Energy dissipation in drought-avoiding and drought-tolerant tree species at midday during the Mediterranean summer

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Summary Photosynthetic performance was monitored during two consecutive summers in four co-occurring evergreen Mediterranean tree species growing on a south-facing rocky slope. In response to midday water stress, the drought-avoiding species *Pinus halepensis* Mill. exhibited marked stomatal closure (g_s) but no changes in stem water potential (Ψ_s), whereas the drought-tolerant species *Quercus coccifera* L., *Q. ilex* ssp. *ballota* (Desf.) Samp. and *Juniperus phoenicea* L. displayed declines in midday g_s and Ψ_s. The higher resistance to CO_2 influx in needles of *P. halepensis* compared with the other species did not result in either a proportional increase in non-radiative dissipation of excess energy or photo-inactivation of photosystem II (PSII). No significant differences were found among species either in the de-epoxidation state of the xanthophyll cycle (DPS) or in the pool of its components on a total chlorophyll basis (VAZ). Despite contrasting midday assimilation rates, the three drought-tolerant species all exhibited a pronounced drop in photochemical efficiency at midday that was characterized by a decrease in the excitation capture efficiency of the open PSII centers. Although photoinhibition was not fully reversed before dawn, it apparently did not result in cumulative photo-damage. Thus, the drought-avoiding and drought-tolerant species employed different mechanisms for coping with excess light during the midday depression in photosynthesis that involved contrasting midday photochemical efficiencies of PSII and different degrees of dynamic photoinhibition as a photo-protective mechanism. These behaviors may be related to the different mechanisms employed by drought-avoiding and drought-tolerant species to withstand water deficit.

Keywords: chlorophyll fluorescence, Juniperus phoenicea, midday depression, Pinus halepensis, photo-protection, Quercus coccifera, Quercus ilex, xanthophyll cycle.

Introduction

Co-occurring tree species often differ in their tolerance to drought (Bahari et al. 1985, Castell et al. 1994, Abrams and Mostoller 1995, Goulden 1996). This heterogeneous response to water deficit has been divided into two types of mechanism: avoidance and tolerance (Kramer 1983, Jones 1992). Species that employ a drought-avoidance mechanism prevent damage by early stomatal closure before any change in leaf water status occurs, whereas drought-tolerant species exhibit simultaneous decreases in stomatal conductance and water potential (Guehl et al. 1991, Picon et al. 1996). In drought-tolerant *Quercus* species, drought-induced stomatal closure does not limit carbon assimilation, whereas carbon assimilation is inhibited in the drought-avoiding species of *Pinus* (Grieu et al. 1988, Picon et al. 1996). Furthermore, *Quercus* species maintain significant rates of assimilation even at low leaf and stem water potentials (below –2.0 MPa; Epron and Dreyer 1993, Damesin and Rambal 1995), whereas when *Pinus* species encounter a mild drought stress, carbon assimilation is suppressed because of stomatal closure (Schwanz et al. 1996).

This difference in the ability of drought-avoiding and drought-tolerant species to maintain a significant rate of net CO_2 uptake suggests that drought stress can impose very different restrictions on the availability of CO_2 as a sink for absorbed solar energy. Consequently, both mechanisms are likely to differ in their requirements for excess energy dissipation. Studies carried out in Mediterranean ecosystems, where vegetation is typically subjected to a summer drought, have shown an inverse relationship between photosynthetic and photo-protective capacities in tree species—species with low net photosynthetic rates exhibited high carotenoid to chlorophyll ratios and xanthophyll de-epoxidation rates (Faria et al. 1998). Conversion of violaxanthin to antheraxanthin and zeaxanthin is strongly correlated with an increase in harmless non-radiative energy dissipation (q_N) that lowers the photochemical efficiency of photosystem II (Φ_{PSII}) and provides photo-protection from oxidative damage (Demmig-Adams and Adams 1992, Long et al. 1994, Verhoeven et al. 1997). Lack of photooxidative injury in drought-avoiding species has also been attributed to electron transport to O_2, either through the Mehler reaction or the photorespiratory pathway (Schwanz et al. 1996). Thus, even though carbon assimilation is more sensitive to water deficits in drought-avoiding species

than in drought-tolerant species, drought-avoiding species might not be any more prone to photoinhibitory damage than drought-tolerant species.

