimately affect the structure, distribution, composition and productivity of vegetation in semi-arid environments (Klemmedson and Wienhold, 1992; Kutiel and Lavee, 1999; Sternberg and Shoshany, 2001). Other factor of great importance for soil moisture dynamics in semi-arid areas is rainfall pattern, which typically shows a strong degree of within- and inter-year heterogeneity (Le Houérou et al., 1988). This heterogeneity can influence substantially both soil and vegetation responses to slope aspect (Gómez-Plaza et al., 2001). Thus, whole-year monitoring of plants becomes especially relevant for an accurate assessment of vegetation responses to slope aspect under semi-arid conditions.

Despite the acknowledged importance of slope aspect for vegetation dynamics and performance in semi-arid areas, and the increasing body of studies describing vegetation responses to this factor, few studies so far have evaluated the effect of slope aspect on the physiology of a plant community (Monson et al., 1992). Small-scale differences in climate can have strong effects on physiological variables related to carbon fixation and water use of evergreen woody species (Flexas et al., 2001; Balaguer et al. 2002), affecting plant productivity and species distribution in semi-arid areas. Thus, the analysis of the effects that both slope aspect and temporal variations in climate have on plant physiological status may be of great importance to improve our knowledge about the functioning of semi-arid plant communities. In addition, it can help to understanding their potential responses to climate change, and to define effective measurements for the management and restoration of these communities.

In this study we evaluated the effect of slope aspect on the chlorophyll fluorescence features of three Mediterranean species in a semi-arid shrubland located in SE Spain during a 2-year period. We selected two Mediterranean sprouting shrubs (*Quercus coccifera* L. and *Pistacia lentiscus* L.), and one Mediterranean tree (*Pinus halepensis* L.) for the experiment. These species share a common strategy to cope with drought stress (‘‘drought avoidance’’), but show important differences in the mechanisms underlying it (Martínez-Ferri et al., 2000; Vilagrosa, 2002). Our main objectives were to: (i) assess the effect of small-scale differences in slope aspect on the physiological status of these species, and (ii) evaluate how the effect of slope aspect is influenced by temporal variations in climatic conditions. We hypothesize that small-scale differences in environmental conditions between north- and south-facing slopes will affect the chlorophyll status of evaluated shrubs, improving plant performance in the north-facing slope.

2. Materials and methods

2.1. Study area

We conducted our study in two experimental sites located at the Ventós catchment, in the province of Alicante, in SE Spain (Ventós-1 site, $38^\circ 29'$N, $0^\circ 37'$W, 600 m a.s.l., 330° azimuth; Ventós-2 site, $38^\circ 27'$N, $0^\circ 37'$W, 550 m a.s.l., 220° azimuth). The area has a Mediterranean semi-arid climate, with a 30-yr mean annual precipitation of 302 mm, and a mean annual temperature of 18.2°C (Pérez, 1994). Vegetation is a shrubland dominated by species such as *Q. coccifera*, *P. lentiscus*, *Rhamnus lycioides* L. subsp. *lycioides* and *Erica multiflora* L. Soils are *Cambisols* and *Lythic Leptosols*.

2.2. Sampling design and measurements

We performed chlorophyll fluorescence measurements seasonally on eight occasions from December 1997 to December 1999. Measurements at both sites were performed with similar climatic conditions and separated by 1–3 days of difference. At the beginning of the experiment, we randomly selected three individuals per species (except in *Quercus* and *Pinus* at the Ventós-2 site, where only two individuals were available) that were measured in all sampling dates. Measurements were replicated 3–4 times in each plant using randomly selected single leaves (except in the case of *Pinus*, in which we used five attached leaves) formed the previous year to reduce age effects. The same leaves were used during measurements throughout a determined sampling date, but leaves were randomly selected in each sampling date.

Chlorophyll fluorescence measurements were performed with a portable, pulse-modulated fluorometer (PAM-2000, Walz, Effeltrich, Germany) equipped with a leaf clip holder (2030-B; Walz) and a micro-quantum sensor to measure incident PAR as described in Bilger et al. (1995). Predawn and midday (1300−1400 h solar time) measures of maximal (F_m) and minimal (F_0) fluorescence were used to calculate maximum efficiency of the photosynthetic energy conversion of photosystem II ($F_v{:}F_m = [F_m - F_0]/F_m$). Predawn determinations were performed under complete darkness before sunrise; midday measurements were made after 30-min dark adaptation. The relationship between the fluorescence maximum in the light (F'_m), and the steady-state value of fluorescence immediately prior a saturating flash of light (F_t) was used to estimate the estimated effective quantum yield of photosystem II ($\Phi_{PSII} = [F'_m - F_t]/F'_m$). Yield determinations were performed under natural light conditions from predawn to dusk at 2-h intervals (from 7:00 to 19:00 solar time in spring and summer measurements, and from 7:00 to 17:00 solar time in autumn and winter measurements). See Maxwell and Johnson (2000) for a complete description of the evaluated chlorophyll fluorescence parameters.

