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Does *Pinus halepensis* facilitate the establishment of shrubs in Mediterranean semi-arid afforestations?

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Abstract

Aleppo pine (*Pinus halepensis*) dominates forest ecosystems in dry and semi-arid areas of the Mediterranean Basin. In addition to its natural distribution, this species has been used extensively in afforestation projects during this century. The improvement in soil fertility and microclimate provided by the *P. halepensis* canopy is known to facilitate the establishment of perennial grasses, but little is known about the interactions of this species with woody species in natural stands and afforestations under semi-arid climate. In this study, we analyze the effects of the *P. halepensis* canopy on the survival and ecophysiological features of experimentally planted seedlings of several Mediterranean shrub and tree species in two semi-arid afforestations of SE Spain.

Soils under *P. halepensis* (pine microsite) showed small differences in nutrient content relative to those outside the canopy (open microsite). Radiation reaching pine microsites was four times lower than in open microsites. Soil moisture did not show significant differences between both microsites during most of the year. One year after planting, survival of the introduced seedlings was significantly higher in the open microsites than in the pine microsites. Predawn and midday water potentials and chlorophyll fluorescence of seedlings measured before the summer did not show any microsite effect. Our results suggest that the changes in understorey microclimate associated with *P. halepensis* are not sufficient to facilitate the establishment of shrubs under semi-arid conditions.

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1. Introduction

Changes in resource flow and microclimate conditions resulting from plant growth have long been recognized (Zinke, 1962; Rhoades, 1997; Binkley and Giardina, 1998). Through these changes, some plant species can affect inter-specific interactions (Morris and Wood, 1989; Callaway, 1995) and com-

munity composition and dynamics (Connell et al., 1987; Holmgren et al., 1997). The identification of these species and of the mechanisms involved in the changes that they generate is a question of great interest (Jones et al., 1997). Facilitative interactions between plants have been identified as one of the main processes affecting community structure and composition (Bertness and Callaway, 1994). Facilitation has been mainly described under harsh environmental conditions, such as those prevailing in arid and semi-arid environments. In these areas, positive interactions between plants are mediated by a combination

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of differences in microclimate, soil fertility, water availability and substrate modification (Callaway, 1995).

One of the most important forest species in the Mediterranean Basin is the Aleppo pine (*Pinus halepensis* Miller). This species is the most widely distributed pine in this region, where it covers more than 25,000 km² and dominates the forest formations in semi-arid and dry areas (Quézel, 2000). It is also expanding as an alien in some areas of the Southern Hemisphere (Richardson and Higgins, 1998). *Pinus halepensis* has been extensively planted in the western Mediterranean Basin during this century, because it is a pioneer drought-resistant species that can survive in a wide range of conditions (Barbéro et al., 2000; Quézel, 2000). In the Iberian Peninsula alone, over 43% of current *P. halepensis* forests derive from afforestations (Vélez, 1986). Many of the afforestations performed in semi-arid areas have replaced woody Mediterranean shrublands, dominated by species such as mastic tree (*Pistacia lentiscus* L.) and kermes oak (*Quercus coccifera* L.), with *P. halepensis* monocultures. These plantations often result in slow-growing stands that have not increased vegetation cover significantly (Chaparro and Esteve, 1996), and that suffer from frequent insect plagues (Mendel et al., 1997). In addition, *P. halepensis* afforestations have a high frequency of fires (Agee, 2000), one of the main factors that influence the increase in erosion and desertification rates worldwide (Thornes, 1990). In Spain alone, 26% of the area burned during the 1974–1994 period (4.6 million hectares) corresponds to *P. halepensis* afforestations (Moreno, 1999).

Isolated trees and shrubs can play a relevant role in the colonization of Mediterranean lands because they can change microclimatic and soil conditions and because they attract seed-disperser birds (Herrera, 1984). *Pinus halepensis* can improve soil fertility (Kutiel and Naveh, 1987) and structure (Cerdà, 1998). The improved soil conditions, together with shading, can facilitate the establishment of grasses under its canopy (Bautista, 1999). A positive relationship between holm oak (*Quercus ilex*) seedlings and *P. halepensis* trees has been reported under dry Mediterranean conditions (Lookingbill and Zavala, 2000), although this may not always be the case (Vilagrosa et al., 1997). On the other hand, pine canopies intercept and redistribute rainfall (Bellot and Escarré, 1991), and they may have

relatively shallow rooting systems (Breshears et al., 1997); thus, the surface soil under the canopy of pine individuals could be drier than the surroundings. To our knowledge, direct tests for facilitation under the canopy of *P. halepensis* have not yet been conducted in either natural stands or afforestations.