We determined whether co-occurring drought-avoiding and drought-tolerant evergreen tree species differ in their ability to cope with excess energy and consequently in their susceptibility to photoinhibition. The pioneer *Pinus halepensis* Mill., which behaves as a drought-avoiding species, was compared with a late-successional, drought-tolerant gymnosperm species, *Juniperus phoenicea* L., and with the late-successional, drought-tolerant angiosperms *Quercus coccifera* L. and *Q. ilex* ssp. *ballota* (Desf.) Samp. The study was conducted during the continental Mediterranean summer in a rupicolous environment where differences between drought-avoiding and drought-tolerant mechanisms were expected to be particularly marked.

Materials and methods

Field site and plant material

The study was conducted on a south-facing calcareous rocky slope (27°) located in Teruel, Spain (40°52′ N, 00°07′ W; central-east Spain) at 750 m above sea level. The area has a typical Mediterranean-type climate. Mean annual precipitation is 381.9 mm (1960–1994) and the mean maximum temperature is 31.7 °C. During the experiment, air temperature (T), photosynthetic photon flux density (PPFD) and relative humidity (RH) were gathered every 2 min throughout the day with cross-calibrated temperature sensors (Grant Instruments Ltd., Cambridge, U.K.), quantum sensors (SKP210; Skye Instruments Ltd., Powys, U.K.) and relative humidity probes (HMP 35A; Vaisala Oyj, Helsinki, Finland), respectively, that were all connected to a Squirrel 1200 data logger (Grant Instruments Ltd.). Air vapor pressure deficit (VPD) was calculated from air temperature and air humidity data.

Juniperus phoenicea, *Pinus halepensis*, and the evergreen oaks *Quercus coccifera* and *Q. ilex* ssp. *ballota* co-occurred throughout the rupicolous ecotone. None of the trees was taller than 1.8 m, indicating that tree growth was being restricted. Photosynthetic performance of three plants per species was monitored over eight clear days chosen from 25 days of field measurements from June to September of 1996 and 1997. All measurements were made on current-year exposed foliage located at regular intervals around the outer crown.

Stem water potential

During summer 1997, stem water potential (Ψ_s) was determined at predawn (0230–0430 h solar time) and midday (1100–1300 h solar time; Ψ_{spd} and Ψ_{smd}, respectively) with a pressure chamber (Skye Instruments Ltd.) as described by Scholander et al. (1965). Briefly, two twigs of three plants per species were enclosed in a plastic bag and covered with aluminum foil for 2 h before measurements. In this way, leaf transpiration was blocked to allow the xylem water potential of the twigs to equilibrate with that of the main stem (cf. Begg and Turner 1970). We measured stem water potential because it is a sensitive and reliable plant-based measure of water stress in woody plants, and is less variable than leaf water potential (Garnier and Berger 1985, McCutchan and Shackel 1992).

Gas exchange measurements

Leaf gas exchange was measured at 0700–0900 h solar time and at midday in two fully expanded current-year leaves or twigs of two plants per species on two consecutive days in August and September 1997. Measurements were made with a portable, open gas-exchange system (Heinz Walz GmbH, Effeltrich, Germany) equipped with a differential CO_2/H_2O IRGA-porometer (Binos-100, Leybold Heraeus, Hanau, Germany). The central unit recorded incident PPFD and cuvette temperature, while air temperature and relative humidity were measured simultaneously with an external microclimatic unit (Heinz Walz GmbH). Temperature inside the cuvette was controlled by a Peltier unit and never exceeded the external air temperature by more than 2.0 °C. Net CO_2 assimilation rate (A), stomatal conductance (g_s) and intercellular CO_2 concentration (C_i) were calculated with DIAGAS software (Heinz Walz GmbH) according to the equations of von Caemmerer and Farquhar (1981). Both A and g_s were expressed on a projected leaf area basis, which was measured with an automatic image analyzer (Inco 10, Microm España S.A., Barcelona, Spain). Projected leaf areas of twigs of *J. phoenicea* and needles of *P. halepensis* were multiplied by $\pi/2$, as recommended by Cregg (1992).