Climatic variables during the period of study were continuously recorded by a solar powered meteorological station (CDR10, Campbell Scientific, Logan, USA) located in an open area of each of the two study sites. Air temperature, relative humidity, photosynthetic photon flux density (PFFD) and precipitation were measured at 15 min intervals and were automatically stored as half-hourly and daily means.

2.3. Statistical analyses

Maximum efficiency of the photosynthetic energy conversion of photosystem II (F_v:F_m) was analysed separately for each date and moment of the day (predawn/midday) with three-way (Slope Aspect, Species, and Individual) nested ANOVA, with Aspect and Species as fixed effects and Individual as random effect nested within Species. The diurnal patterns of effective quantum yield of photosystem II were compared separately for each sampling date using a four-way (Slope Aspect, Species, Individual, and Time) nested ANOVA, with repeated measures of one of the factors (Time) and Individual nested within Species. Data were log-transformed when necessary to correct deviations from normality and heterogeneity of variances. In addition to these analyses, we evaluated the effect of slope aspect on F_v:F_m using a meta-analysis approach (Gurevitch and Hedges, 2001). We defined the effect of slope aspect as positive when F_v:F_m was higher in the north-facing slope as compared to the south-facing one. We obtained the effect size and its confidence interval for each sampled date using the "Hedges' d index" (all calculations below were performed according to Gurevitch and Hedges, 2001):

$$d_{12} = \frac{X_1 - X_2}{s_{12}} J,$$

where X_1 and X_2 are the F_v:F_m values for the two sites, and S_{12} is the pooled standard deviation, calculated as

$$s_{12} = \sqrt{\frac{(N_1 - 1)(s_1)^2 + (N_2 - 1)(s_2)^2}{N_1 + N_2 - 2}},$$

where N_1 and N_2 are the number of replicates in the zones to be compared. J is a factor that corrects for small sample sizes, and is computed as

$$J = 1 - \frac{3}{4(N_1 + N_2 - 2) - 1}.$$

The variance around d was used to obtain 95% confidence intervals by using standard statistical methods (Gurevitch and Hedges, 2001). Values of d with confidence intervals not overlapping zero indicate the presence of a significant effect.

This variance was calculated as

$$v_{12} = \frac{N_1 + N_2}{N_1 N_2} + \frac{d_{12}^2}{2(N_1 + N_2)}.$$

All the statistical analyses were performed using the SPSS 9.0 package (SPSS Inc., Chicago, USA).

3. Results

Rainfall in the study sites during the 1998–1999 period ranged between 215 and 289 mm yr^{-1}, a 71–96% of the 30-yr average annual rainfall (Fig. 1). Rainfall patterns of both years were characterized by a strong summer drought, especially evident in 1998, and two peaks during spring and autumn. Total annual rainfall in 1998 was below 15% at the south-facing slope as compared to the north-facing slope. These differences were mainly evident in the rainiest months of the year. In 1999, the total amount registered was nearly equal at both sites and the pattern did not show strong differences. Daily values of photon flux density and air temperature were usually higher at the south-facing site throughout the period of study, but most clearly during 1999 (Fig. 2). In consequence, the relative air humidity was usually higher at the north-facing site. However, in Spring 1999, higher values of relative air humidity were found in the south-facing site.

Seasonal patterns of F_v:F_m showed usually higher values at the north-facing site at both predawn and midday throughout the period of study (Fig. 3). The effect of slope aspect was significant for most part of that time, but showed important differences between evaluated species, as suggested by the significant Species × Slope Aspect interactions (Table 1). Strong differences between north- and south-facing slopes were observed for predawn values of all the species in both summer and winter

