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Characteristic patterns of chronic and dynamic photoinhibition of different functional groups in a Mediterranean ecosystem

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Abstract. To analyse characteristic patterns of dynamic and chronic photoinhibition within a plant community, a new technique is proposed, which is based on the long- and short-term recovery time of maximum photochemical efficiency of PSII (F_v/F_m) after environmental stress. Chronic photoinhibition was determined as a sustainable decrease in predawn F_v/F_m , occurring during periods of prolonged stress, whereas dynamic photoinhibition was assessed from the fully reversible diurnal decline in F_v/F_m . Applied to a Mediterranean macchia ecosystem, this definition allowed the characterization of typical annual patterns of chronic and dynamic photoinhibition. Both types of photoinhibition were highest during summer drought. However, differences emerged among the ten dominant macchia species regarding their susceptibility to chronic photoinhibition during different seasons. Chronic and dynamic photoinhibition were dependent on leaf orientation. Semi-deciduous species avoided enhanced chronic photoinhibition through a reduction of excessive light interception by vertical foliage orientation during summer, whereas evergreen sclerophylls did not exhibit pronounced structural photoprotective mechanisms. Chronic and total photoinhibition were significantly correlated with predawn and midday water potentials, respectively, and a grouping of the macchia species into three functional groups is proposed according to this relationship.

Keywords: chlorophyll fluorescence, chronic and dynamic photoinhibition, drought semi-deciduous species, evergreen sclerophylls, leaf orientation, Mediterranean macchia, water potentials.

Introduction

Photoinhibition is a common phenomenon in environments with high radiation fluxes, especially when plants are exposed to additional environmental stresses. Many arguments and terminology have been developed to quantify photoinhibition. Nowadays there is profound knowledge of a variety of processes within the chloroplast that mediate the controlled dissipation of excess light energy, for example, non-radiative dissipation in the antenna, the xanthophyll cycle (Demmig-Adams 1990; Demmig-Adams and Adams 1992), and inactivation of PSII reaction centres, the repair of which involves turnover of the D1 protein (Krause and Weiss 1991; Aro *et al.* 1993; Bilger *et al.* 1995).

In this work we apply a definition that aims to evaluate the ecological significance of photoinhibition rather than the physiological mechanisms, and may be used to characterize community responses under natural conditions. The

definition is based on the concept of dynamic and chronic photoinhibition, first introduced by Osmond (1994) and Osmond and Grace (1995). They defined dynamic photoinhibition as a short-term reversible, regulatory process for the controlled dissipation of excessive light energy, and chronic photoinhibition as a slowly reversible process that may occur following prolonged exposure to excessive photon fluxes and under environmental stress conditions. These concepts have been criticized due to the lack of objective differentiation between dynamic and chronic photoinhibition (Critchley 1999). However, regarding the plant functioning under natural conditions, there might be a pronounced difference in short- and long-term reversible photoinhibition. Several authors have reported evidence suggesting that F_v/F_m may remain downregulated under environmental stress, resulting in a sustained decrease in predawn F_v/F_m (e.g. Adams and Demmig-Adams 1995; Werner *et al.* 1999).

Abbreviations used: F_v/F_m , maximum photochemical efficiency of PSII; PI_{chr} , PI_{dyn} , chronic and dynamic photoinhibition, respectively; Ψ , water potential; Ψ_{pd} , Ψ_{mid} , predawn and midday water potential, respectively.

Here, we present a definition based on the recovery time of F_v/F_m , which is one of the most reliable measurements of photoinhibition under field conditions and allows rapid screening of a plant community (Björkman and Demmig 1987; Ball *et al.* 1994). It has been shown that diurnal changes in F_v/F_m are related to cumulative light interception over several hours (Ögren and Sjöström 1990; Werner *et al.* 2001a) and therefore represent an integrative parameter even under conditions of rapid fluctuations of incident radiation that are frequently encountered under natural conditions.

In the present work, chronic photoinhibition is determined from the long-term sustainable decrease F_v/F_m , measured as a decrease in predawn F_v/F_m . Dynamic photoinhibition is assessed from the diurnal decline in F_v/F_m that is fully reversible overnight, occurring, for example, on sunny days even under otherwise favourable environmental conditions. Total photoinhibition of a plant may be composed of both types. This definition relates dynamic photoinhibition to a flexible adjustment to actual environmental conditions, whereas chronic photoinhibition reflects the integrated response to long-term environmental stress.

This concept was evaluated in a Mediterranean macchia ecosystem, which repeatedly experiences high temperatures and excessive radiation during summer drought. Within the macchia community, plants have developed a variety of adaptations to these environmental conditions, for example, reduction of stomatal conductance and net photosynthesis during summer, which increases water-use efficiency (e.g. Beyschlag *et al.* 1986, 1987; Tenhunen *et al.* 1987, 1990). The high incident radiation intensity enhances the vulnerability of these communities to photoinhibition, especially during periods when low water availability limits photosynthetic energy conversion (e.g. Angelopoulos *et al.* 1996; Werner and Correia 1996; García-Plazaola *et al.* 1997; Valladares and Pearcy 1997). These species show a variety of photoprotective mechanisms such as high xanthophyll cycle activity (e.g. Kyprisiss *et al.* 2000; Martinez-Ferri *et al.* 2000), or structural adaptations such as enhanced pubescence (Correia *et al.* 1992), leaf abscission and adjustment of leaf orientation (Valladares and Pearcy 1999; Werner *et al.* 1999, 2001b).

The proposed definition of chronic and dynamic photoinhibition was applied in order to characterize different functional groups in a macchia ecosystem, to identify periods of enhanced stress, and to analyse characteristic annual patterns of plant responses. Therefore, seasonal courses of predawn and midday water potentials (Ψ_{pd} and Ψ_{mid} respectively) and F_v/F_m of ten dominant macchia species were evaluated regarding their adaptive strategies towards excessive radiation and water stress. Furthermore, the importance of structural regulation of light interception by seasonal changes in leaf orientation was evaluated, both on the single-leaf and whole-canopy level. Different func-

tional groups of species were identified regarding the relationship between photoinhibition and Ψ .

Materials and methods

Study site and plant material

The study was performed during 1996–1998 in the Parque Natural da Serra da Arrábida in southwest Portugal (see Catarino *et al.* 1982). The study site is a well-preserved macchia, a dense evergreen sclerophyllous shrub formation, situated on a southeast-facing slope at the coast (Convento da Arrábida; 38°28'40" N, 8°59'33" W; elevation 280 m). To characterize the ecosystem, all dominant species were studied, namely the evergreen sclerophylls *Quercus coccifera* L., *Arbutus unedo* L., *Olea europaea* var. *silvestris* Brot., *Phillyrea latifolia* L., *Phillyrea angustifolia* L., *Erica arborea* L. and *Juniperus phoenicea* L., and the drought semi-deciduous shrubs *Cistus albidus* L., *Cistus monspeliensis* L. and *Rosmarinus officinalis* L.