Chlorophyll a fluorescence

In vivo chlorophyll a fluorescence signals of five attached current-year leaves (or twigs of *J. phoenicea*) of three plants per species were monitored from predawn to dusk with two cross-calibrated portable fluorometers (PAM-2000, Heinz Walz GmbH) equipped with leaf-clip holders to monitor incident PPFD ($PPFD_{leaf}$) and leaf temperature (T_{leaf}). Predawn measures of maximal (F_m) and minimal fluorescence (F_o) were used to calculate maximal photochemical efficiency of PSII (F_v/F_m). The F_m values were also used to calculate diurnal non-photochemical quenching ($q_N = (F_m-F_m')/(F_m-F_o')$; Buschman 1995). Daily variation in quantum yield of noncyclic electron transport (Φ_{PSII}), photochemical quenching (q_P) and photochemical efficiency of the open reaction centers of PSII (F_v'/F_m') were calculated according to Genty et al. (1989). For quenching analysis, minimal fluorescence yield of a pre-illuminated sample (F_o') was assessed in leaves darkened immediately after every saturation pulse and subsequently exposed to far-red light for 5.5 s.

Pigment analyses

Three pooled samples from three plants per species were taken before dawn and at noon and immediately stored in liquid nitrogen until analyzed for pigments. Samples were extracted with cool acetone (20 mg of leaf tissue per ml of solvent) in the presence of sodium ascorbate with a mortar and pestle. After filtering through a 0.2 μm nylon filter syringe, 30 μl of acetone extract was subjected to HPLC by injecting it into a Spherisorb ODS2 reverse-phase steel column (25 cm, 5 μm particle diameter) (Waters Corp., Milford, MA). Solvents for

HPLC analyses (LabScan Ltd., Dublin, Ireland) were degassed before use by bubbling helium through them (Quality U, Air Liquide America Corp., Houston, TX). Chlorophylls and carotenoids separated by HPLC, as described by Val et al. (1994), were detected with a Waters 996 photodiode array detector. For the identification and quantification of peaks, pure commercial standards (VKI, Denmark) were used. Leaf concentrations of violaxanthin, antheraxanthin and zeaxanthin as well as the total pool (VAZ) were expressed in relation to total chlorophyll (Chl a + b) concentration. The de-epoxidation state of the xanthophyll cycle (DPS) was calculated as the ratio of antheraxanthin + zeaxanthin to the total xanthophyll cycle pool as described by Adams et al. (1995).

Statistical analyses

Data were analyzed with the software program STATISTICA 4.5 (Statsoft Inc., Tulsa, OK). Effects of species on chlorophyll fluorescence-based variables, $PPFD_{leaf}$ and T_{leaf} were assessed by a multifactorial repeated measures analysis of variance (ANOVA). In this model, species was the between-groups factor and plant was nested under species. Within subjects, sampling date was considered as a repeated measures factor when data were analyzed at a given point during the diurnal course, or as a second within-subjects factor under time of day when differences between predawn and midday were tested. Statistical analyses of chlorophyll fluorescence-based variables incorporated a linear combination of climatic variables as a changing covariate to account for effects of climatic variation across leaves, time of day, and field campaigns. We calculated this covariate by principal component analysis. Because a different batch of leaves was selected every year, the corresponding data sets were analyzed separately. Where differences were detected, a least significance difference test (LSD) was used for all pairwise comparisons. Differences in the diurnal course of pigment composition among species were also evaluated by repeated measures ANOVA, using species and time of day as between-group and within-subject factors, respectively. Differences in gas exchange and stem water potential among species during the day were tested by two-way ANOVA. Assumptions of normality and homoscedasticity were tested by the Kolmogorov-Smirnov test and Cochran's C test, respectively. In the event of heteroscedasticity, variables were either log-transformed or analyzed with the nonparametric Kruskal-Wallis test.

Results

Weather conditions and stem water potential

The measured climatic variables followed similar time courses on all sampling days, although summer 1997 was warmer and sunnier than summer 1996. Midday PPFD at crown height reached maximum values of 2025 and 2310 µmol m^{-2} s^{-1} in 1996 and 1997, respectively. In 1996 and 1997, air temperature and VPD had maximum values of 31.5 and 36.8 °C and 3.0 and 5.0 kPa, respectively. Before dawn, minimum daily temperatures ranged from 12.3 to 20.5 °C, resulting in a daily temperature oscillation up to 19.5 °C.

All species exhibited their highest Ψ_s values before dawn (Figure 1). These moderately low Ψ_{spd} values indicate that none of the trees suffered severe water stress. Values of Ψ_{spd} were significantly lower for *J. phoenicea* than for the other species ($P < 0.05$). A significant decline (about 50%; $P < 0.05$) in Ψ_s was observed at midday in all species except *P. halepensis* where values of Ψ_{smd} and Ψ_{spd} were similar. Among the study species, *J. phoenicea* had the lowest values of Ψ_{smd} ($P < 0.05$).