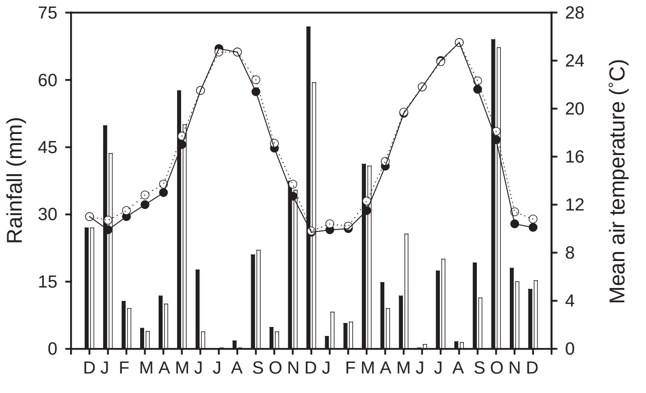

Fig. 1. Main climatic characteristics at the north- and south-facing slopes during the period of study. Monthly rainfall and average temperature are presented as blocks and points, respectively. North- and south-facing slopes are represented with black and white symbols, respectively.

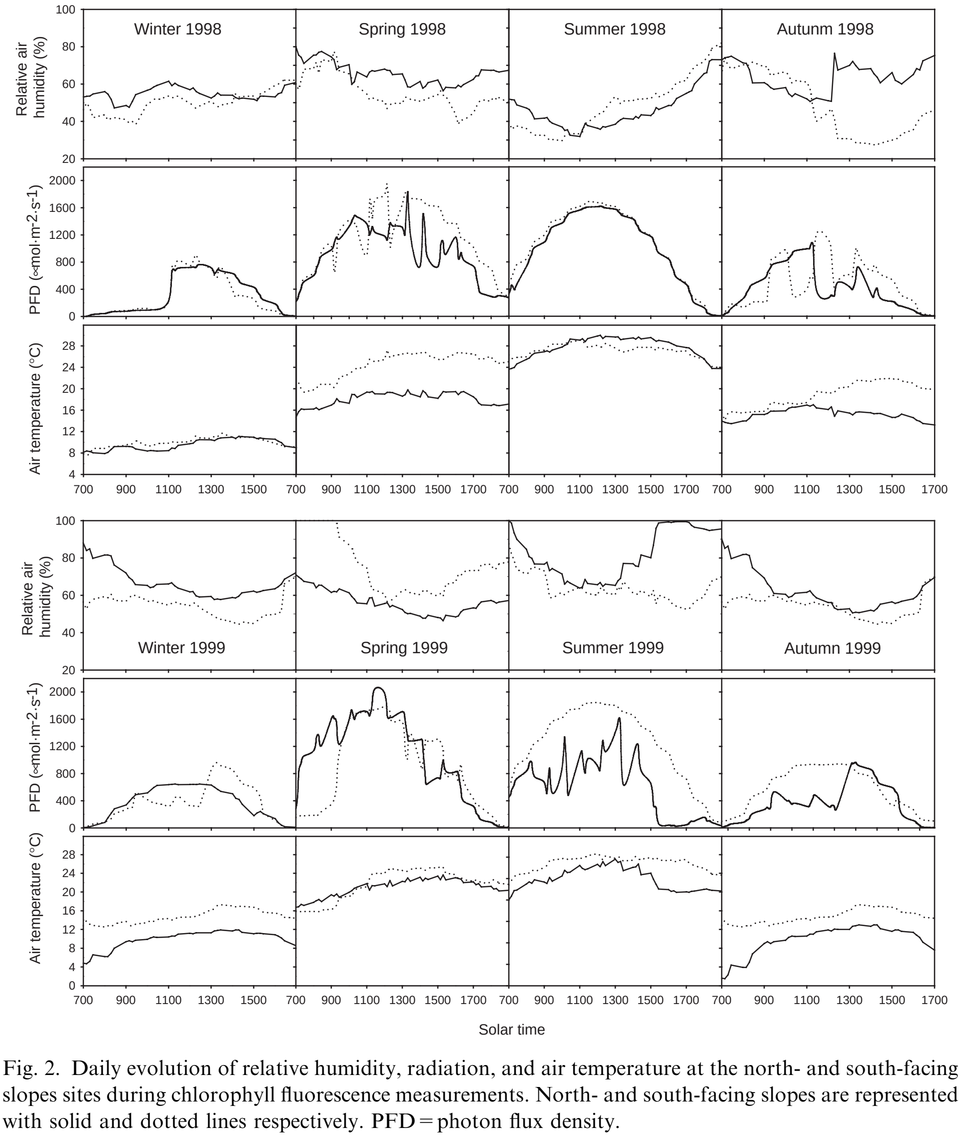

Fig. 2. Daily evolution of relative humidity, radiation, and air temperature at the north- and south-facing slopes sites during chlorophyll fluorescence measurements. North- and south-facing slopes are represented with solid and dotted lines respectively. PFD = photon flux density.

of 1998, and these differences were especially evident for *Pinus* during summer (Fig. 3). The strong effect of slope aspect was not so evident in 1999, despite marked climatic differences between north- and south-facing slopes. It is interesting to note how the response of evaluated species to summer drought was not the same in the 2 years evaluated. Midday values for all species were considerably lower than predawn ones at the south-facing slope throughout 1999. A strong decrease was not observed for any species in the north-facing slope, except in summer 1999.