Meteorological data

Local weather conditions were continuously recorded by a solar powered meteorological station (data-logger CR10; Campbell Scientific, Logan, UT, USA). Air temperature and precipitation were measured in 10–15 s intervals with a Campbell HMP35AC solid-state relative humidity and temperature probe and a Campbell ARG100 tipping bucket rain gauge, respectively, and were automatically stored as half-hourly and daily means.

Water potentials

Ψ of single leaves (*A. unedo*) or small terminal shoots (all other species) were measured once per month before dawn and at noon (Ψ_{pd} and Ψ_{mid} respectively), using Scholander-type pressure bombs (Manofrigido, Portugal). Measurements were performed within 1–2 min of sample collection. Water loss from excised leaves was limited by moistening the pressure chamber air with a wet paper towel. Ψ below -5.5 MPa could not be determined in 1996 due to the limited measuring range of the pressure bomb available in the first year.

Chlorophyll a fluorescence

Measurements of F_v/F_m (i.e. the ratio of variable to maximal fluorescence) were conducted *in situ* on attached leaves with a pulse-modulated fluorometer (PAM-2000; Walz, Effeltrich, Germany). Leaves were dark-adapted with leaf clips for 15 min, which was determined to be sufficient to allow complete re-oxidation of PSII reaction centres. It was the minimum time to assure complete relaxation of energy-dependent quenching, and a compromise to reduce the duration of withholding natural daylight during diurnal course measurements.

Fluorescence parameters were recorded on vertically ($90^\circ \pm 10^\circ$) and horizontally ($0^\circ \pm 10^\circ$) south-orientated sun leaves of the current years growth. In *E. arborea* and *J. phoenicea* small terminal shoots with predominantly vertical orientation were used instead of single leaves. Diurnal courses of F_v/F_m were recorded on cloudless days on six (naturally vertical and horizontally orientated) leaves on 1–3 plants per species. An additional 9–10 south-facing leaves with either vertical or horizontal orientation were measured during maximum solar radiation (11:00–14:00 true solar time). Predawn fluorescence measurements were performed once per month under complete darkness before dawn, either on the same day as midday measurements or the following morning (before Ψ_{pd} measurements). Care was taken that the signal amplitude allowed maximum signal resolution, particularly when fluorescence signals were low during summer. Measurement settings were adjusted frequently for each species.

Chronic photoinhibition (PI_{chr}) was calculated as percentage reduction in predawn F_v/F_m relative to the annual maximum F_v/F_m of each species [$(F_v/F_m)_{max}$; see below], and dynamic photoinhibition (PI_{dyn}) was calculated from midday F_v/F_m as the additional decrease, i.e.:

$$PI_{chr} = [(F_v/F_m)_{max} - (F_v/F_m)_{pd}] / (F_v/F_m)_{max} \times 100 \quad (1)$$

$$PI_{dyn} = [(F_v/F_m)_{pd} - (F_v/F_m)_{mid}] / (F_v/F_m)_{max} \times 100 \quad (2)$$

where $(F_v/F_m)_{pd}$ and $(F_v/F_m)_{mid}$ are predawn and midday F_v/F_m values, respectively. $(F_v/F_m)_{max}$ is the annual maximum F_v/F_m value, which was calculated for each species as the average from the three months with highest predawn F_v/F_m . Values were expressed as percentage reduction in $(F_v/F_m)_{max}$ values. Any photoinhibitory reduction in F_v/F_m at any time of the day may be composed of both chronic photoinhibition, in the case that predawn F_v/F_m values are depressed, and dynamic photoinhibition resulting in a further (fully reversible) decrease during the day. The annual course of chronic and dynamic photoinhibition was calculated from all predawn and midday F_v/F_m values measured during 1996–1998, which were averaged for each month. Since predawn values were not determined in January, values were interpolated between December and February measurements. Total photoinhibition is the sum of chronic and dynamic photoinhibition.

For the correlation of photoinhibition and Ψ , mean monthly Ψ_{pd} and Ψ_{mid} were calculated from all measurements recorded in 1996–1998, by pooling data for each month. Since Ψ was not determined for different leaf orientations, mean photoinhibition values of vertical and horizontal leaves were used.

Leaf angles

Leaf angles were measured relative to the horizon (0°) using a compass protractor (see Norman and Campbell 1989). Approximately equal numbers of randomly selected leaves from different heights, depths and azimuth directions within the respective plant canopies were used for the measurements. All leaf angle data were tested for significant differences between canopy position (height, depth and azimuth orientation, exposition) and time of year (ANOVA, Duncan post-hoc test). No significant differences of leaf angles from different exposures (south, west, east, and north side of the canopy) could be found. Therefore, leaf angle data were pooled from all compass directions at a given canopy height. For the sake of presentation clarity, results from one plant per species are shown, since no significant differences were found between plants of the same species (ANOVA, $P=0.7$). In *E. arborea*, measurements were performed on small terminal shoots in spring and summer, but on single leaves in autumn.

Statistical analysis

Statistical analyses were performed with Statistica (StatSoft Inc., Tulsa, OK, USA). Leaf angle data were analysed by means of multifactorial ANOVA with post-hoc comparisons (Duncan's multiple range test), or by multiple regression analysis. Data sets were tested for normality and variance homogeneity, and log transformations were used if significant deviations from normal distributions were found. Spearman's rank order correlation test was used to evaluate changes in leaf angle and total photoinhibition.

Correlations between photoinhibition and Ψ of the three functional groups were analysed by multiple regression analysis. Differences in slopes of the regression lines were tested by a method described by Zar (1996). Analysis of covariance was used to compare the three slopes by testing for homogeneity of regression coefficient, followed by Tukey's multiple comparison test.

Results

Climatic conditions

Precipitation was very high in the preceding winter of 1995/96, which was followed by a rainy spring. The drought period with only a few minor precipitation events lasted from 20 May to 11 September in 1996 (114 d) and from 11 June to 29 September (110 d) in 1997 (Fig. 1). An extreme rainfall event was recorded in October 1997, when peak daily rainfall amounted to 112 mm. March was very dry and hot, with nearly no rainfall in 1997 and 1998. A significant reduction in March rainfall has been previously reported for Portugal (Zhang *et al.* 1997). The variability of precipitation in Portugal is related to changes in the circulation patterns of the North Atlantic Oscillation (Ulbrich *et al.* 1999). The first short drought period in early spring 1997 and 1998, which was followed by a rainy and cooler period, altered the phenological development of some species.