Leaf temperature and leaf photon flux density

In all species, mean midday values of T_{leaf} and $PPFD_{leaf}$ were lower in 1996 than in 1997 (Figure 2A). In both years, *J. phoenicea* had the highest mean T_{leaf} at midday and *Q. ilex* had the lowest mean T_{leaf} and the difference in mean T_{leaf} between the two species was significant ($P < 0.01$). *Pinus halepensis* and *Q. coccifera* displayed intermediate T_{leaf} values. Mean midday values of T_{leaf} were correlated with those of $PPFD_{leaf}$ ($r^2 = 0.82$) (Figure 2A) in both sampling years. At midday, $PPFD_{leaf}$ of leaves sampled from around the outer surface of the crowns in 1996 and 1997 ranged from 214 and 561 µmol m^{-2} s^{-1} (lower quartile) to 1223 and 1520 µmol m^{-2} s^{-1} (upper quartile), respectively. Significant differences in midday $PPFD_{leaf}$ among species were only found in summer 1997, when values for *Q. ilex* were significantly lower than those of the other species ($P < 0.05$).

Gas exchange

In the morning, *Quercus* species displayed significantly higher g_s values than the other species ($P < 0.05$); however, there were no significant differences in *A* between *P. halepensis* and the *Quercus* species at mid-morning (Figure 3). In all species except *J. phoenicea*, g_s declined significantly at midday ($P < 0.05$). In *Q. coccifera* and *P. halepensis*, the midday reduction in g_s was accompanied by a significant decrease in *A* (Figure 3). Midday g_s in *Q. ilex* was 2- to 5-times higher than in the other species and was accompanied by proportionally higher *A* (Figure 3). In *P. halepensis*, a low g_s and
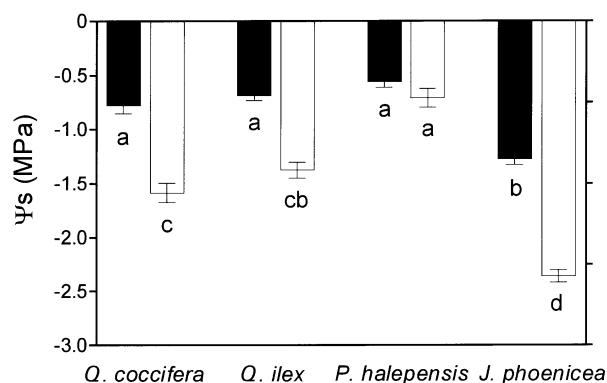
Figure 1. Predawn (Ψ_{spd}, solid bars) and midday stem water potential (Ψ_{smd}, open bars) of twigs of *Quercus coccifera*, *Q. ilex*, *Pinus halepensis* and *Juniperus phoenicea* measured in summer 1997. Bars represent means ± SE ($n = 24$). Statistical differences ($P < 0.05$) between species and times of day are indicated by different letters.
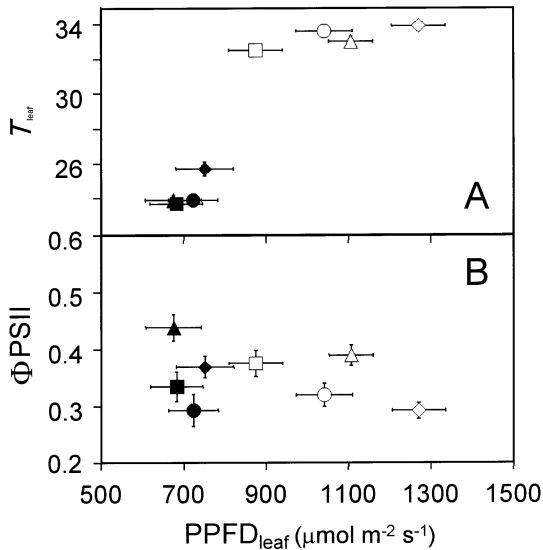
Figure 2. Mean values (± SE) of (A) leaf temperature (T_{leaf}; $n = 85$) and (B) quantum yield of noncyclic electron transport (Φ_{PSII}; $n = 45$–75) versus incident photon flux density ($PPFD_{leaf}$) at midday in current-year leaves of *Quercus coccifera* (●, ○), *Q. ilex* (■, □), *Pinus halepensis* (▲, △) and *Juniperus phoenicea* (◆, ◇) in summer 1996 (solid symbols) and 1997 (open symbols).

a relatively high A from mid-morning to midday resulted in significantly lower values of C_i (199 ± 13 mmol mol^{-1}; $P < 0.01$) than those observed in *Q. coccifera* (275 ± 21 μmol mol^{-1}), *Q. ilex* (247 ± 8 μmol mol^{-1}) and *J. phoenicea* (256 ± 16 μmol mol^{-1}).