Facilitative interactions can be used for the introduction of shrubs into degraded semi-arid ecosystems (Maestre et al., 2001). The introduction of these species in *P. halepensis* afforestations could stimulate successional processes, increase diversity, improve ecosystem resilience against disturbances, and have a positive effect on faunal communities (Cortina and Vallejo, 1999; Vallejo et al., 1999, 2000). The main objective of this study is to evaluate the effect of *P. halepensis* on the establishment of native woody species in semi-arid afforestations. To achieve this objective, we carried out experimental plantings of shrubs and trees under the canopy of *P. halepensis* and in the inter-canopy areas, and assessed the performance of introduced seedlings in terms of survival and ecophysiological response. Our initial hypothesis was that the microsite provided by *P. halepensis* could facilitate the establishment of shrubs. We expected that water use and rainfall interception by *P. halepensis* could be offset by stemflow inputs, by reduced evaporation due to shading, and by higher infiltration capacity under the pine canopy. In addition, *P. halepensis* was expected to enhance soil nutrient content and improve soil structure by adding organic matter to the soil under its canopy. We thus interpreted that an improvement in the performance of seedlings planted under the *P. halepensis* canopy would indicate the prevalence of facilitation over competitive interactions.

2. Methods

2.1. Study area

We conducted our study in two 30-year old Aleppo pine (*P. halepensis*) afforestations located in the province of Alicante, in SE Spain (Orgegia site 38°23'N, 0°28'W, 80 m a.s.l.; Xirau site 38°26'N, 0°37'W, 320 m a.s.l.). The two sites have a Mediterranean semi-arid climate, with a 30-year average annual precipitation of 302 mm (Xirau) and 358 mm (Orgegia), and an average

annual temperature of 18 °C (Pérez Cueva, 1994). The pines were planted during the early 1970s, using seedlings of a Spanish provenance. They were planted in a uniform pattern, with a between-row distance of 5.6 ± 0.4 and 4.8 ± 0.6 m, and a between-tree distance of 3.8 ± 1.8 and 2.3 ± 1.3 m in Orgegia and Xirau, respectively (mean \pm S.D., $n = 12$). Most trees are poorly developed and are less than 3 m in height. Understorey vegetation is sparse and composed mainly of the perennial sprouting grass *Brachypodium retusum* (Pers.) P. Beauv., which concentrates underneath the canopy of *P. halepensis*, as well as several isolated individuals of common Mediterranean shrubs such as *Globularia alypum* L., *P. lentiscus*, and *Q. coccifera*. There is no evidence of spontaneous colonization by sprouting shrubs from the thorny shrubland community. Most of the inter-canopy area is covered with a biotic crust consisting of lichens and cyanobacteria.

2.2. Species employed

We selected three Mediterranean sprouting shrubs (*Q. coccifera*, *P. lentiscus* and *Rhamnus lycioides* L.) and one Mediterranean tree (*Ceratonia siliqua* L.) for the experiment. The carob tree (*C. siliqua*) is a drought-resistant species that forms part of the Mediterranean evergreen sclerophyllous shrublands in coastal areas (Tomaselli, 1981). The mastic tree (*P. lentiscus*) belongs to climax semi-arid shrublands in coastal areas (Tomaselli, 1981). It forms tall, dense-leaved shrubs that tend to develop a compact cushion-like canopy, thereby shading and protecting the soil and creating favorable conditions for litter decomposition, humus formation and biological soil enrichment. Kermes oak (*Q. coccifera*) is a tall shrub that characterizes the garrigue-type shrublands in the Western Mediterranean (Tomaselli, 1981) and is especially abundant in the semi-arid shrublands of SE Spain (Rivas Martínez, 1987). It is able to resprout after fire (Lloret and Vilà, 1997) and develop a deeply-penetrating root system that allows the plant to reach deep soil water reserves (Rambal, 1984). Like the former species, *R. lycioides* belongs to the Mediterranean macchia and can thrive in areas with average annual precipitation below 300 mm (Tomaselli, 1981).

Seeds were collected from local provenances in the Valencia Region (E Spain) by the local Forest Services

(Forest Seed Bank, Conselleria de Medio Ambiente, Generalitat Valenciana). Before planting, seedlings were grown in the open air in a nursery for 9 months in 330 ml containers (Roottrainer Ash limited, Roxburghshire, Scotland) with a mixture of peat, coconut fiber, and sand as the growing medium (50, 45 and 5%, respectively). Slow-release fertilizer (Osmocote plus, The Scotts Company, Columbus, OH, USA) was also included in the mix.

2.3. Experimental design

We conducted experimental plantings in 1998 and 1999 at two sites (Orgegia and Xirau) representative of typical *P. halepensis* afforestations performed under Mediterranean semi-arid conditions. In 1998, we used three species (*P. lentiscus*, *R. lycioides*, and *C. siliqua*); in 1999, we used two species (*P. lentiscus* and *Q. coccifera*). In both experiments, we selected two types of planting microsites: pine and open. The pine microsite refers to the planting points located under the canopy of *P. halepensis* individuals (one planting point per individual). The open microsite refers to the planting points located in the inter-pine areas outside the crown projection. Within each site, we prepared 300 (1998) and 140 (1999) replicated planting points per microsite, and we randomly assigned each species to them (100 and 70 planting points per each combination of species, microsite and site in 1998 and 1999, respectively). We also characterized soil properties and recorded microclimatic conditions in order to explore the potential mechanisms behind the interactions between *P. halepensis* and the introduced seedlings.