Water potentials

Ψ (Fig. 2) followed the seasonal patterns of precipitation (Fig. 1) with a pronounced decline during summer drought. Only two evergreen sclerophylls (*Q. coccifera* and *A. unedo*) maintained minimum Ψ_{pd} above -3.5 MPa in summer. Both species were obviously able to avoid major water losses during the day, showing only a small decline at noon. In all other species, summer Ψ_{mid} declined far below these values. In several species even Ψ_{pd} declined below -5.5 MPa (please note that values below this range could not be measured during the first year). With the onset of autumn rains, Ψ recovered rapidly. The first short drought period in early spring 1997 and 1998 (Fig. 1) was reflected in a decrease of Ψ_{pd} in all semi-deciduous and some evergreen species (Fig. 2).

Chlorophyll fluorescence

A diurnal depression of PSII efficiency was found on all sunny days, with the minimum reached at midday or early afternoon. Figure 3 presents the seasonal course of F_v/F_m measured at solar noon in horizontal and vertical sun leaves of each species. F_v/F_m exhibited a pronounced depression during drought, but seemed more responsive to short-term changes in environmental conditions as compared with Ψ , resulting in higher data variability. Some species exhibited a depression during the first drought period in March (e.g. *R. officinalis*). Species-specific differences were apparent regarding their susceptibility to photoinhibition. *A. unedo* was the least susceptible species, *Q. coccifera* and *Phillyrea* spp. revealed intermediate responses, whereas the semi-deciduous species were highly photoinhibited during summer drought. However, the semi-deciduous species maintained higher F_v/F_m under non-limiting environmental conditions.

The importance of leaf orientation became visible under drought conditions: steeply-orientated leaves were less photoinhibited than horizontally-orientated ones. This was most pronounced in the semi-deciduous species. Exposure to excessive radiation led to irreversible photodamage and leaf bleaching of many horizontal leaves, followed by leaf abscission. Vertical leaf orientation generally protected the leaf from severe photodamage, which was particularly evident in *C. monspeliensis*. This functional group differed further from the evergreen sclerophylls in its rapid recovery from drought stress after the first autumn rainfalls. In contrast, evergreen species recovered only slowly, and reached high F_v/F_m values only a month after drought-release (Fig. 3).

Due to a late timing of growth and the irregular climate course in spring 1996, *Ph. latifolia* produced almost no new leaves in 1997. Since fluorescence parameters are age-dependent (see Šesták 1999), the older leaves might have been more susceptible to photoinhibition.

Predawn F_v/F_m exhibited a similar seasonal course as midday F_v/F_m , though with a much smaller amplitude, and a pronounced depression was only found during summer (Table 1). Some species also exhibited a small decline during winter. To illustrate the range of variations in predawn F_v/F_m , the peak annual values are presented in Table 1. Highest predawn F_v/F_m were reached in spring and autumn, and minimum values occurred in summer and winter. The effect of winter cold stress was not pronounced, and some species reached similar or even higher F_v/F_m values in winter as compared with spring and autumn

(e.g. *E. arborea*). During summer, differences between leaf orientations (Fig. 3) were also maintained during predawn measurements (Table 1).

Leaf angles

To evaluate the importance of leaf orientation for photo-protection, the leaf orientation of the whole canopy has to be considered. All species showed statistically significant differences in seasonal changes of mean leaf angle (Table 2). However, remarkable changes in leaf angle were only found in the semi-deciduous species, exceeding 40° in *Cistus* spp. and 30° in *R. officinalis*. These semi-deciduous species maintained pronounced horizontal orientation in spring and autumn, and a nearly vertical leaf orientation during summer drought (Table 2). This was achieved by shedding most of the horizontal leaves with the onset of summer drought, maintaining only the apical, rather erect leaves. After drought release in autumn, new, horizontally-orientated leaves emerged.

The evergreen sclerophylls maintained steeper leaf angles during the favourable seasons, with only minor seasonal variations (Table 2). *O. europaea* was the only evergreen species with leaf angle changes exceeding 10° . High standard deviations indicate a broad range of leaf angle classes. *A. unedo*, the species with the largest leaves, maintained the steepest leaf angles (Table 2). Leaf angles were significantly correlated with canopy height in nearly all species and seasons, with steeper orientation of the leaves at the upper and outer, exposed canopy positions (data not shown; Werner 2000).

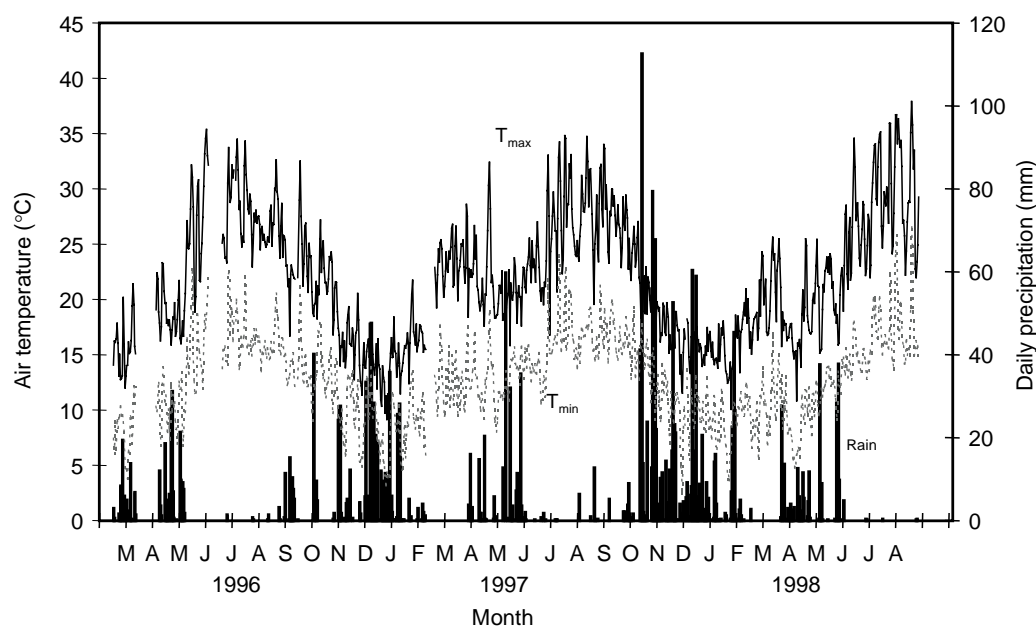


Fig. 1. Climatic conditions during the study at Convento da Arrábida. Daily minimum and maximum air temperature (T_{\min} , T_{\max} , dotted and solid line, respectively) and daily total precipitation (bars) were recorded with a climate station at the field site from 1996 to 1998.