Chlorophyll fluorescence parameters

Predawn F_v/F_m did not differ among species and ranged from 0.731 ± 0.009 to 0.785 ± 0.003 during 1996 and 1997 (Figure 4), except in *P. halepensis*, which had significantly higher predawn F_v/F_m values in 1997 (0.833 ± 0.002; $P < 0.05$).
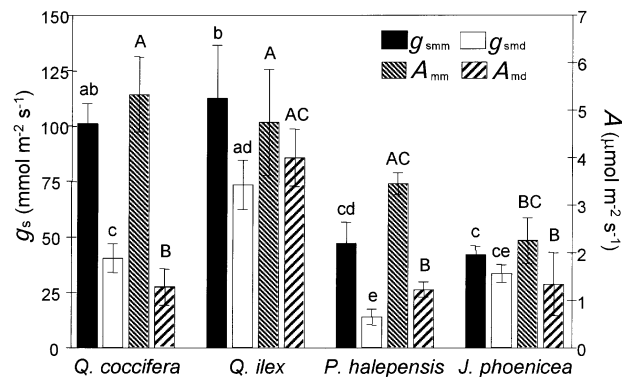

Figure 3. Mid-morning and midday stomatal conductance (g_{smm} and g_{smd}, respectively) and net CO_2 assimilation rate (A_{mm} and A_{md}, respectively) measured in leaves of *Quercus coccifera*, *Q. ilex*, *Pinus halepensis* and *Juniperus phoenicea* during summer 1997. Bars represent means ± SE ($n = 6$). Bars with different letters within a gas exchange variable are significantly different at $P < 0.05$.
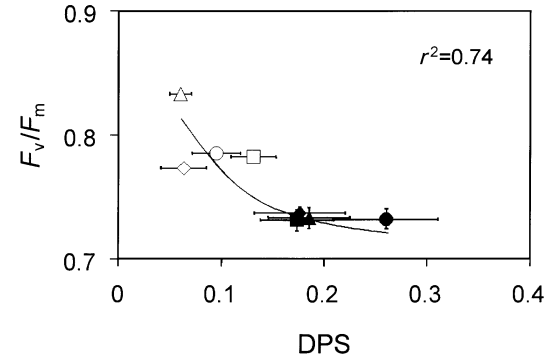

Figure 4. Relationship between the maximum photochemical efficiency of PSII (F_v/F_m) and de-epoxidation index (DPS) at predawn in leaves of *Quercus coccifera* (●, ○), *Q. ilex* (■, □), *Pinus halepensis* (▲, △) and *Juniperus phoenicea* (◆, ◇) in summer 1996 (solid symbols) and 1997 (open symbols). Each data point represents the mean ± SE ($n = 45$–75).

In all species in both years, there was a progressive and significant decrease in Φ_{PSII} ($P < 0.001$) from maximum values at predawn to minimum values at midday. Among these minimum Φ_{PSII} values, *P. halepensis* had significantly higher values ($P < 0.001$) than the other species in 1996, but had values comparable with those of *Q. ilex* in 1997 (Figure 5A). Species differences in midday Φ_{PSII} were not explained by differential light interception at midday (Figure 2B), nor by differential reductions in q_P (Figure 5B). However, the midday decline in Φ_{PSII} paralleled a marked decrease in F_v'/F_m' that was associated with an increase in q_N (Figure 5C). Midday values of F_v'/F_m' were significantly higher in *P. halepensis* than in the other species in both sampling years (0.605 ± 0.019 in 1996 and 0.563 ± 0.014 in 1997; $P < 0.001$). Among the species, *Q. coccifera* and *J. phoenicea* had the lowest midday values of F_v'/F_m'.

Pigment content and diurnal variation

There were no changes in Chl a + b concentration expressed on a leaf area basis between years (Figure 6). The concentration of Chl a + b in gymnosperms was consistently around half that in angiosperms ($P < 0.001$), but did not vary much within each group (Figure 6A). Although xanthophylls per chlorophyll unit showed a consistent tendency to increase in all species in 1997 (Figure 6B), VAZ did not differ among species within years ($P > 0.2$).