Site preparation was done manually in autumn 1998 and 1999. It consisted in digging a 25 cm \times 25 cm \times 25 cm hole to avoid soil disturbance and damage to pine roots as much as possible. We planted the seedlings in late autumn (December 1998 and 1999). The 1998 experiment was conducted under natural conditions with no watering or weeding. In the 1999 experiment, seedlings were irrigated with an equivalent of 10 mm rainfall 3 weeks after planting. This paper reports seedling-response results for the first year after planting, as this time period is crucial for the establishment of woody Mediterranean species (Vilagrosa et al., 1997; Rey Benayas, 1998; Maestre et al., 2001).

2.4. Microsite characterization

In early autumn 1998, we sampled ten 20 cm deep soil cores per site and microsite. In each sample, we determined total N content (Kjeldahl method; [Bremner and Mulvaney, 1982](#)), organic C content (Walkley-Black method; [Nelson and Sommers, 1982](#)), total carbonate content (Bernard calcimeter method; [Nelson, 1982](#)), soil particle distribution (pipette method), and pH (in a 1:2.5 w:v soil and water suspension). We measured the midday (12:00–13:00 h solar time) solar radiation at the two sites on 15 August 1999. We randomly selected 20 points per microsite and site, and we measured photosynthetic active radiation (PAR) radiation as the average of 10 instantaneous measurements at a height of 20 cm using a ceptometer (model Sunfleck, Decagon, Pullman, Washington, USA). Additional PAR data were taken during the ecophysiological survey (see below). During the year 2000, we measured soil moisture monthly at the two experimental sites. We randomly selected five planting holes for each sampling date, and we determined the gravimetric soil moisture at two depths (0–10 and 10–20 cm). Water interception was measured during September–November 2000 in the Orgegia site. Six small rainfall gauges with a recording capacity of 35 mm were located under the canopy of randomly selected pine and open microsites, and the amount of water in each was recorded within 24 h of each rainfall event. On 16 October 2000, a strong rainfall (65 mm) filled all the rainfall gauges; thus, the data for this event are missing.

2.5. Seedling response

We used seedling survival, water status, and chlorophyll fluorescence as response variables to evaluate seedling response to microsite. Survival was recorded four times during the first year after plantation in the two experimental plantings (January, May, October and December). We carried out physiological measurements during late spring 2000 (chlorophyll fluorescence and xylem water potentials) on introduced seedlings in the Xirau site (1999 plantation). Five individuals per microsite and species were randomly selected for these measurements.

We measured predawn and midday (12:00–13:00 h solar time) xylem water potential in situ on small

terminal shoots using a pressure bomb (Soilmoisture Corp., Santa Barbara, CA, USA). Chlorophyll fluorescence was measured by using a portable, pulse-modulated fluorometer (PAM-2000, Walz, Effeltrich, Germany), equipped with a leaf clip holder (2030-B; Walz) and a micro-quantum sensor to measure incident PAR. Predawn and midday (11:00–13:00 h solar time) measures of maximal (F_m) and minimal (F_0) fluorescence were used to calculate maximum efficiency of the photosynthetic energy conversion of PSII ($F_v/F_m = (F_m - F_0)/F_m$). Predawn measurements were performed before sunrise; midday measurements were made after 30 min dark adaptation. We estimated effective quantum yield of PSII ($\Delta F/F_m'$) according to [Genty et al. \(1989\)](#), using exposure to natural light conditions. Yield determinations were performed between 11:00 and 13:00 solar time, taking care to keep the natural leaf exposure on the plant.

2.6. Statistical analyses

Soil and PAR data were analyzed separately for each site by one-way ANOVA. Monthly soil moisture was analyzed separately for each site and sampling period by three-way nested ANOVA, with microsite and depth as fixed effects and planting hole (nested within microsite) as a random effect. Survival was analyzed separately for each plantation and sampling period using hierarchical log-lineal models. Survival data were first analyzed in a four-way table (survival, species, microsite, and site). Since the four-factor interaction term was significant for most of the sampling periods, we made separate three-way tests of independence (survival, microsite, and site) for each species. When the three-way interaction was significant we analyzed survival separately for each site. Water potential and fluorescence variables were analyzed by two-way (species and microsite) ANOVA, with both factors as fixed effects. To analyze the effective quantum yield of PSII, we used PAR as a covariate. Variations between predawn and midday values were analyzed separately for each species by using one-way ANOVA. Interception data were analyzed by two-way (microsite and time) repeated-measures ANOVA. Data were log-transformed when necessary to correct deviations from normality. All the statistical analyses were performed using the SPSS 9.0 package (SPSS Inc., Chicago, IL, USA).

