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Comparative field summer stress of three tree species co-occurring in Mediterranean coastal dunes

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Abstract

Chlorophyll *a* fluorescence, water potential (Ψ_s), and root system of *Juniperus oxycedrus* ssp. *macrocarpa*, *Juniperus phoenicea* ssp. *turbinata*, and *Pinus pinea* were studied in Mediterranean coastal dunes of SW Spain during summer drought and after fall rains in 1999, the driest year in the 90's. A strong and reversible depression in the photochemical efficiency of photosystem 2 of the three species was recorded, which happened concomitantly with the diurnal increase and decrease in radiation. *J. phoenicea*, with superficial root system, was the most affected species by summer drought. It showed high rates of down-regulation of photosynthesis by photoinhibition and positive correlation between Ψ_s and F_v/F_p, with Ψ_s lower than −7 MPa. However, it tolerated this high stress, showing a fast recovery of its physiological state after fall rains. On the other hand, *J. oxycedrus* and *P. pinea*, both with deep root systems, kept their Ψ_s values up to −3 MPa, showing lower stress during summer drought. On the other hand, *J. oxycedrus* and *J. phoenicea* were more sensible to changes in edaphic water content than *P. pinea*. These specific responses to summer drought would be determined by their root distributions and stomatal control of transpiration, conditioning the efficiency in getting and using the available water resources. Ecophysiological responses indicate that these species are well-adapted to long periods of drought in Mediterranean climate areas, developing different strategies: *J. phoenicea* tolerates high stress with a fast recovery after fall rains, while *J. oxycedrus* and *P. pinea* are less affected by summer drought since their deep root systems would allow them to reach deep water resources.

Additional key words: chlorophyll fluorescence; fall rain; *Juniperus phoenicea*; *Juniperus oxycedrus*; *Pinus pinea*; photoinhibition; root system; water potential.

Introduction

Mediterranean coastal dunes are highly diverse and variable environments, characterised by a strong seasonality, with warm and wet winters and hot and dry summers. Vegetation is exposed to high stress in summer caused by drought, large evaporative demand, and high irradiance at high temperatures (Figueroa *et al.* 1997, Fernández-Baco *et al.* 1998, Lloret *et al.* 1999).

In this context, drops in net photosynthetic rate have been described frequently in Mediterranean environments during summer (Lange *et al.* 1985, Damesin and Rambal 1995) provoked mainly by CO_2 uptake limitation (Tognetti *et al.* 2000). The fitness of Mediterranean species is determined by their capacities to confront summer drought. Many of them have adaptations such as midday stomatal enclosure (Tenhunen *et al.* 1987), high leaf mass per area (Levitt 1972), low leaf conductance for water vapour (Pugnaire *et al.* 1993), and deep rooting (Jeffrey 1987).

The South West Atlantic coastline of Spain is under Mediterranean climate, where *Juniperus oxycedrus* ssp. *macrocarpa* (Sibth. and Sm.) Ball (*Cupressaceae*), *Juniperus phoenicea* ssp. *turbinata* (Guss.) Nyman (*Cupressaceae*), and *Pinus pinea* L. (*Pinaceae*) coexist. These species show very contrasted distributions and conservation states in SW Iberian Peninsula: Nowadays, *J. oxycedrus* ssp. *macrocarpa* appears only in a few populations throughout the seaboard in the Gulf of Cadiz, with low seed cone production and low seed viability (Ortiz *et al.* 1998). Andalusia Government (1994) catalogues it as species in risk of extinction. On the other hand, *J. phoe-*

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Abbreviations: Chl = chlorophyll; F_p, F_0, F_v = peak, initial, and variable Chl fluorescence; PPFD = photosynthetically active photon flux density; PQ = plastoquinone; PS = photosystem; SEM = standard error of mean; $T_{1/2}$ = half-rise time for peak fluorescence; Ψ_s = stem water potential.