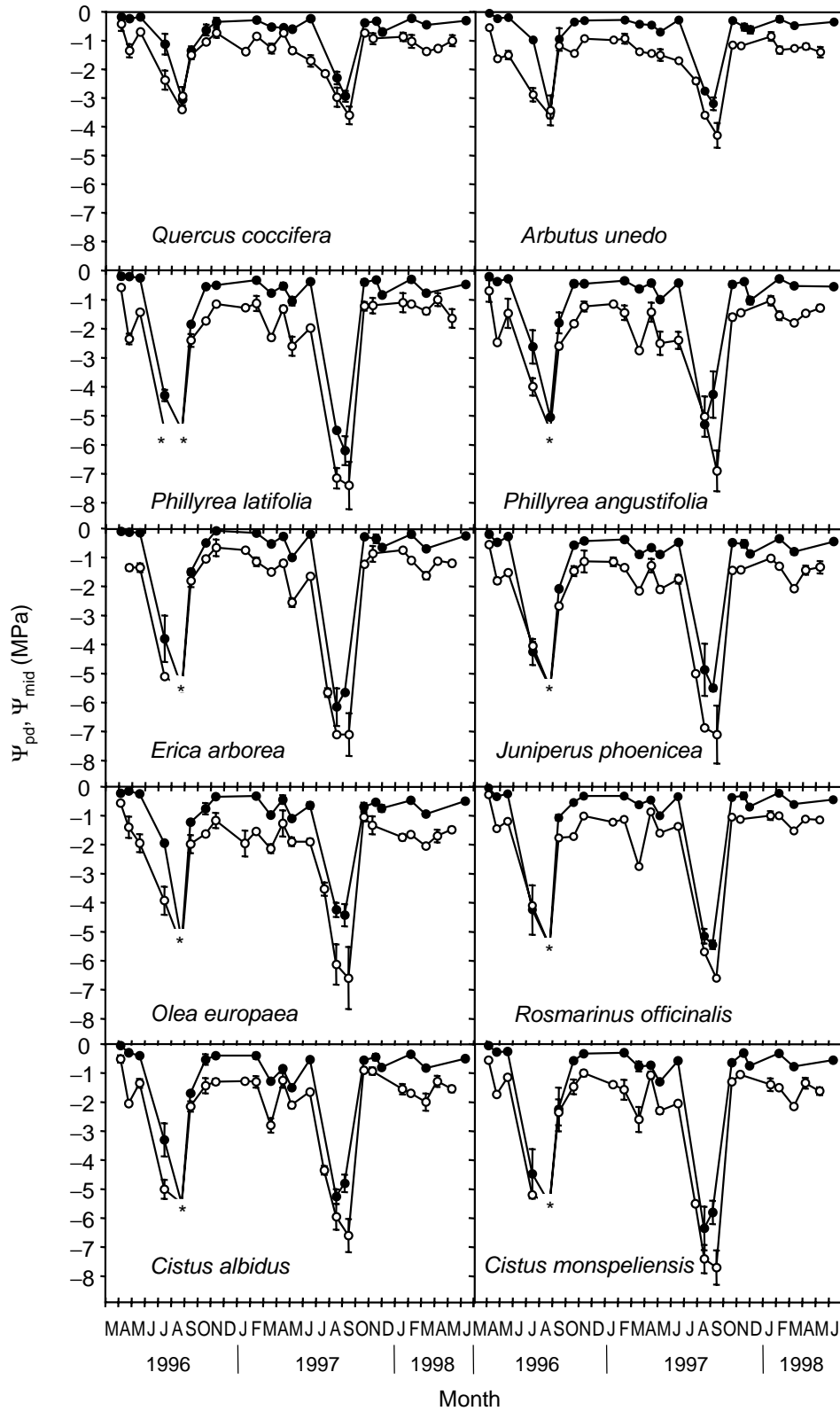


Fig. 2. Seasonal progression of Ψ_{pd} and Ψ_{mid} (closed and open symbols, respectively) of dominant macchia species from March 1996 to June 1998. Data are means of 2–6 measurements per species \pm s.d. In 1996, Ψ below -5.5 MPa exceeded the measuring range of the pressure bomb and could therefore not be determined (*).