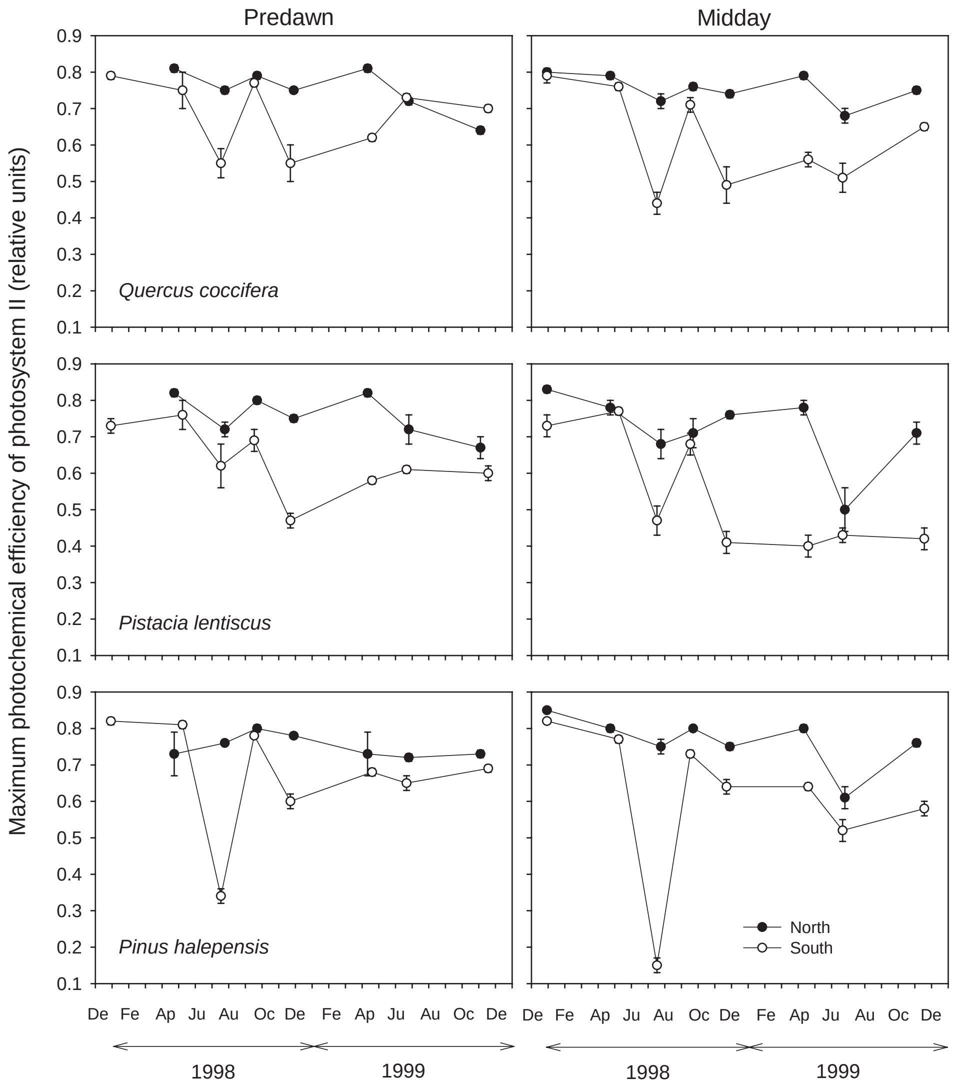

Fig. 3. Seasonal variation in predawn and midday values of maximum efficiency of photosystem II at the north- and south-facing slopes. Data represent mean ± 1 S.E. ($n = 6-9$).