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nicea ssp. *turbinata* is a typical species from semi-dry Mediterranean climate, appearing on mountains (Arista and Ortiz 1995, Arista *et al.* 1997) and on stable coastal dunes, where juniper woodlands represent the original ecosystem (Granados *et al.* 1988). Nowadays, due to human influence, *J. phoenicea* ssp. *turbinata* only occupies negligible areas. The third species, *P. pinea*, appears throughout the coast of SW Spain in large afforestations started in 18th century (Granados *et al.* 1987). At the moment, it is increasing its distribution by natural seed dispersion (Muñoz 1997). However, there are no comparative studies about the ecophysiology of these three tree species.

The aim of this study was to analyse stress levels, water status, and root system of these Mediterranean tree species in an extreme summer and after fall rains, to obtain a better understanding of their levels of summer drought tolerance. Chl *a*-fluorescence was used, together with water potential measurements, since stress measured as changes in Chl fluorescence provides a valuable non-destructive window into the physiological status of plants in the field (Castillo *et al.* 2000). Furthermore, root distribution was recorded in the three species to explore their possibilities of water uptake.

Materials and methods

Study area: This study was carried out in the natural reserve "Enebrales de Punta Umbría" located in Southwest Iberian Peninsula (37°13´N, 6°57´W; altitude 0-15 m a.s.l.). It is a prograding coastal dune system parallel to the coastal line with an eolic origin. Soils contain *ca.* 92 % of sand, have acid pH of 5.5, and poor nutrient contents (0.1 % C and 0.02 % N).

This area is under Mediterranean climate. Irradiance and temperature are high during summer (August mean temperature is 25 °C; highest temperatures reach 40 °C), with practically no rainfall between June and September, whereas winters are wet and mild (January mean temperature is 11 °C; frosts do not occur most years). Mean annual rainfall is *ca.* 505.6 mm with a variation coefficient of 31 % (Nieva and Luque 1995). The vegetation is composed of the trees *J. oxycedrus* ssp. *macrocarpa*, *J. phoenicea* ssp. *turbinata*, and *P. pinea*.

Environmental matrix: Climatic values were obtained from Punta Umbría meteorological station (n° 555), about 2 km from the research site (37°10´N, 6°57´W; altitude 5 m a.s.l.). Air temperature and relative humidity (*Elka FTM10* thermohygrometer, Lüdenscheid, Germany) (n = 2), potential evapotranspiration (Piche´s evaporimeter, *Wilh. Lambrecht*, Göttingen, Germany) (n = 2), relative soil humidity (*Rotronic M1* thermohygrometer, Huntington, USA) in surface (0-5 cm) and depth (5-20 cm) (n = 2), and PPFD (quantum sensor meter *LiCor LI-189*, Lincoln, USA) were measured at the same time as Chl fluorescence.

Chl *a* fluorescence of intact leaves were measured using a portable non-modulated fluorimeter (Plant Stress Meter, *PSM Mark II, Biomonitor S.C.I.,* Umeå, Sweden) and a white lightweight clamp cuvette (*Biomonitor 1020*) for dark adaptation (Bolhàr-Nordenkampf *et al.* 1989, Mohammed *et al.* 1995). Leaves were dark pre-treated for 30 min before measurement. The Chl fluorescence transit over 2 s was determined after an actinic pulse of 400 µmol m^{-2} s^{-1}. All measurements at a sampling time were made on adult leaves with the same orientation to avoid possible effects of microclimatic variations.

Measurements were made in 8 randomly chosen trees per species, with 3 measures per tree (n = 24), at the prevailing air temperature in the field, every 2 h from predawn to sunset on 21 July, 29 August, 30 September, and 30 October 1999.

Initial fluorescence (F_0) was determined when all photosystem 2 (PS2) reaction centres were in an "open" state. F_0 depends on the size of PS2 Chl antenna and on the functional integrity of PS2 reaction centres (Krause and Weis 1991). Superimposing a flash of actinic radiation yielded a peak of fluorescence (F_p) dependent on the level of actinic stimulation. Variable fluorescence (F_v) was determined as the change in florescence emission between the two defined states, F_0 and F_p. The half time for the transition from F_0 to F_p ($T_{1/2}$) was determined, and it has been used to determine the effective size of PQ pool (Bolhàr-Nordenkampf and Öquist 1993). The ratio of variable to peak Chl fluorescence [$F_v/F_p = (F_p - F_0)/F_p$] was used as an estimate of optimal photochemical efficiency of PS2 (Björkman and Demmig 1987, van Kooten and Snel 1990). This ratio correlates with the number of functional PS2 reaction centres (Öquist *et al.* 1992) and has been used to quantify photoinhibition (Krivosheeva *et al.* 1996).