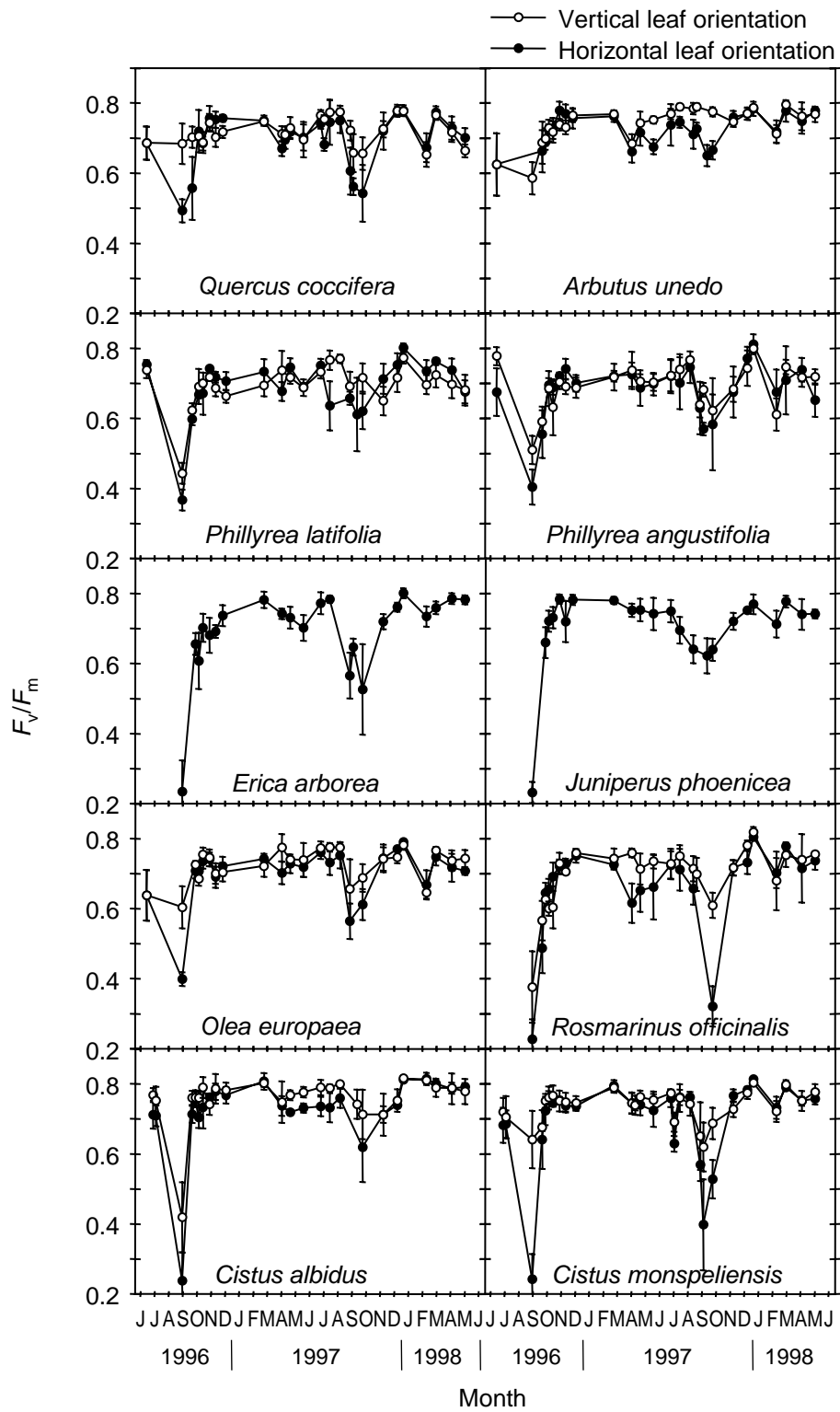


Fig. 3. Seasonal progression of midday F_v/F_m of vertical ($90^\circ \pm 10^\circ$; open symbols) and horizontal ($0^\circ \pm 10^\circ$; closed symbols) sun leaves of dominant macchia species. In *E. arborea* and *J. phoenicea*, small terminal shoots were measured instead of single leaves. Dark-adapted leaves were measured at solar noon on sunny days from June 1996 to May 1998. $n = 4-10 \pm$ s.d. per species and leaf orientation.

Table 1. Predawn F_v/F_m

Maximum seasonal variation of mean predawn F_v/F_m values of horizontal and vertical sun leaves (or terminal shoots for *E. arborea* and *J. phoenicea*) of all macchia species studied. Mean values for each month were calculated from measurements recorded during 1996–1998. Maximum values occurring under favourable environmental conditions (spring and autumn), and minimum values reached under environmental stress (winter and summer), are shown for each species. $n = 6–18$; s.d. ranged between 0.010–0.050

Species	Leaf orientation	Spring maximum (May–July)	Summer minimum (Aug–Sep)	Autumn maximum (Oct–Nov)	Winter minimum (Dec–Feb)
Evergreen sclerophylls					
<i>Quercus coccifera</i>	Horizontal	0.834	0.737	0.809	0.772
	Vertical	0.806	0.767	0.827	0.784
<i>Arbutus unedo</i>	Horizontal	0.815	0.749	0.819	0.819
	Vertical	0.837	0.777	0.839	0.803
<i>Olea europaea</i>	Horizontal	0.790	0.659	0.819	0.796
	Vertical	0.842	0.736	0.812	0.789
<i>Phillyrea angustifolia</i>	Horizontal	0.790	0.753	0.818	0.781
	Vertical	0.816	0.746	0.811	0.749
<i>Phillyrea latifolia</i>	Horizontal	0.764	0.703	0.802	0.775
	Vertical	0.802	0.766	0.806	0.767
<i>Erica arborea</i>	Vertical	0.830	0.591	0.791	0.805
<i>Juniperus phoenicea</i>	Vertical	0.809	0.620	0.817	0.777
Semi-deciduous species					
<i>Rosmarinus officinalis</i>	Horizontal	0.834	0.465	0.821	0.807
	Vertical	0.806	0.556	0.833	0.827
<i>Cistus albidus</i>	Horizontal	0.829	0.500	0.802	0.812
	Vertical	0.866	0.563	0.839	0.824
<i>Cistus monspeliensis</i>	Horizontal	0.843	0.379	0.823	0.823
	Vertical	0.847	0.650	0.845	0.817

Chronic and dynamic photoinhibition

Annual patterns of chronic and dynamic photoinhibition (Fig. 4) were calculated from the seasonal courses of midday (Fig. 3) and predawn F_v/F_m measurements (Table 1). The drought period in summer can be easily identified as the major stress period, however, differences between the functional groups emerged. Chronic photoinhibition (filled

portion of bars, Fig. 4) was most enhanced in semi-deciduous species during summer, whereas some of the evergreens (e.g. *Q. coccifera* and *A. unedo*) revealed only slight chronic photoinhibition, even during summer drought.

In general, there was a gradient of responses among the evergreen species. For example, *O. europaea* and *Phillyrea* spp. displayed intermediate behaviour, i.e. photoinhibition

Table 2. Seasonal changes of mean canopy leaf angles

Mean whole-plant leaf orientation ($^{\circ}$ to horizon \pm s.d.) of all dominant macchia species during 1996 (pooled leaf angles from all canopy subsections). Different letters indicate significant differences in mean leaf angle between seasons within each species (ANOVA, Duncan post-hoc test, $P < 0.01$). For *E. arborea*, measurements were performed on small terminal shoots in spring and summer, but on single leaves in autumn (*)

Species	Spring (May–July)		Summer (Aug–Sep)		Autumn (Oct–Nov)	
	Mean \pm s.d.	n	Mean \pm s.d.	n	Mean \pm s.d.	n
Evergreen sclerophylls						
<i>Quercus coccifera</i>	51.4 \pm 17.2a	845	53.8 \pm 19.9b	1420	55.4 \pm 17.2c	1202
<i>Arbutus unedo</i>	57.7 \pm 18.8a	900	66.1 \pm 15.9b	961	61.7 \pm 17.4c	900
<i>Olea europaea</i>	42.4 \pm 15.7a	450	64.5 \pm 16.5b	922	53.4 \pm 13.6c	850
<i>Phillyrea latifolia</i>	43.9 \pm 16.1a	2528	48.8 \pm 19.8b	1925	45.1 \pm 16.2c	2041
<i>Phillyrea angustifolia</i>	42.8 \pm 13.9a	300	48.6 \pm 14.9b	552	46.6 \pm 15.5c	951
<i>Erica arborea</i>	51.1 \pm 16.1a	1000	50.3 \pm 18.7b	848	33.5 \pm 16.0*	750
<i>Juniperus phoenicea</i>	41.2 \pm 18.9a	898	42.2 \pm 19.7b	1012	42.9 \pm 17.8b	1000
Semi-deciduous species						
<i>Cistus albidus</i>	34.9 \pm 18.8a	580	76.0 \pm 12.1b	247	33.8 \pm 18.6a	562
<i>Cistus monspeliensis</i>	31.6 \pm 13.6a	550	71.7 \pm 12.0b	497	27.5 \pm 8.8a	500
<i>Rosmarinus officinalis</i>	37.2 \pm 13.8a	655	55.6 \pm 19.3b	574	22.3 \pm 9.8c	600

was enhanced during summer but some chronic photoinhibition occurred also during winter and early spring. *E. arborea* and *J. phoenicea* showed a pattern similar to the semi-deciduous species, with high chronic and dynamic photoinhibition in summer, but rather low and predominantly dynamic photoinhibition during the rest of the year. Vertical

and horizontal leaves differed not only in the total extent of photoinhibition, but horizontal leaves of most species showed enhanced levels of chronic photoinhibition during summer as compared with vertically-orientated leaves. These differences between leaf orientations were less pronounced during non-water-limiting environmental conditions.