Over the course of the day, the increase and subsequent decrease in PAR radiation was followed quite closely by a pronounced decrease and subsequent increase of effective quantum yield of photosystem II (Φ_{PSII}, Fig. 4). This response was consistent throughout all the sampling dates except in Winter 1999, where an increase was registered from 7:00 to 9:00 AM (Fig. 4). For all species, reduction in Φ_{PSII} was less accentuated at the north-facing slope, and differences promoted by slope aspect were significant throughout the period of study (Table 2). However, the

Table 1
Results of a three-way (species, aspect and individual) nested ANOVA showing the significance of the species and slope aspect effects, and their interaction, on log-transformed predawn and midday values of maximum efficiency of photosystem II

Time of the day	Year	Season	ANOVA results								
			Slope aspect			Species			Slope aspect × species		
			F	df.	*p*	*F*	df.	*p*	*F*	df.	*p*
Predawn	1998	Spring	0.57	1.26	0.459	0.28	2.7	0.765	5.81	2.26	0.008
		Summer	62.50	1.30	<0.001	9.45	2.8	0.007	10.09	2.30	<0.001
		Autumn	15.70	1.33	<0.001	2.92	2.5	0.142	6.93	2.33	0.003
	1999	Winter	107.48	1.37	<0.001	3.01	2.5	0.137	2.39	2.37	0.106
		Spring	154.53	1.29	<0.001	0.18	2.7	0.839	19.32	2.29	<0.001
		Summer	8.48	1.28	0.007	0.48	2.6	0.638	2.71	2.28	0.084
		Autumn	0.29	1.30	0.60	2.79	2.8	0.123	6.24	2.30	0.005
Midday	1998	Winter	16.97	1.29	<0.001	1.62	2.6	0.281	3.86	2.29	0.033
		Spring	3.72	1.31	0.063	0.88	2.7	0.460	4.49	2.31	0.019
		Summer	131.35	1.29	<0.001	16.16	2.7	0.002	24.94	2.29	<0.001
		Autumn	23.77	1.32	<0.001	3.33	2.7	0.084	3.00	2.24	0.070
	1999	Winter	145.71	1.33	<0.001	4.28	2.5	0.080	14.91	2.33	<0.001
		Spring	195.02	1.31	<0.001	20.73	2.6	0.002	17.49	2.31	<0.001
		Summer	15.18	1.28	0.001	3.57	2.5	0.106	0.68	2.28	0.516
		Autumn	78.70	1.33	<0.001	23.60	2.5	<0.001	7.96	2.33	0.002

response differed substantially between evaluated species, as suggested by the significant Species × Slope Aspect interaction found.

The meta-analysis of F_v:F_m data revealed a positive effect of slope aspect for most part of species and sampling dates (Fig. 5). However, the magnitude of this effect showed strong differences between species and years. For predawn data, the highest values of effect size in *Quercus* and *Pistacia* were found during the spring 1999, while those in *Pinus* were found during the summer 1998. With midday values the effect followed a similar trend, but its magnitude was usually higher.

4. Discussion

Accordingly to our initial hypothesis, chlorophyll fluorescence features of shrubs varied substantially between north- and south-facing slopes, with improved values in the former throughout the period of study. Our results agree with and complement other studies performed in semi-arid Mediterranean shrublands, which showed higher values of vegetation properties such as cover, height, volume, species composition, and recovery rates after disturbance in northern slopes as compared with southern ones (Kutiel, 1992; Kutiel and Lavee, 1999; Kadmon and Harari-Kremer, 1999; Sternberg and Shoshany, 2001).