Pre-dawn and midday stem water potential (Ψ_s) was measured, together with Chl fluorescence, in stems of the 3 species (n = 6), similar in maturity to those chosen for Chl fluorescence, using a pressure bomb (*Manofrigido*, Lisbon, Portugal) according to Scholander *et al.* (1965).

Root distribution and the existence of vertical deep roots was explored by digging 55 cm deep hole at the base of one tree of every species on 13 February 2001, and the number and distribution of horizontal and vertical roots were recorded using a direct counting method with a grid of 5×5 cm (Böhm and Köpke 1977, Virginia and Jarrell 1987). Caudal roots were digged until 1.5 m in depth.

Statistical analysis was carried out using the *Statistica* version *5.1* (*Statsoft*). Pearson correlation coefficients were calculated between environmental and physiological variables. Physiological and root measurements were compared between and within species by one-way analysis of variance (*F*-test). Data were tested for normality with the Kolmogorov-Smirnov test ($p<0.05$) and homogeneity of variance with the Levene test ($p>0.05$). Values were transformed when it was necessary by *arcsin* function. Differences in water potential between predawn and midday in every species were compared by the Student test (*t*-test).

Results

Climate and environmental matrix: The annual rainfall from September 1998 to September 1999 was 254 mm (21.2 mm per month) which led to the driest year in the 90's. The two first samples, in July and August 1999, were carried out under summer drought and high temperatures, while the two last samples, in September and October 1999, started 11 d after the first autumn rainfall (19 mm in September and 140 mm in October). Environmental variables at midday varied from summer to fall. Maximum air temperature occurred in July (31.7± 1.1 °C), and decreased gradually until October (26.9± 0.3 °C). Air relative humidity increased from July (49.0±1.1 %) to September (53.2±0.7 %). Potential evapotranspiration fluctuated between 1.5±0.1 mm in August and 0.7±0.1 mm in September. Soil relative humidity at surface (0-5 cm) increased in October by *ca.* 20 % compared with the other samples, and at depth (5-20 cm) achieved seasonal minimum in August (74.0±1.0 %), then increased progressively until October (84.0±0.4 %). PPFD increased from dawn to midday, decreasing during the evening. The maximum oscillated between 2 000 μmol m^{-2} s^{-1} in July and 1 400 μmol m^{-2} s^{-1} in October (Fig. 1).