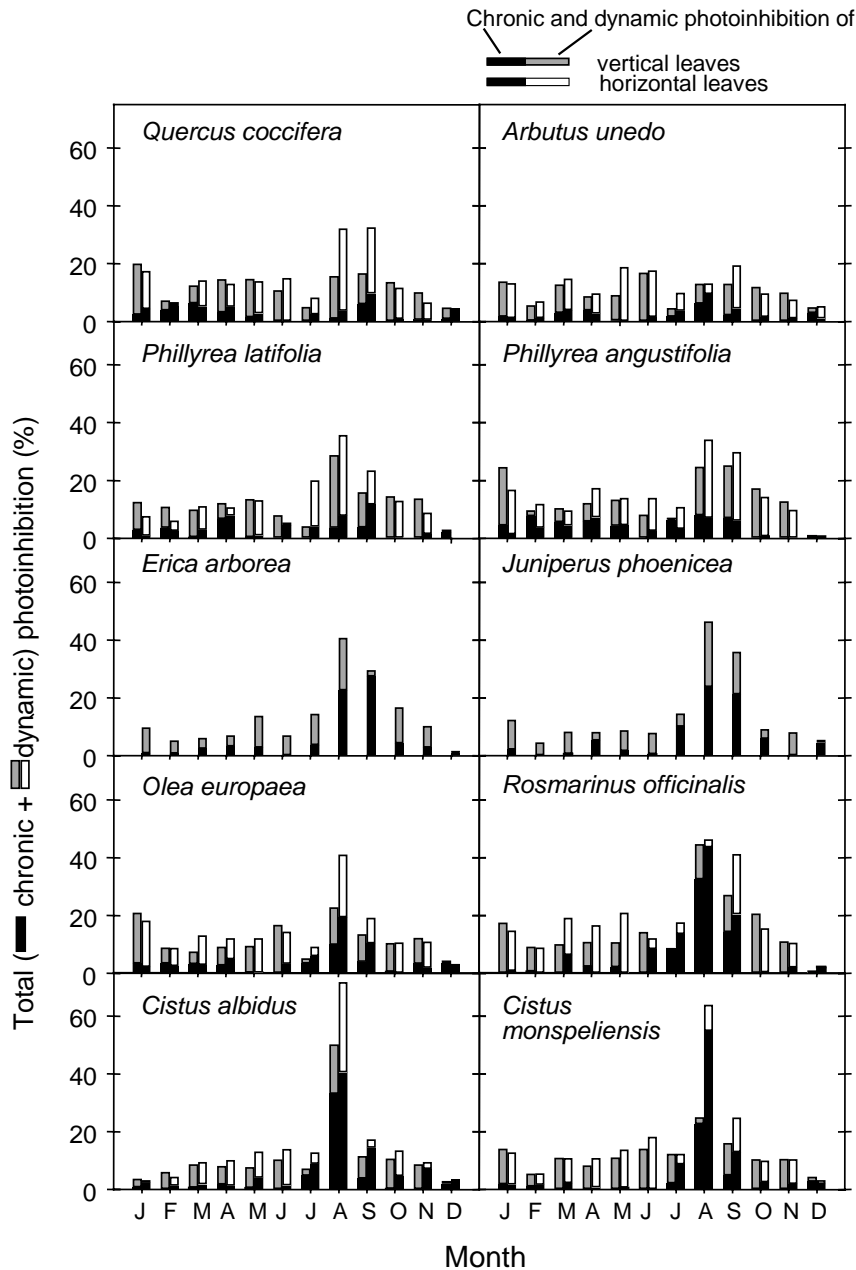


Fig. 4. Annual course of chronic (filled bars) and dynamic (open and shaded bars) photoinhibition of horizontal (open bars) and vertical (shaded bars) sun leaves. Chronic photoinhibition was calculated from the reduction (%) in predawn F_v/F_m relative to maximum F_v/F_m . Dynamic photoinhibition represents the additional, fully reversible, diurnal reduction of F_v/F_m (calculation based on pooled data from 1996–1998). See ‘Materials and methods’ for further details.

A change in leaf orientation would be most beneficial for species that exhibit a pronounced difference in susceptibility to photoinhibition under favourable and stress conditions. As shown in the example in Table 3, a substantial increase in total photoinhibition of horizontally-orientated leaves was found in species that exhibit a concomitant increase in leaf orientation at the canopy level ($P < 0.05$, Spearman's rank order). This was not found for species with small leaf angle changes.

Relationship between photoinhibition and water potentials

Ψ_{pd} and Ψ_{mid} were significantly correlated with chronic and total photoinhibition, respectively ($P < 0.001$, multiple regression analysis; Fig. 5). Three distinct groups were found. Most evergreen species exhibited only a weak correlation (Group I; Figs 5a, d), which explained only 33 and 44% of the variance between Ψ_{pd} and Ψ_{mid} vs chronic and total photoinhibition, respectively. *Phillyrea* spp. exhibited chronic photoinhibition at Ψ above -1.0 MPa (Fig. 5a), indicating that factors other than water availability (e.g. cold stress during winter) induced chronic photoinhibition. A correlation with photoinhibition was always found when Ψ_{pd} declined below a threshold of -1.0 MPa. However, *E. arborea* and *J. phoenicea* were significantly different from all other sclerophylls, and showed a higher correlation explaining 77% of variance between photoinhibition and Ψ (Group II; Figs 5b, e). This pattern was similar to the one found for the semi-deciduous species ($P < 0.01$; Group III; Figs 5c, f). A comparison of slopes of the linear regressions further confirmed these patterns (Table 4). Significant differences were found between the slopes of Group I vs Groups II and III concerning both regression lines, but not between the latter two groups.