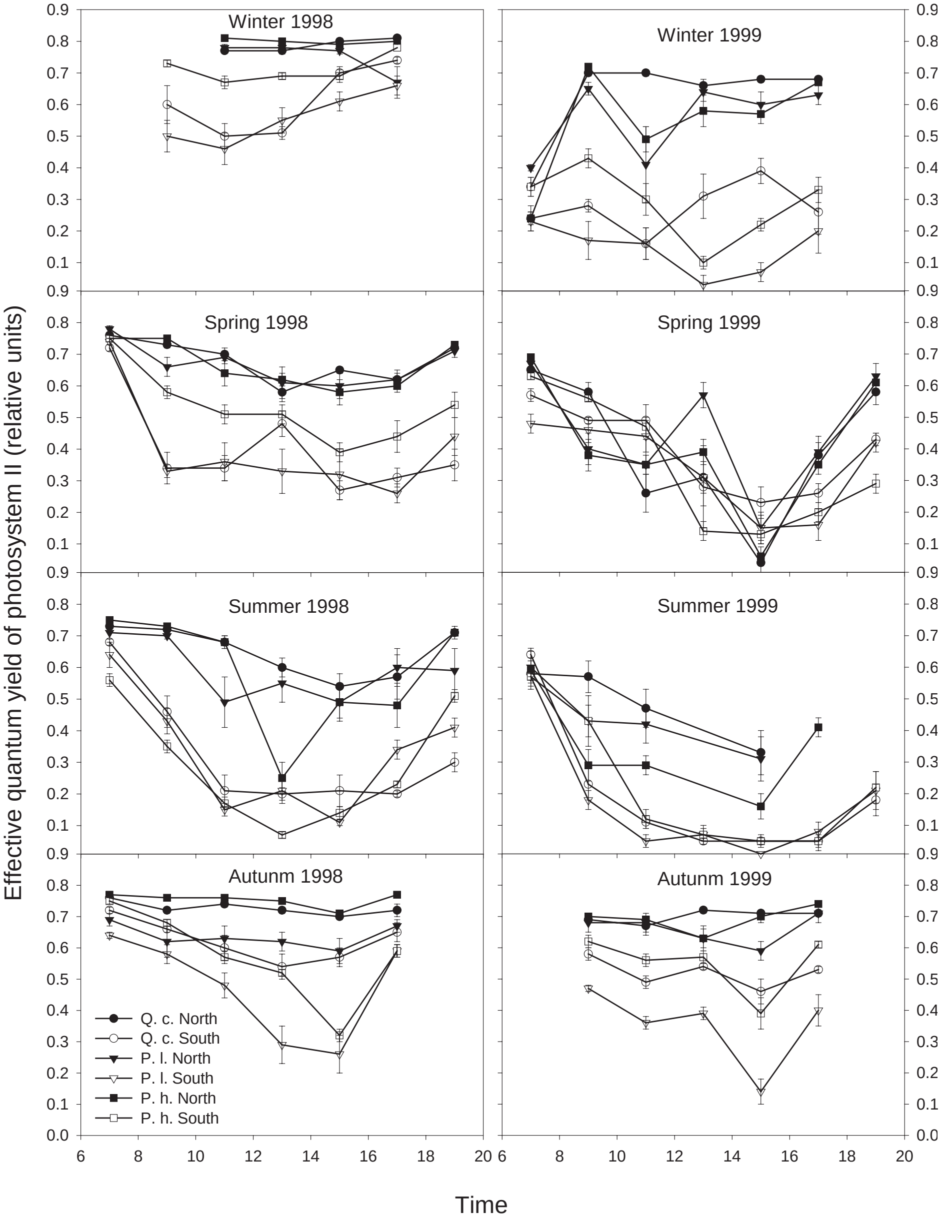

Fig. 4. Diurnal course of effective quantum yield of photosystem II at the north- and south-facing slopes. Data represent mean ± 1 S.E. ($n = 6-9$). Q. c. = *Q. coccifera*, P. l. = *Pistacia lentiscus*, and P. h. = *Pinus halepensis*.

Chlorophyll fluorescence have been revealed as a valid indicator of physiological status in the field (Figueroa et al., 1997; Werner et al., 1999; Oliveira and Peñuelas, 2000), but its use in semi-arid areas is still not as common as in other environments

Table 2
Results of a four-way (species, aspect, individual and time) repeated measures nested ANOVA showing the significance of the species and slope aspect effects, and their interaction, on daily evolution of actual efficiency of photosystem II

Year	Season	ANOVA results								
		Slope aspect			Species			Slope aspect × species		
		F	df.	*p*	*F*	df.	*p*	*F*	df.	*p*
1998	Winter	56.64	1.18	<0.001	9.49	2.18	0.002	3.59	2.18	0.049
	Spring	314.68	1.30	<0.001	11.83	2.30	<0.001	20.44	2.30	<0.001
	Summer	318.48	1.33	<0.001	5.65	2.33	0.008	0.15	2.33	0.857
	Autumn	132.75	1.37	<0.001	47.91	2.37	<0.001	132.75	2.37	<0.001
1999	Winter	321.28	1.34	<0.001	4.42	2.34	0.020	8.47	2.34	0.001
	Spring	18.10	1.26	<0.001	0.21	2.26	0.814	3.97	2.26	0.036
	Summer	63.70	1.29	<0.001	3.86	2.29	0.033	27.48	2.29	<0.001
	Autumn	46.325	1.35	<0.001	0.77	2.35	0.472	0.77	2.35	0.471

(Maestre et al., 2001, 2003). Our results suggest that chlorophyll fluorescence features of evergreen woody species are a useful tool to evaluate the effect of changing environmental conditions on their physiological performance. The values of F_v:F_m and Φ_{PSII} found in this study agree with those obtained for *Pinus*, *Quercus* and *Pistacia* in other studies performed in dry and semi-arid areas (Werner et al., 1999; Martínez-Ferri et al., 2000), and are within the range of those reported for more mesic Mediterranean schlerophyllous species like *Q. ilex*, *Arbutus unedo* and *Juniperus phoenicea* (Werner et al., 1999; Oliveira and Peñuelas, 2000).