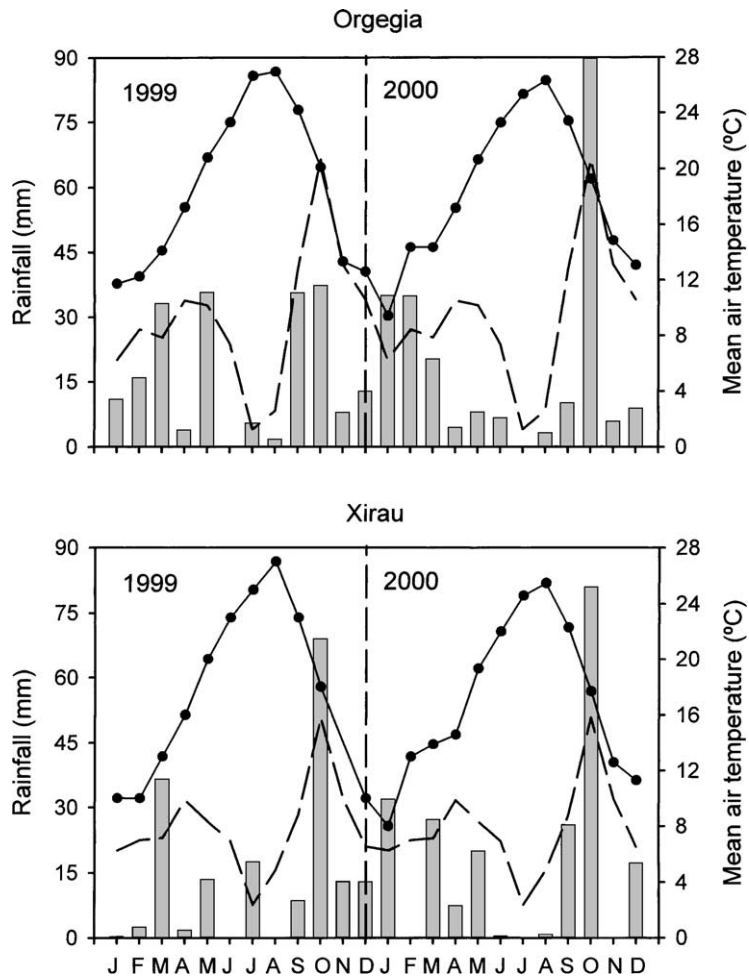


Fig. 1. Monthly rainfall (blocks) and average temperature (solid lines) recorded at the experimental sites. Dashed lines indicate the 30-year average monthly rainfall. Orgegia data come from the Alicante weather station (38°21'N, 0°30'W); Xirau data come from the Agost weather station (38°26'N, 0°38'W).

Table 1

Properties of the surface soil (0–20 cm depth) under the canopy (pine) and outside the canopy (open) of *Pinus halepensis* individuals^a

Variable	Orgegia		Xirau	
	Pine	Open	Pine	Open
pH	8.2 ± 0.0	8.3 ± 0.0	8.4 ± 0.1	8.4 ± 0.1
Organic carbon (mg g ⁻¹)	28.1 ± 1.5	22 ± 1.2	16 ± 1.4	14.2 ± 1.0
Total nitrogen (mg g ⁻¹)	2.4 ± 0.1	2.0 ± 0.1	1.4 ± 0.1	1.4 ± 0.1
C:N	11.7 ± 0.3	11.2 ± 0.3	11.4 ± 0.4	10.2 ± 0.3
Total carbonates (%)	58.3 ± 2.4	69.1 ± 2.5	82.0 ± 1.9	76.1 ± 1.8
Sand (%)	41.4 ± 1.7	40.4 ± 2.4	28.6 ± 1.4	25.4 ± 1.1
Silt (%)	38.4 ± 1.3	38.0 ± 1.6	50.3 ± 1.1	52.1 ± 1.0
Clay (%)	20.2 ± 0.8	20.2 ± 0.8	21.2 ± 0.8	22.6 ± 0.5

^a Data represent means ± 1 S.E. (n = 10).