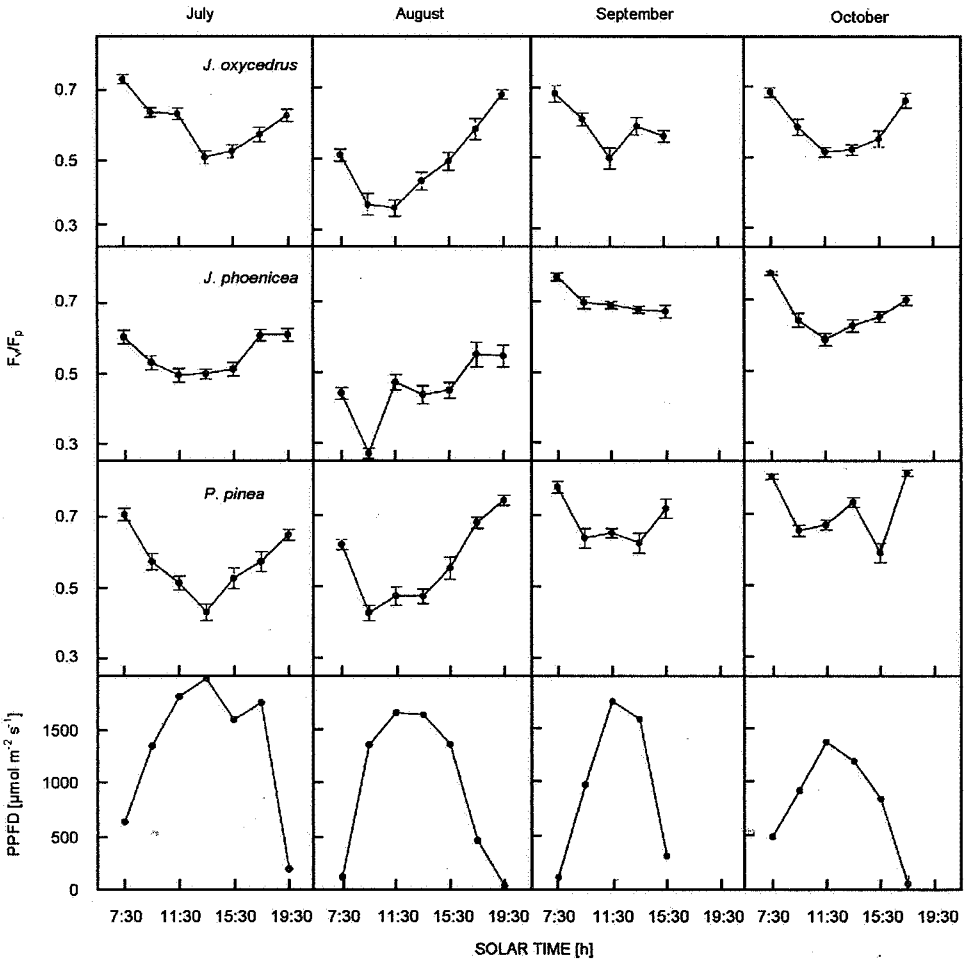

Fig. 1. Diurnal time course of changes in photochemical efficiency (F_v/F_p) ($n = 24$) in *Juniperus oxycedrus*, *Juniperus phoenicea*, and *Pinus pinea*, and photosynthetically active photon flux density (PPFD) [μmol m^{-2} s^{-1}], from July to October 1999. Vertical bars indicate ±SEM.

Chl fluorescence: The three tree species showed a significant midday depression of photochemical efficiency. This drop in F_v/F_p was lower after autumn rainfalls than under summer drought. In summer, F_v/F_p depression was higher in *J. oxycedrus* and *P. pinea* than in *J. phoenicea*, with a decrease of 30-40 and 20 %, respectively, as compared to morning values. Recovery started as soon as PPFD began to fall in the evening in every species (Fig. 1). F_v/F_p showed a negative correlation with PPFD in *J. oxycedrus* ($r = -0.53$, $p<0.01$) and *P. pinea* ($r = -0.74$, $p<0.001$), but not in *J. phoenicea* ($r = -0.38$, $p<0.06$).

F_v/F_p values at dawn, midday, and sunset under summer drought were lower than those raised after autumn rainfalls in the three species (*Anova*; $p<0.0001$ in all cases). On the other hand, F_v/F_p at dawn was lower in *J. phoenicea* than in the other two species in July ($F_{2,66} = 8.14$, $p<0.001$) and August ($F_{2,66} = 30.00$, $p<0.0001$). These differences in F_v/F_p decreased at midday, when the three species achieved their minimum (*ca.* 0.4) (Fig. 1).

Both F_0 and F_v reached their minimum under summer drought and their maximum after rainfalls. F_0 values were very constant throughout the day in every species (*ca.* 0.15), with a slight increase in August. On the other hand, F_v tended to decrease at midday, except in *J. phoenicea* in August. In *P. pinea*, F_v was higher in August, September, and October than in *Juniperus* species (*Anova*; $p<0.0001$ in all cases) (Fig. 2).

$T_{1/2}$ values raised to maximum after fall rains, increasing significantly from August to October in the three species (*Anova*; $p<0.001$). The highest oscillations in $T_{1/2}$ throughout the day in *J. oxycedrus* and *P. pinea* were recorded under summer drought, while in *J. phoenicea* this occurred in September and October (Fig. 3).