Despite the effect of slope aspect was consistent, it is interesting to note how its magnitude, as revealed by the meta-analysis, changed throughout the studied period. This reflects the importance that small-scale changes in the temporal distribution of resources, mainly rainfall, may have on shrub physiological status in semi-arid areas. The strong differences found in the effect of slope aspect during summer drought in the 2 years evaluated is worth noting. Despite climatic conditions obtained during measurements in summer 1998 were very similar in north- and south-facing slopes, the effect of slope aspect was substantially higher as compared to that obtained in summer 1999, when climatic conditions were less stressing in the former. These differences may be related with temporal variability in rainfall patterns and amounts, since during July 1999 over 20 mm were received in both sites, and virtually no rainfall was recorded in July 1998.

Increasing diurnal light intensities led to decreased Φ_{PSII} in all evaluated species, but this decline was for most part of cases less pronounced in the north-facing slope. Diurnal decline in Φ_{PSII} was generally reversible in all seasons, suggesting that there was no chronic damage to this photosystem (Oliveira and Peñuelas, 2000). Predawn values of F_v:F_m obtained in the north-facing slope were close to the optimal range (0.83 according to Maxwell and Johnson, 2000), and remained relatively constant for all evaluated species and sampling dates. This was not found in the south-facing

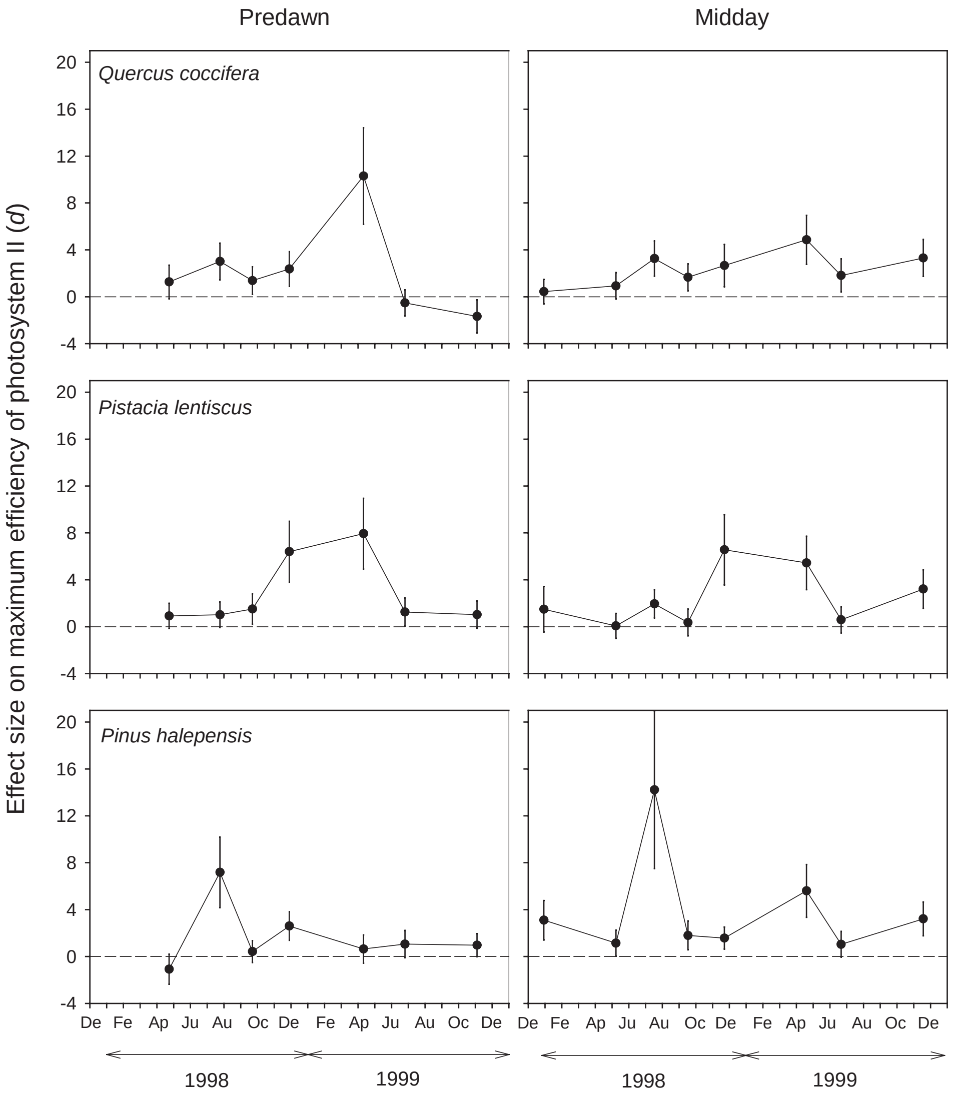

Fig. 5. Effect of slope aspect on the response of predawn and midday values of maximum efficiency of photosystem II. Closed circles and vertical lines are mean effect ± 95% confidence intervals (see text for details).

slope, where values were substantially lower, especially during summer and winter, and the variability between seasons was higher than in the north-facing slope. These results suggest that the individuals located in the north-facing slope were less stressed than those located in the south-facing one (Maxwell and Johnson, 2000). The less variability found in the predawn values of F_v:F_m obtained in the north-facing slope also suggest that the environmental conditions are more stable as compared to those in the south-facing slope.

In Mediterranean environments, typical light intensities experienced by leaves during spring and summer exceed the capacity for orderly energy dissipation by the photosynthetic system, resulting in enhanced photoinhibition (Long et al., 1994). Although very few studies exist, conditions that are commonly present during winter and autumn in Mediterranean semi-arid areas, such as relatively cold temperatures combined with moderate light intensities, can also produce photoinhibition in evergreen woody species (Oliveira and Peñuelas, 2000). For all evaluated species, midday values of F_v:F_m at the south-facing slope were lower than predawn ones, suggesting the presence of sustained diurnal photoinhibition in all seasons. Contrarily, diurnal photoinhibition at the north-facing slope was found only in Summer 1999, despite the relatively low radiation and high air humidity found during measurements. These results reinforce again the idea of a greater stability of environmental conditions at the north-facing slope as compared to the south-facing one.