Discussion

In this work, a definition of chronic and dynamic photoinhibition was applied, which aimed to clarify the ecological

Table 3. Ranking of changes in leaf angle and total photoinhibition Maximum annual changes (Δ = annual max – annual min values) of whole-plant leaf angle and total photoinhibition of horizontally-orientated leaves, sorted by increasing Δ leaf angle. *E. arborea* and *J. phoenicea* are not shown, since terminal shoots were measured instead of single leaves. $n = 8$; $P < 0.05$ (Spearman's rank order correlation)

Species	Δ Leaf angle ($^{\circ}$)	Δ Total photoinhibition
<i>Quercus coccifera</i>	2.4	36.9
<i>Phillyrea latifolia</i>	4.9	37.6
<i>Phillyrea angustifolia</i>	5.8	26.4
<i>Arbutus unedo</i>	8.4	23.4
<i>Olea europaea</i>	22.1	
<i>Rosmarinus officinalis</i>	33.4	61.7
<i>Cistus albidus</i>	42.2	67.5
<i>Cistus monspeliensis</i>	44.2	68.8

significance of photoinhibition under natural conditions. The proposed classification is based on a concept originally introduced by Osmond (1994) and Osmond and Grace (1995) that distinguishes between short- and long-term photoinhibition — chronic photoinhibition refers to a sustainable decrease in predawn F_v/F_m , whereas dynamic photoinhibition describes the fully reversible diurnal decrease of F_v/F_m . This concept allows evaluation of the duration and intensity of stress in terms of reversibility of the flexible adjustment of maximum photochemical efficiency. It further overcomes problems that may result from the calculation of quenching coefficients (e.g. nonphotochemical quenching, qN), which arise when predawn fluorescence values do not correspond to maximal F_v/F_m under stress conditions. Since maximum fluorescence (F_m) is required for calculation of some quenching coefficients, they may be underestimated under these conditions (Demmig-Adams *et al.* 1996; Verhoeven *et al.* 1998a, b).

Applied to a Mediterranean macchia ecosystem, chronic and dynamic photoinhibition reflected seasonal environmental changes, as well as species-specific susceptibilities. Highest predawn F_v/F_m ratios were found in new, fully-developed leaves in late spring in most species, but a pronounced depression occurred during summer (Table 1).

In general, different strategies could be identified between drought-tolerant and drought-avoiding species. The drought-resistant sclerophylls (e.g. *Q. coccifera* and *A. unedo*) revealed mainly dynamic photoinhibition, providing photoprotection against excessive incident radiation. For *A. unedo*, it has been shown that the diurnal decline of photochemical efficiency of PSII is accompanied by a pronounced increase of zeaxanthin (Demmig-Adams *et al.* 1989). The xanthophyll cycle might mediate the process of de-excitation of excited chlorophyll from PSII reaction centres, and probably protects photosynthetic membranes against the adverse effects of excess excitation energy.

In contrast, semi-deciduous species suffered from enhanced chronic photoinhibition during summer. This long-term depression has been related to slowly reversible loss of PSII reaction centre function, which also promotes dissipation of excess photons as heat from non-functional PSII centres. Following prolonged exposure to excess radiation, this may ultimately result in irreversible photo-damage and pigment destruction (Long *et al.* 1994; Osmond and Grace 1995), as was found in horizontally-exposed leaves during summer.

Within the community, a gradient of intermediate responses was observed. Some evergreen sclerophylls (*O. europaea* and *Phillyrea* spp.) revealed slightly enhanced photoinhibition during winter. These species are well adapted to summer drought [e.g. via high rates of de-epoxidation of violaxanthin, and high carotenoid contents (e.g. Faria *et al.* 1998; Kypris *et al.* 2000)], but may be susceptible to winter cold stress (Tretiach 1993; Larcher

2000). Clear winter days with low temperatures can induce photoinhibition in Mediterranean species (e.g. Karavatas and Manetas 1999; Oliveira and Peñuelas 2001). Gilmore and Ball (2000) did show that evergreens can protect their chlorophyll by forming special complexes that are unique to the winter-acclimated state and increase thermal energy dissipation of the PSII antenna. Interestingly, the structural photoprotection by vertical leaf orientation during summer (Fig. 4; Werner *et al.* 1999) was also shown to be an efficient photoprotective mechanism in *C. albidus* during winter at a colder site (Oliveira and Peñuelas 2000). Chilling stress was probably not a determining factor during the present work,

because minimum air temperatures rarely declined below 5°C, frost was absent due to the proximity of the Atlantic Ocean, and sunny days induced a remarkable increase in air temperature on the south-facing slopes even during winter (Fig. 1).

Photoinhibition was significantly correlated with Ψ in all species. Low water availability may predispose leaves to photoinhibition, probably through stomatal restriction of CO₂ supply to photosynthetic reaction centres and, hence, a reduction of photosynthetic energy dissipation (e.g. Björkman and Powles 1984). Ψ_{pd} revealed differential availability, and temporal utilization, of site water reserves