In 1996 and 1997, the sizes of the Chl a + b and VAZ pools did not vary from predawn to midday. Predawn de-epoxidation state (DPS) values were slightly higher in the cooler summer of 1996 than in 1997 (from 0.17 ± 0.04 to 0.26 ± 0.05 in 1996; and from 0.05 ± 0.02 to 0.13 ± 0.02 in 1997; Figure 4). However, within years, there were no significant differences in predawn DPS values between species. All of the species exhibited a highly significant ($P < 0.001$) diurnal increase in DPS, reaching maximum values at midday. No species differences were found in the degree of photo-conversion of epoxidized forms at midday (Figure 5D).
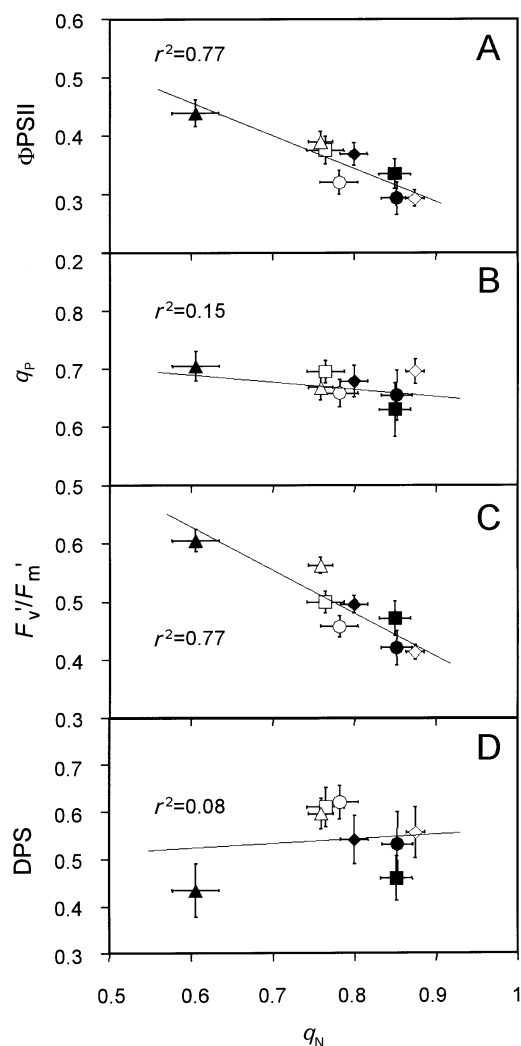
Figure 5. Relationship between non-photochemical quenching of fluorescence (q_N) and: (A) quantum yield of noncyclic electron transport (Φ_{PSII}), (B) photochemical quenching (q_P), (C) photochemical efficiency of the open reaction centers of PSII (F_v'/F_m') and (D) de-epoxidation index (DPS), at midday measured in leaves of *Quercus coccifera* (●, ○), *Q. ilex* (■, □), *Pinus halepensis* (▲, △) and *Juniperus phoenicea* (◆, ◇) in summer 1996 (solid symbols) and 1997 (open symbols). Each data point represents the mean ± SE (n = 45–75).
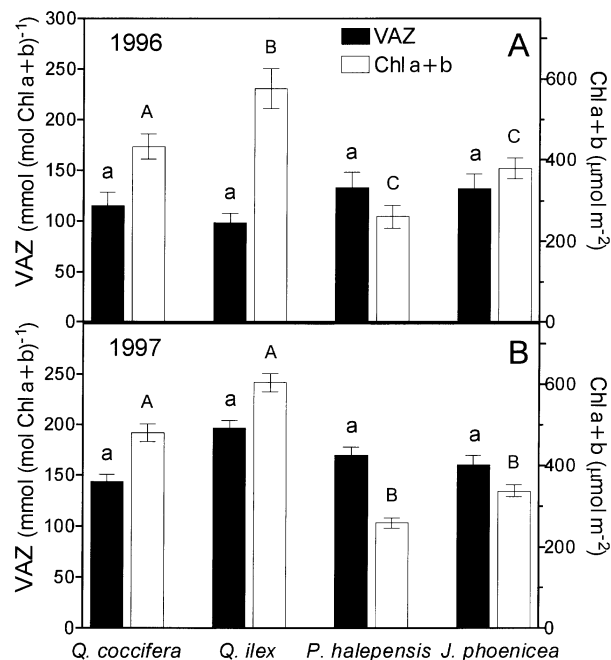

Figure 6. Pool of xanthophyll cycle pigments on a total chlorophyll basis (VAZ) and total chlorophyll concentration on a leaf area basis (Chl a + b) in leaves of *Quercus coccifera*, *Q. ilex*, *Pinus halepensis* and *Juniperus phoenicea* in (A) summer 1996 and (B) summer 1997. Bars are means ± SE (n = 18–27). Bars followed by different letters within a variable are significantly different at $P < 0.05$.