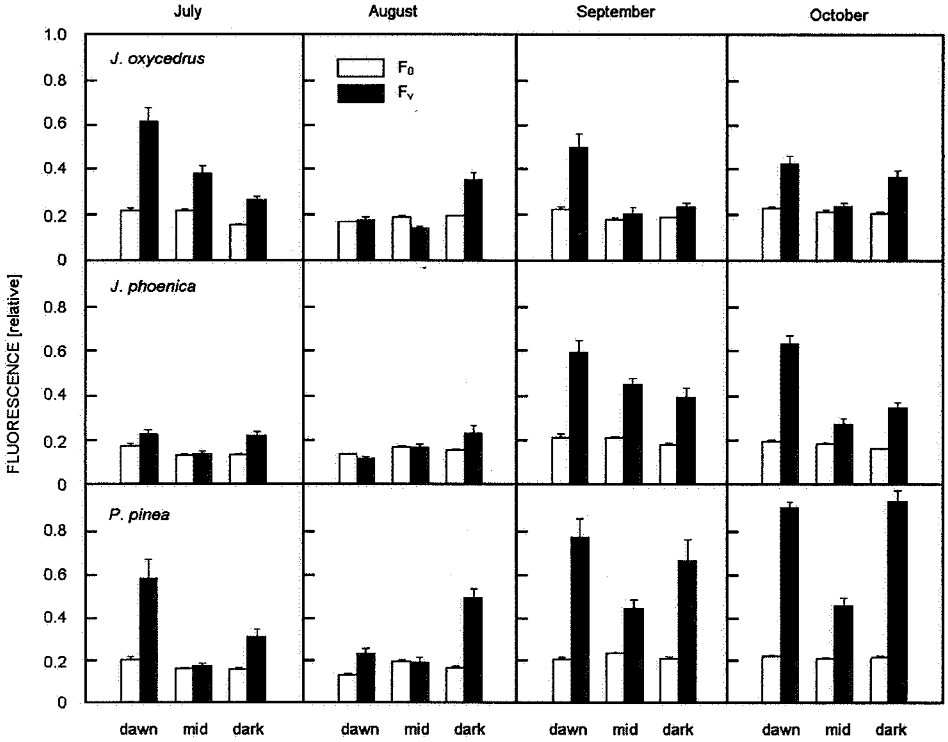

Fig. 2. Changes in initial fluorescence (F_0) and variable fluorescence (F_v) in *Juniperus oxycedrus*, *Juniperus phoenicea*, and *Pinus pinea* at morning, midday and evening ($n = 24$), from July to October of 1999. Vertical bars indicate ±SEM.

Water potential: In *J. oxycedrus*, Ψ_s showed a slight increase from July to October, more pronounced at midday ($F_{3,19} = 14.12$, $p<0.0001$) than at pre-dawn ($F_{3,21} = 6.38$, $p<0.01$). Ψ_s at midday oscillated between −2.9 and −1.8 MPa. Differences between pre-dawn and midday were constant (*ca.* 1 MPa) and larger than those recorded in *J. phoenicea* in July and August, and in *P. pinea* during the whole study (Fig. 4).

In *J. phoenicea*, Ψ_s showed a high positive correlation with F_v/F_p ($r = 0.73$, $p<0.0001$, $n = 62$). Thus, Ψ_s decreased in August to values lower than −7.0 MPa, coinciding with the lowest F_v/F_p values, to surpass its initial values after the rains, together with an increase in F_v/F_p. *J. phoenicea* showed lower Ψ_s values than *J. oxycedrus* and *P. pinea* in July ($F_{2,22} = 12.74$, $p<0.001$) and August ($F_{2,31} = 13.01$, $p<0.0001$). After autumn rainfalls, Ψ_s values decreased significantly at midday, compared with pre-dawn values ($t_{24} = 6.51$, $p<0.0001$) (Fig. 4).