In addition to the variability found in the magnitude of response to slope aspect caused by temporal variations of climatic conditions, we found important differences in this magnitude between the evaluated species, despite they share a general strategy to cope with situations of stress (Martínez-Ferri et al., 2000; Vilagrosa, 2002). The strongest effect of slope aspect on F_v:F_m was found in *Pinus* during summer 1998. These results contrast with those obtained by Martínez-Ferri et al. (2000), who did not find the presence of photoinhibition in a semi-arid site of Central Spain. For both *Pistacia* and *Quercus*, the strongest effect of slope aspect was found during spring 1999, after main Winter and Spring rainfalls. We would have expected to find a less pronounced effect of slope aspect in *Quercus* as compared to *Pistacia* in relation to their physiological characteristics. *Pistacia* has a very efficient system of water transport from roots to leaves (Vilagrosa, 2002), which allows it to maintain high levels of water in leaves when soil water is available. On the other hand, *Quercus* has a more conservative strategy, and spend less water even during period of high availability with the aim to maintain acceptable rates of water in leaves during water stress periods (Vilagrosa, 2002). It is interesting to note how, during measurements of spring 1999, radiation was higher in the north-facing slope than in the south-facing one. This fact could have over-emphasized the effect of slope aspect in a moment of high water availability, but observed results may be also consequences of increased water availability in the north-facing slope as consequence of the higher rainfalls registered at this site during winter and early spring.

Despite variability promoted by differences in the ecological behavior of the species evaluated, our findings indicate that slope aspect has a prevailing role on the chlorophyll fluorescence dynamics of a semi-arid evergreen shrubland, and that its effect is consistent throughout all seasons. However, they also suggest that temporal variability in rainfall patterns influence the magnitude of shrub response to slope aspect. Detailed information about the spatio-temporal dynamics of plant physiological performance, such as reported in this study, may be of great significance to understand the functioning of semi-arid Mediterranean shrublands.

This information, combined with an accurate understanding of the physiological basis for this response may also be used to improve the outcome of process-oriented models examining ecological vegetation shifts under various climate change scenarios (Pausas, 2003).

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