Discussion

The marked midday reduction in g_s in the absence of changes in Ψ_s indicates that *Pinus halepensis* behaved as a drought-avoiding species. Such behavior, previously observed in other taxa of this genus (DeLucia and Schlesinger 1991, Picon et al. 1996), contrasts with the drought-tolerance characteristics exhibited by the *Quercus* and *Juniperus* species. However, drought avoidance in *P. halepensis* was not associated with a higher susceptibility to dynamic photoinhibition at midday. On the contrary, *P. halepensis* exhibited higher midday values of photochemical efficiency of PSII (Φ_{PSII}) than the other species. Higher midday Φ_{PSII} in *P. halepensis* than in *Quercus* species has also been reported by Méthy et al. (1997). The

higher values of F_v'/F_m' in *P. halepensis* than in the *Quercus* and *Juniperus* species indicate that the low degree of photoinhibition observed in *P. halepensis* was associated with less severe photo-inactivation of PSII (cf. Genty et al. 1989).

Previous studies on crown architecture of woody species in Mediterranean environments have documented structural avoidance of excess light (Valladares and Pearcy 1997, 1998, Valladares 1999). However, in *P. halepensis*, the low sensitivity to photoinhibition exhibited by the needles was not the result of differentially lower light interception at midday. Both *Q. ilex* and *J. phoenicea* exhibited significantly more severe PSII photo-inactivation than *P. halepensis* even though their midday PPFD$_{leaf}$ values were lower and higher, respectively, than the midday PPFD$_{leaf}$ values of *P. halepensis*.

Furthermore, the lower sensitivity to photoinhibition observed in *P. halepensis* compared with the other species was not the result of a differential increase in the relief of electron pressure at the PSII acceptor site, because photochemical quenching was similar among the species (cf. Schreiber et al. 1994). However, the absence of such a difference might mask differences in photochemical flux partitioning among five possible destinations: (1) nitrate or sulfate reduction or both, (2) cyclic electron transport around PSII, (3) photosynthetic carbon assimilation, (4) CO_2 recycling associated with photorespiration, and (5) O_2 consumption by way of the Mehler reaction. With reference to these possibilities we note the following. First, the proposed role of increased allocation of the photochemical flux to nitrate or sulfate reduction as effi-

cient photo-protective mechanisms has been ruled out (Park et al. 1996). Second, protection against overexcitation of the reaction center could have been achieved by cyclic electron transport around PSII (Long et al. 1994, Allakhverdiev et al. 1997). Third, midday carbon assimilation in *P. halepensis* did not differ from that of *Q. coccifera* and *J. phoenicea*, suggesting that reduced mesophyll resistance ameliorated the effect of the low stomatal conductance on the photochemical flux to CO_2. Fourth, the maintenance of high photochemical efficiency might also result from sustained electron flux for recycling CO_2 derived from both photorespiration and mitochondrial respiration. The low intercellular CO_2 concentration observed in the needles of *P. halepensis* would have stimulated photorespiration as a result of a decline in the CO_2/O_2 ratio at the carboxylation sites. Thus, photorespiration and CO_2 recycling should channel a larger fraction of the photochemical flux in *P. halepensis* than in the other study species; however, we found that needle respiration and photorespiration were not stimulated by a rise in leaf temperature as a result of the low g_s. On the contrary, needle surface temperature remained close to air temperature, as observed in previous studies with conifers (Waring and Running 1976), and did not differ from the leaf surface temperatures of species with significantly higher stomatal conductances. Fifth, a higher photochemical efficiency of PSII could also be the consequence of electron flux to O_2. Previous reports have observed an increase in superoxide dismutase activity in *P. halepensis* during the summer months (Elvira et al. 1998). Nevertheless, this flux would be associated not only with an increased q_P but also with a high ΔpH-dependent radiation-less energy dissipation (Park et al. 1996).