In *P. pinea*, Ψ_s showed a positive correlation with F_v/F_p ($r = 0.27$, $p<0.05$, $n = 61$). Ψ_s at midday did not vary monthly, with values of *ca.* −2 MPa. Ψ_s showed significant differences between pre-dawn and midday only in October ($t_{12} = 5.56$, $p<0.01$) (Fig. 4).

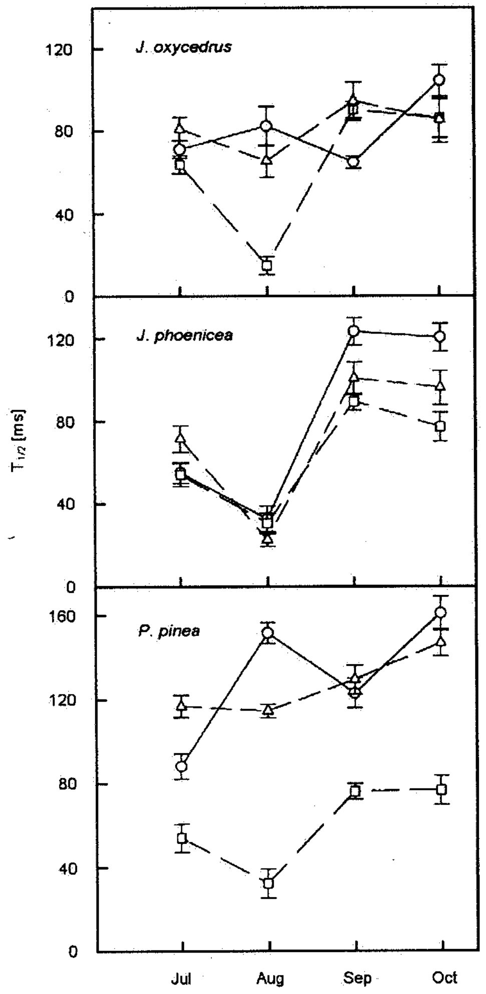

Fig. 3. Changes in $T_{1/2}$ [ms] in *Juniperus oxycedrus*, *Juniperus phoenicea,* and *Pinus pinea* at dawn (○), midday (□), and sunset (Δ) ($n = 24$), from July to October of 1999. Vertical bars indicate ±SEM.

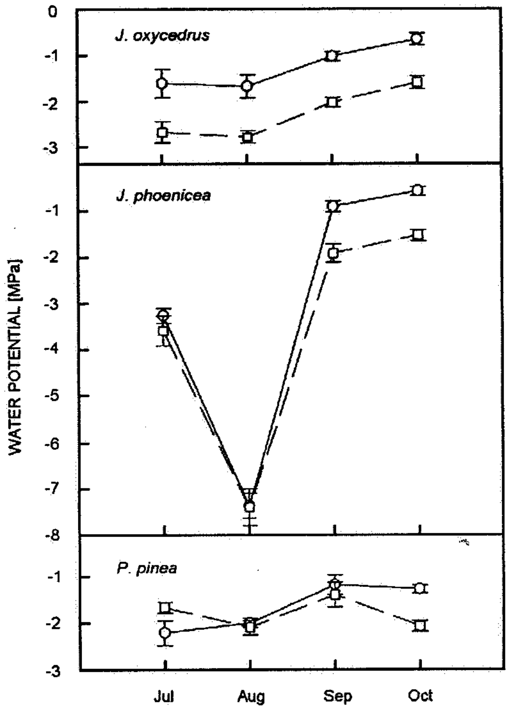

Fig. 4. Changes in stem water potential [MPa] in *Juniperus oxycedrus*, *Juniperus phoenicea,* and *Pinus pinea* at morning (○) and midday (□) ($n = 6$), from July to October of 1999. Vertical bars indicate ±SEM.

Root distribution: In *J. phoenicea*, most of the horizontal roots were located between 35 and 45 cm in depth, without showing any caudal root. In contrast, in *J. oxycedrus* and *P. pinea ca.* 70 % of horizontal roots were located between 0-15 cm, vertical caudal roots appearing deeper than at 1.5 m in both species (Fig. 5).