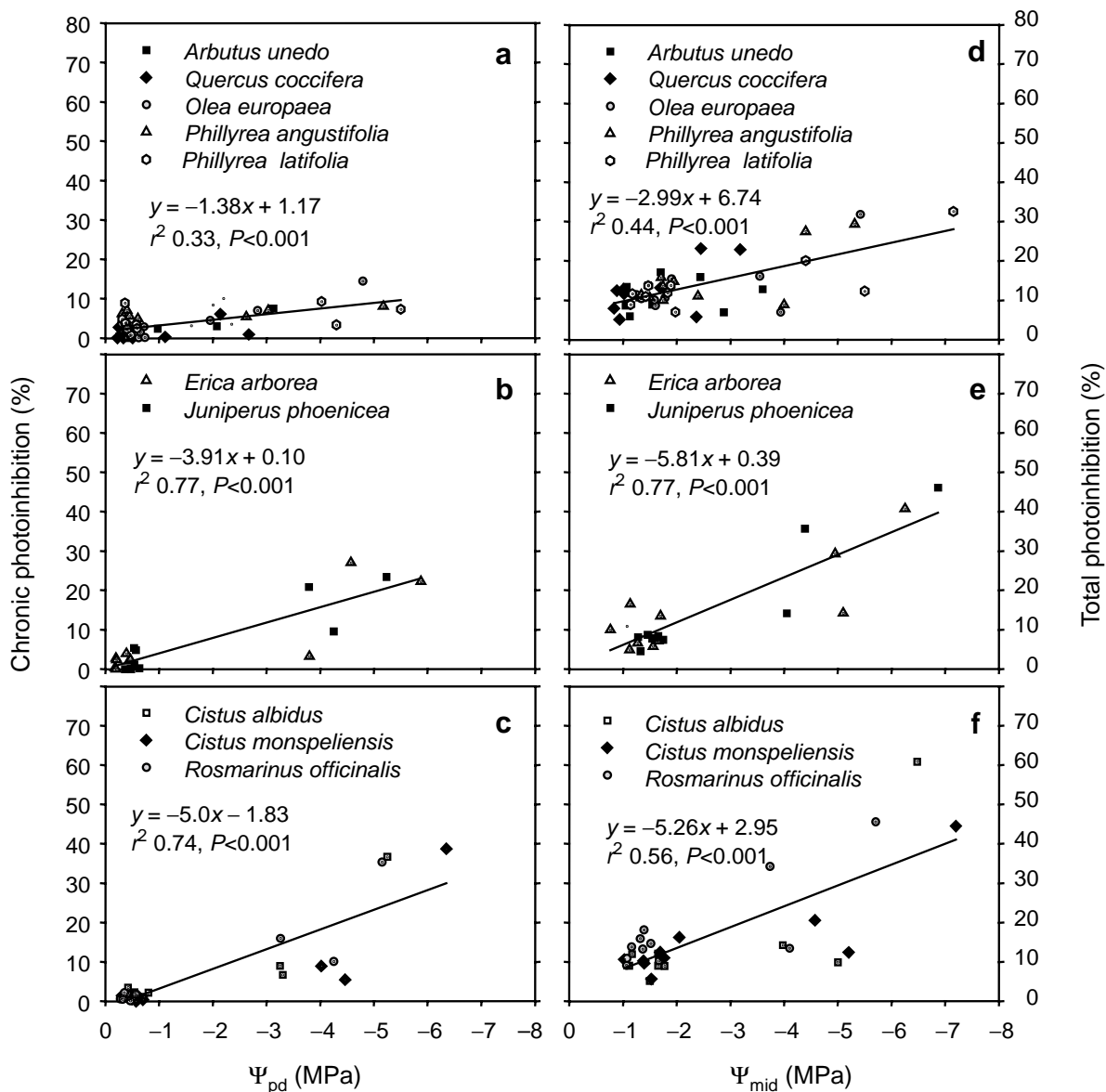


Fig. 5. Relationship between Ψ_{pd} and Ψ_{mid} vs chronic (a–c) and total (e–f) photoinhibition. Chronic and total (chronic + dynamic) photoinhibition were derived from Table 1 and Fig. 4, and were plotted against mean Ψ calculated for each month from data presented in Fig. 2. For the grouping of species see text.

among species. Highly drought-tolerant sclerophylls (*Q. coccifera* and *A. unedo*) showed a high capacity for the extraction of a considerable amount of water from the soil for nighttime recovery (Fig. 2) due to their deep and well-developed root system (Kummerow 1981; Margaris 1981). Unless soil water deficits are severe and persist for a long period, woody perennials usually experience only moderate water deficits and acclimate to water shortage (Pereira and Chaves 1995). However, in other evergreen sclerophylls, particularly *E. arborea*, *J. phoenicea* and the semi-deciduous species, Ψ declined markedly. Ψ reported here is consistent with other results [e.g. Beyschlag *et al.* 1987; Rhizopoulou *et al.* 1991 (although they reported lower Ψ for *A. unedo*); Correia and Catarino 1994] but lower than that reported by Rhizopoulou and Mitrakos (1990).

Acclimation involves changes in plant structure and function that enhance the ability of the plant to avoid dehydration, for example, an increase in the ratio of root biomass to leaf biomass, osmotic adjustment, and stomatal closure (Rambal 1992; Osório *et al.* 1998). Semi-deciduous *Cistus* spp. reduced their transpirational surface through leaf abscission (Werner *et al.* 1999) and display several morphological adaptations [e.g. pubescence, high leaf reflectance and leaf dimorphism (Correia *et al.* 1992; Kyparissis and Manetas 1993; Baldini *et al.* 1997)]. An effective way to reduce photoinhibition is vertical leaf orientation, which lowers the amount of excessive light interception and serves as a photoprotective mechanism (e.g. Adams *et al.* 1992; Ögren and Evans 1992; Björkman and Demmig-Adams 1994; He *et al.* 1996; Kao and Tsai 1998; Valladares and Pearcy 1998; Werner *et al.* 1999). This strategy was most pronounced in the semi-deciduous species, which showed a flexible adjustment of leaf angle in summer (Table 2). In general, there seems to be a tendency of increasing structural regulation with increasing susceptibility to photoinhibition (Table 3). The adjustment of leaf orientation is a growth-related process in these species. Most evergreens,

which produce their long-lived leaves during a short growing period in spring (and sometimes in autumn), did not rely on structural photoprotection. Only *O. europaea*, which has an extended growth period, exhibited some seasonal adjustment in leaf orientation.

Whole-plant simulations have shown that the high variability in leaf orientation within a *Q. coccifera* canopy results in optimization of whole-plant carbon gain and photoprotection, whereas the steep leaf orientation of *C. monspeliensis* reduces the amount of carbon lost due to photoinhibition in summer (Werner *et al.* 2001b).

Differences between species were also apparent in the correlation between photoinhibition and water stress (Fig. 5). Most evergreen sclerophylls (Group I) exhibited a poor though significant correlation, whereas Ψ_{pd} and chronic photoinhibition accounted for 74% of the variance in semi-deciduous species. The two sclerophylls *E. arborea* and *J. phoenicea* displayed a response that was similar to the drought semi-deciduous species rather than to the other evergreen sclerophyllous species, and they could have been joined into the same group on the basis of this ecophysiological behaviour. However, since they deviate strongly in their structural adaptations and growth form, the presented grouping seemed to be justified. Furthermore, it is consistent with other studies, where these species have been separated into the same three functional groups, even when based on different parameters like phenological and morphological traits, pollination types, and disturbance and fire resilience (Médail *et al.* 1998; Pausas 1999).

The present data show that susceptibility to photoinhibition is strongly increased by water stress. However, the extent of chronic and dynamic photoinhibition is species specific, and dependent on the amount of excessive radiation intercepted by the foliage, as suggested by the differences between vertical and horizontal leaves. The proposed parameters may therefore be useful in revealing characteristic response patterns to excessive radiation within an ecosystem.

Table 4. Analysis of the slopes of linear regressions

Test for significant differences between slopes of the linear regression lines of Ψ_{pd} vs chronic photoinhibition (PI_{chr} ; Figs 5a–c) and Ψ_{mid} vs total photoinhibition (PI_{tot} ; Figs 5d–f), by covariance analysis followed by a Tukey post-hoc test. Group I: *Arbutus unedo*, *Quercus coccifera*, *Olea europaea*, *Phillyrea latifolia*, *Phillyrea angustifolia*; Group II: *Erica arborea*, *Juniperus phoenicea*; Group III: *Cistus monspeliensis*, *Cistus albidus*, *Rosmarinus officinalis*. For each comparison, degrees of freedom (d.f.), critical value (F or q value), and significance level (P) are given

	Ψ_{pd} vs PI_{chr}		Ψ_{mid} vs PI_{tot}	
Covariance analysis of slopes: d.f. = 94; $F_{0.05(1)2.94} \cong 3.10$				
All groups	$F = 21.78$	$P < 0.001$	$F = 5.01$	$P < 0.01$
Multiple comparisons between groups (Tukey's test): d.f. = 94; $q_{0.05,94,3} \cong 3.37$				
Group I vs Group II	$q = 7.63$	$P < 0.001$	$q = 5.00$	$P < 0.01$
Group I vs Group III	$q = 9.41$	$P < 0.001$	$q = 3.52$	$P < 0.05$
Group II vs Group III	$q = 1.99$	$P > 0.25$	$q = 0.64$	$P > 0.25$

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