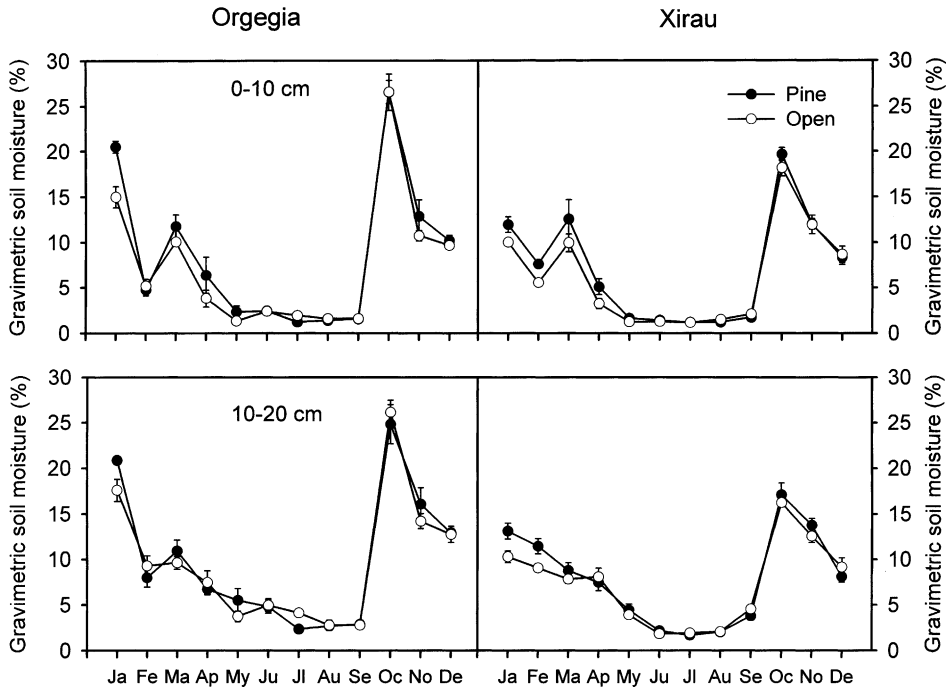


Fig. 2. Monthly changes in gravimetric soil moisture under the canopy (pine) and outside the canopy (open) of *Pinus halepensis* individuals in 2000. Data represent mean \pm 1 S.E. ($n = 5$).

3. Results

Rainfall in the study area during the 1999–2000 period ranged between 177 and 227 mm per year, 56–70% of the 30-year average annual rainfall

(Fig. 1). In both the years, there was a strong summer drought from June to August, in which less than 9% of the total annual rainfall was recorded. These drought years are not uncommon in the study area; 60% of the years comprising the 1960–1990 period

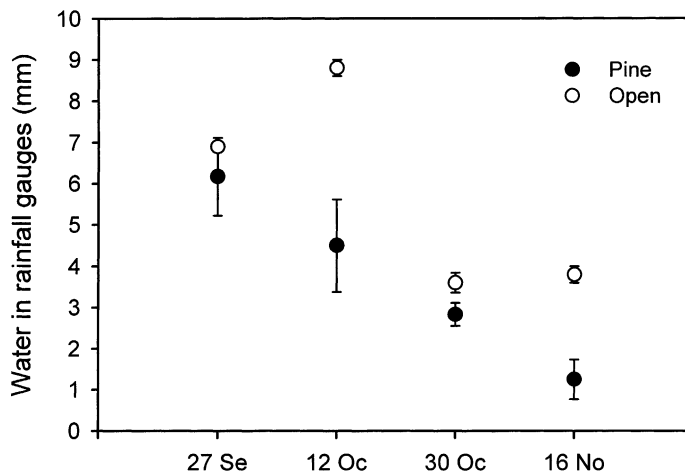


Fig. 3. Rainfall (open) and throughfall (pine) collected during autumn 2000 on the Orgegia site. Data represent mean \pm 1 S.E. ($n = 6$). Se: September, Oc: October, and No: November.

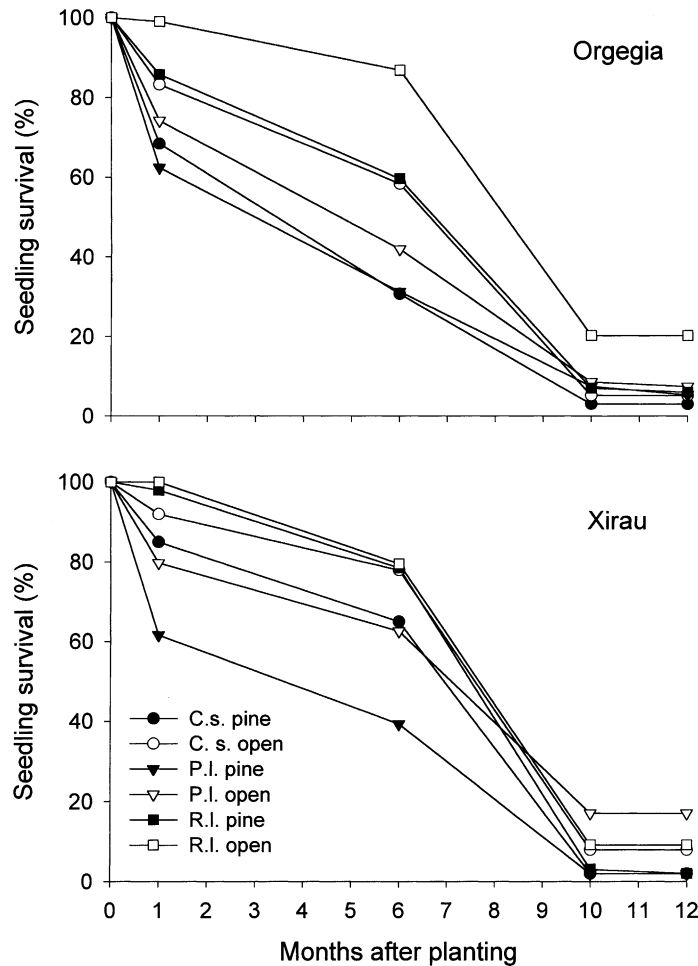


Fig. 4. Survival of seedlings planted in 1998 under the canopy (pine) and outside the canopy (open) of *Pinus halepensis* individuals. For all species and microsites, initial $n = 100$. C.s.: *Ceratonia siliqua*, R.a.: *Rhamnus lycioides*, and P.I.: *Pistacia lentiscus*.

show below-average mean rainfall values (Pérez Cueva, 1994).