Discussion

A strong and reversible depression in the photochemical efficiency of PS2 of three Mediterranean tree species was recorded in the field, which happened concomitantly with the diurnal increase and decrease in radiation. This depression is believed to be dynamic photoinhibition (Epron *et al.* 1992, Figueroa *et al.* 1997), gradual and reversible so as not to damage the photosystems permanently (Long *et al.* 1994).

This reversible depression of F_v/F_p at midday was due, in the three species, to a quenching in F_0 and F_v. It has the characteristics of an increase in the rate of radiation-less energy dissipation in the antenna pigments, which should be accompanied by an increase in zeaxanthin content or other quenching mechanisms (Demmig-Adams *et al.* 1989, Schindler and Lichtenthaler 1994). This depression in F_v/F_p at midday was not exclusively due to irradiance, but to its interactions with other stress factors such as high temperature and drought. Thus, drop in F_v/F_p at midday was higher, under the same irradiance, in August than in September in every species. It was higher than 40 % of 0.835, the value for unstressed plants of many species measured at low irradiance (Björkman and Demmig 1987). In plants not subject to any other stress, the fluctuations in irradiance during the days in this study would be expected to result in dynamic photoinhibition that should decrease this value by 15-20 % (Ögren and Rosenqvist 1992, Krause and Winter 1996, Fernández-Baco *et al.* 1998).

Thus, this work points out that environmental factors such as summer drought, high temperature, and high irradiance have a substantial effect on the performance of photosynthetic apparatus of the three species under study. However, every species showed different strategies to face summer drought.

J. phoenicea was the species most affected by summer drought, showing F_v/F_p values lower than those recorded after fall rains and for *J. oxycedrus* and *P. pinea*. These low values of F_v/F_p, even at dawn, together with low records in $T_{1/2}$ throughout the day under summer drought indicate down-regulation of photosynthesis by photoinhibition, with a reduction in the transmission of energy between photosystems (Bolhàr-Nordenkampf *et al.* 1991). At this time, the main useful ways to divert energy were related to non-photochemical deactivation mechanisms such as thermal deactivation in the inactive PS2 reaction centres and to xanthophylls (Long *et al.* 1994, Griffiths and Maxwell 1999). In *J. phoenicea* these low morning F_v/F_p values led to a less pronounced reduction of this ratio, as a response to oscillation of radiation throughout the day, than in the other two species which achieved higher F_v/F_p values at dawn.