Photo-protection of PSII in *P. halepensis* was not achieved by an increase in non-radiative energy dissipation (q_N), because q_N values in *P. halepensis* were lower than or not significantly different from those of the other study species. However, increased global values of q_N might result from different contributions of its components (Krause and Weis 1991). We found no evidence of a higher contribution of the quenching component associated with the xanthophyll cycle activity (q_E). Furthermore, all the study species showed similar midday values of DPS and VAZ. Moreover, in contrast to a previous report (Faria et al. 1998), we found no inverse relationship between VAZ size and photosynthetic capacity among species. On the other hand, the contribution of photoinhibited but intact reaction centers of PSII as quenchers of excitation energy (q_I) would result in a differential increase in q_N in those species (i.e., *Quercus* and *Juniperus*) that experienced more severe photo-inactivation of PSII. We found a positive correlation between the degree of PSII photo-inactivation and the value of q_N. Dynamic photo-inactivation has been viewed as a photo-damage avoidance mechanism that involves increased thermal dissipation of excess energy (Long et al. 1994). In this context, we note that midday q_N values in *P. halepensis* during the warmer and sunnier summer of 1997 were similar to those in *Quercus* species, even when the *P. halepensis* needles showed significantly less PSII photo-inactivation (significantly higher F_v'/F_m' values). This

finding indicates that non-photochemical mechanisms other than those associated with q_E and q_I might be of greater significance in *P. halepensis* than in the other study species. Previous studies of *Pinus* species have reported avoidance of photoinhibitory damage through decreases in chlorophyll contents in summer (Elvira et al. 1998) and through reversible reorganization of PSII and the light-harvesting chlorophyll complexes (Ottander et al. 1995). The low chlorophyll concentrations observed in *P. halepensis* in our study are consistent with the former mechanism. However, the daily recovery of the photochemical efficiency of PSII before dawn (i.e., maximum F_v/F_m at predawn) clearly contrasts with the several days required for full recovery from the quenched state through reversible reorganization of PSII (Ottander et al. 1995).

With the exception of *P. halepensis* during summer 1997, PSII efficiency did not return to optimum values before dawn in any species. However, the significant correlation observed between DPS and F_v/F_m before dawn ($r^2 = 0.74$; $P < 0.01$; Figure 4) suggests that the low PSII efficiency was probably the result of sustained energy dissipation activity associated with the xanthophyll cycle rather than the result of photodamage to the leaves. Retention of high DPS values overnight in association with a low F_v/F_m ratio has been attributed to the inhibitory effect of low temperatures on the enzymatic conversion of zeaxanthin and antheraxanthin to violaxanthin during winter (Adams and Demmig-Adams 1994, Adams et al. 1995). However, less attention has been paid to the ecological implications of low DPS values on maximum PSII efficiency at dawn. Our findings suggest that the low predawn DPS values observed in summer, which were similar to those reported in previous studies (Adams et al. 1995), resulted in a slight nocturnal quenching that persisted throughout the summer months.

Our results support the division of the study species into two groups on the basis of their mechanisms for coping with excess light during the midday depression of photosynthesis. Photoinhibition-avoiding species are able to avoid photoinactivation by maintaining a sustained PSII photochemical efficiency, whereas photoinhibition-tolerant species tolerate a more pronounced dynamic photoinhibition of PSII that is associated with high non-radiative energy dissipation. We did not obtain any information on the efficiency of these photo-protective strategies in avoiding permanent photodamage. We observed tolerance to photoinhibition in drought-tolerant and late-successional species. Previous studies have associated drought-tolerance with late-successional species that maintain high assimilation rates at midday (see Dreyer et al. 1993). However, our results in *Q. coccifera* and *J. phoenicea* indicate that tolerance to photoinhibition and drought was not linked to the maintenance of high midday photosynthetic rates. Avoidance of photoinhibition and drought was observed in *Pinus halepensis*, which has been described as a pioneer species (Méthy et al. 1997), and is consistent with the previously proposed relationship between drought avoidance and early successional behavior (Dreyer et al. 1993).

We conclude that co-occurring tree species do not share common mechanisms for withstanding the multiple stresses imposed by the Mediterranean summer. Differences in field photosynthetic performance at supra-saturating light intensities observed among *Q. ilex*, *Q. coccifera* and *J. phoenicea* were only quantitative; however, these species differed qualitatively from *P. halepensis*. Heterogeneity in the ecological behavior of evergreen trees under stress may be of great significance in describing the functional complexity of Mediterranean ecosystems and in helping to understand future changes in these ecosystems.

Acknowledgments

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