3.1. Microsite characteristics

Soil fertility underneath *P. halepensis* canopies was somewhat higher than in open areas (Table 1). Soil organic carbon and total nitrogen content were higher beneath the pine canopies in the Orgegia site (one-way ANOVA, $F_{\text{organic carbon}} = 10.24$, d.f. = 1, 18, $P = 0.005$; $F_{\text{total nitrogen content}} = 5.82$, d.f. = 1, 18, $P = 0.027$), as was C:N in the Xirau site (one-way ANOVA, $F = 5.71$, d.f. = 1, 18, $P = 0.028$). Total carbonate content showed contrasting results between

sites, with higher values under *P. halepensis* in Xirau (one-way ANOVA, $F = 4.86$, d.f. = 1, 18, $P = 0.041$), and in the open microsites in Orgegia (one-way ANOVA, $F = 10.01$, d.f. = 1, 18, $P = 0.027$). Aleppo pine reduced radiation by more than 75% ($229.8 \pm 26.7 \text{ E m}^{-2} \text{ s}^{-1}$ [SE, pine] versus $1856.4 \pm 8.5 \text{ E m}^{-2} \text{ s}^{-1}$ [SE, open] for Orgegia; $427.5 \pm 32.9 \text{ E m}^{-2} \text{ s}^{-1}$ [SE, pine] versus $1934.9 \pm 15.3 \text{ E m}^{-2} \text{ s}^{-1}$ [SE, open] for Xirau). These differences were strongly significant at both sites (one-way ANOVA: $F_{\text{Orgegia}} = 3408.51$, d.f. = 1, 38, $P < 0.001$; $F_{\text{Xirau}} = 1726.03$, d.f. = 1, 38, $P < 0.001$). Gravimetric soil moisture content showed similar trends on both sites (Fig. 2). During January 2000, soil moisture in the pine

microsites was significantly higher than in the open microsites at both locations (three-way nested ANOVA: Orgegia— $F_{\text{microsite}} = 12.36$, d.f. = 1, 8, $P = 0.008$; $F_{\text{microsite} \times \text{depth}} = 7.94$, d.f. = 1, 8, $P = 0.023$; Xirau— $F_{\text{microsite}} = 5.63$, d.f. = 1, 8, $P = 0.045$; $F_{\text{microsite} \times \text{depth}} = 4.67$, d.f. = 1, 8, $P = 0.063$). The same result was obtained for Xirau during February 2000 ($F_{\text{microsite}} = 5.63$, d.f. = 1, 8, $P = 0.045$; $F_{\text{microsite} \times \text{depth}} = 4.67$, d.f. = 1, 8, $P = 0.063$). During July 2000, soil moisture in the open microsites was significantly higher than in the pine microsites at Orgegia (three-way nested ANOVA: $F_{\text{microsite}} = 21.19$, d.f. = 1, 8, $P = 0.002$; $F_{\text{microsite} \times \text{depth}} = 7.78$, d.f. = 1, 8, $P = 0.024$). There were no significant differences in soil moisture at

any of the experimental sites for the rest of the year. *Pinus halepensis* individuals intercepted an average of 2 mm of water in each rainfall event surveyed during the autumn of 2000 (Fig. 3). Differences in rainfall amount between pine and open microsites were statistically significant (repeated-measures ANOVA: $F_{\text{microsite}} = 10.93$, d.f. = 1, 9, $P = 0.009$).

3.2. Seedling survival

Seedling mortality was very high; after 1 year, survival was below 30% in all cases (Figs. 4 and 5). Except for *P. lentiscus*, mortality occurred mostly during summer, coinciding with a strong drought