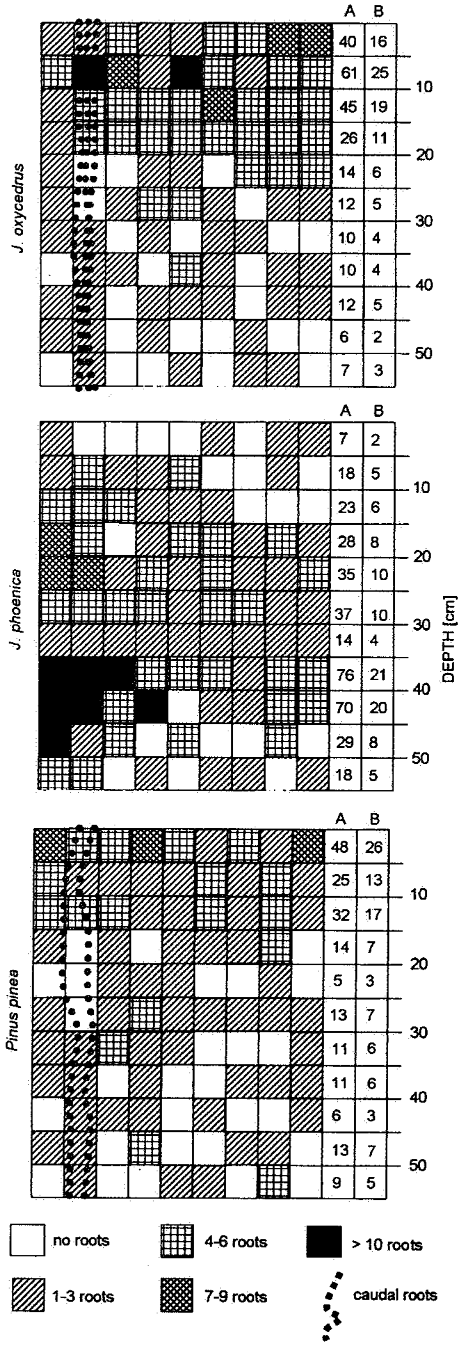

Fig. 5. Root density and distribution of *Juniperus oxycedrus*, *Juniperus phoenicea*, and *Pinus pinea*. A = number of roots; B = % of roots.

The low Ψ_s values recorded throughout the days in *J. phoenicea* in summer (*ca.* –7.5 MPa), and the positive correlation of these with the photochemical efficiency point, together with high irradiance, to summer drought as the main cause of photoinhibition. In this sense, other authors have pointed out in different *Juniperus* species that gas exchange is strongly influenced by water stress (Miller and Shultz 1987, Miller *et al.* 1993, Moore *et al.* 1999). The Ψ_s values obtained for *J. phoenicea* are similar to that reported for *Juniperus* sp. by Scholander *et al.* (1965) and lower than those reported for this species on littoral sandy dunes in the Camargue (France) during summer (Berger and Heurteaux 1985). They could be due to a relative inability of their stomata to restrict water loss when soil water resources are limited, as Miller *et al.* (1993) pointed out in *Juniperus occidentalis*, and to a limitation of water uptake to soil surface as shown by the lack of deep roots. The absence of marked diurnal variations in water potential during drought and the fairly fast response to new input of soil moisture in *J. phoenicea*—recorded 11 d after first fall rain—agree with records of a shallow root system (Gucci *et al.* 1997). Martínez García and Rodríguez (1988), Martínez García *et al.* (1998), and Tsiourlis (1992) suggested that the root biomass of this species is superficial. In this species both a superficial root system deep enough to avoid soil surface, where dehydration and temperatures are high during summer, and reduction of transpiration surface by shedding of leaves were observed (Lansac *et al.* 1994, Streb *et al.* 1997). They or the xeromorphic structure of leaves (Miller and Shultz 1987) probably have some survival value under summer drought. *J. phoenicea* is a well-adapted species to the seasonality of Mediterranean climate, showing fast restoration of its physiological activities in response to pulses of water, similar to other species in arid environments (Lebkuecher and Eickmier 1993, Pugnaire *et al.* 1996) and to *Juniperus communis* (Tognetti *et al.* 2000).

J. oxycedrus and *P. pinea*, both with deep vertical roots and abundant superficial roots, were less affected by summer drought. They kept their midday Ψ_s greater than –3.0 MPa and down-regulation of photosynthesis by photoinhibition was much lower than in *J. phoenicea*.

On the other hand, larger daily and monthly variations in Ψ_s for *J. oxycedrus* and *J. phoenicea* point out that these species are more sensible to changes in soil water content than *P. pinea*, probably due to a relative inability to control water loss by their stomata (Miller *et al.* 1993) and to a superficial root system in *J. phoenicea* (Lansac *et al.* 1994). *P. pinea* kept its Ψ_s of *ca.* –2 MPa, similar to *Pinus edulis, Pinus sylvestris,* and Mediterranean evergreen sclerophylls under summer drought, which is probably associated with a deep root system (Hellkvist and Parsby 1976, Oliveira *et al.* 1992, Lansac *et al.* 1994, Werner *et al.* 1998) and osmotic adjustment and high stomatal restriction of transpiration (Beadle *et al.* 1985, Linton *et al.* 1998).

This work shows that different co-occurring tree species, even related species of the same genus, have contrasted strategies to face summer drought in Mediterranean costal dunes of SW Spain. *P. pinea* and *J. oxycedrus* try to avoid water stress with deep roots, while *J. phoenicea* sustains high stress with very low water potential during drought, showing a fast recovery after fall rains.

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