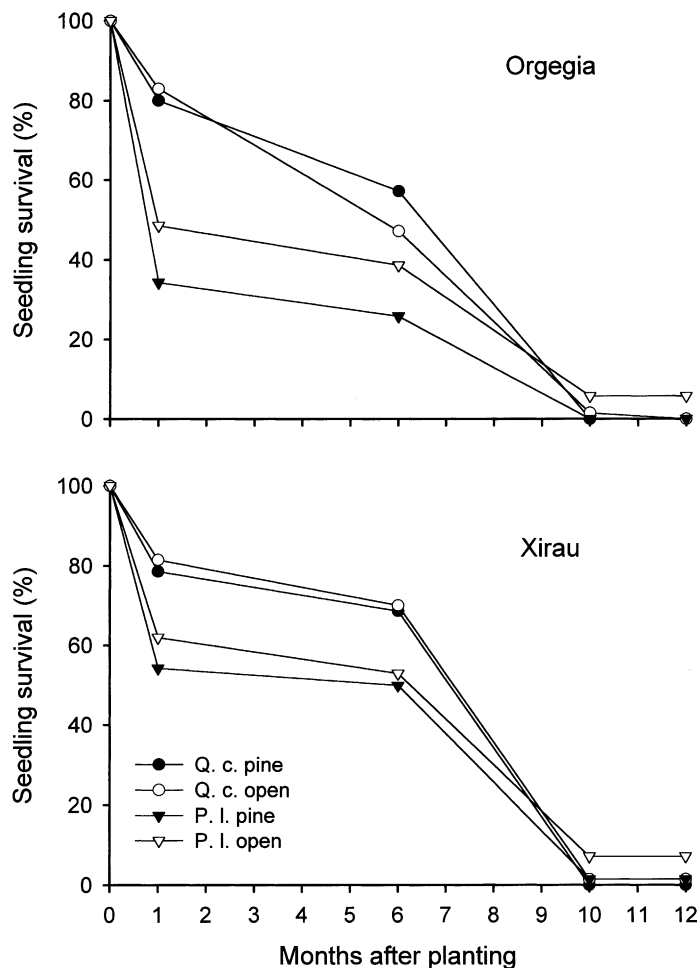


Fig. 5. Survival of seedlings planted in 1999 under the canopy (pine) and outside the canopy (open) of *Pinus halepensis* individuals. For all species and microsites, initial $n = 70$. Q.c.: *Quercus coccifera*, and P.l.: *Pistacia lentiscus*.

Table 2

Partitioned likelihood ratio statistic (G^2) and P values of the hierarchical log-linear analysis describing seedling survival for the 1998 plantation^a

Period	Species	M × U		S × U		M × S × U	
		G^{2b}	P	G^2	P	G^2	P
January 1999	<i>C. siliqua</i>	8.393	0.004	11.123	<0.001	0.051	0.821
	<i>P. lentiscus</i>	10.427	0.001	0.274	0.601	0.590	0.442
	<i>R. lycioides</i>	16.933	<0.001	11.938	<0.001	0.126	0.723
May 1999	<i>C. siliqua</i>	18.147	<0.001	31.459	<0.001	1.340	0.247
	<i>P. lentiscus</i>	11.827	<0.001	1.913	0.167	1.288	0.256
	<i>R. lycioides</i>	11.139	<0.001	11.827	<0.001	8.370	<0.001
October 1999	<i>C. siliqua</i>	3.932	0.047	0.167	0.683	0.684	0.408
	<i>P. lentiscus</i>	8.573	0.003	6.556	0.011	6.157	0.013
	<i>R. lycioides</i>	10.849	0.001	0.286	0.593	0.002	0.963
December 1999	<i>C. siliqua</i>	1.754	0.185	1.754	0.185	2.558	0.109
	<i>P. lentiscus</i>	10.711	0.001	6.952	0.008	4.528	0.033
	<i>R. lycioides</i>	14.124	<0.001	1.325	0.250	0.052	0.819

^a $n = 100$ cases per each site × microsite combination. Total n per species: 400. M: microsite (pine or open), S: site (Orgegia and Xirau), and U: survival (%).

^b Results for unsaturated model containing two-order terms after backward elimination of three-order non-significant term. Results for saturated model in the cases with a significant three-order term.

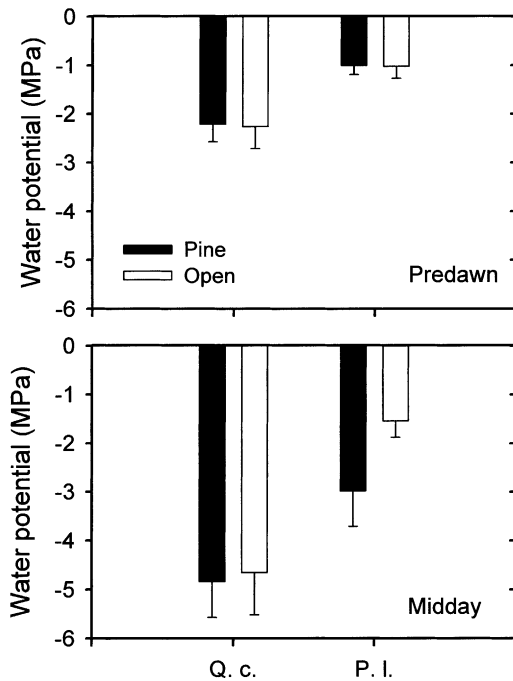


Fig. 6. Late spring xylem water potential in seedlings planted under the canopy (pine) and outside the canopy (open) of *Pinus halepensis* individuals at the Xirau site. Data represent mean ± 1 S.E. ($n = 5$). Q.c.: *Quercus coccifera*, and P.l.: *Pistacia lentiscus*.

period that lasted more than 3 months in both the years (Fig. 1). For the 1998 plantation, we found a clear microsite effect on seedling survival, with higher survival values at the open microsite for all the sampled periods (Table 2). *Ceratonia siliqua* showed significantly higher survival in open microsities except in December, when most seedlings were dead. *Rhamnus lycioides* showed a strong microsite effect in all the sampled periods. The interaction found in May reflected the contrasting effect of microsite on seedling survival in both experimental sites (Orgegia: $G^2_{\text{microsite} \times \text{survival}} = 10.479$, $P < 0.001$; Xirau: $G^2_{\text{microsite} \times \text{survival}} = 0.031$, $P = 0.861$). *Pistacia lentiscus*

Table 3

Predawn and midday measurements of photochemical efficiency of PSII (F_v/F_m) of the seedlings measured under the canopy (pine) and outside the canopy (open) of *Pinus halepensis* individuals on the Xirau site in May 2000^a

	Predawn		Midday	
	<i>Q. coccifera</i>	<i>P. lentiscus</i>	<i>Q. coccifera</i>	<i>P. lentiscus</i>
Pine	0.58 ± 0.09	0.64 ± 0.02	0.55 ± 0.09	0.56 ± 0.04
Open	0.63 ± 0.01	0.63 ± 0.04	0.60 ± 0.01	0.53 ± 0.05

^a Data represent means ± 1 S.E. ($n = 5$).

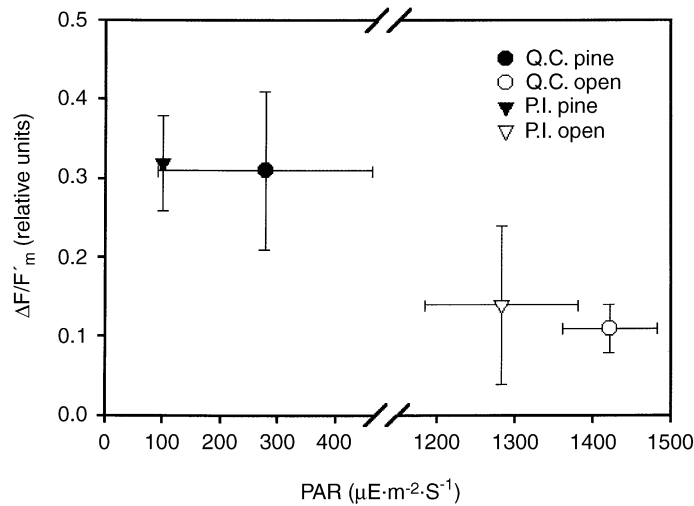


Fig. 7. Effective quantum yield of PS II ($\Delta F/F'_m$) versus PAR in late spring for seedlings planted under the canopy (pine) and outside the canopy (open) of *Pinus halepensis* individuals at Xirau site. Data represent mean \pm 1 S.E. ($n = 5$). Q.c.: *Quercus coccifera*, and P.l.: *Pistacia lentiscus*.

cus behaved similarly, but by the end of the summer the microsite effect disappeared in Orgegia (October 1999: $G^2_{\text{microsite} \times \text{survival}} = 0.073$, $P = 0.788$; December 1999: $G^2_{\text{microsite} \times \text{survival}} = 0.358$, $P = 0.549$), but not in Xirau (October 1999: $G^2_{\text{microsite} \times \text{survival}} = 14.811$, $P < 0.001$; December 1999: $G^2_{\text{microsite} \times \text{survival}} = 14.811$, $P < 0.001$). In the 1999 plantation, the microsite effect was not so evident. Log-linear analysis showed no significant effect of microsite on *Quercus coccifera* survival for any sampling period. *Pistacia lentiscus* survival was higher in the open microsites in October and December 2000 ($G^2_{\text{microsite} \times \text{survival}} = 7.608$, $P = 0.006$; $G^2_{\text{microsite} \times \text{site} \times \text{survival}} = 1.085$, $P = 0.298$).

3.3. Seedling ecophysiology

Predawn and midday water potentials measured by the end of spring did not significantly differ between microsites (Fig. 6). But it is interesting to note the decrease in water potential between predawn and midday in *P. lentiscus* in the pine microsite, which was significantly higher than that observed in the open microsite (one-way ANOVA: $F = 5.657$, d.f. = 1, 8, $P = 0.045$). Maximum photochemical efficiency of PSII did not differ among microsites at both predawn and midday (Table 3). The effective quantum yield of PSII was not significantly different between micro-

sites (Fig. 7), despite the significant reduction in PAR in the pine microsite during these measurements (one-way ANOVA: $F = 111.993$, d.f. = 1, 18, $P < 0.001$).

4. Discussion

Contrary to our initial hypothesis, our results suggest that *P. halepensis* does not facilitate the establishment of shrubs under semi-arid conditions. The lack of differences in most seedling ecophysiological features and the increased survival observed in the open microsite suggest the presence of a negative interaction between *P. halepensis* and introduced seedlings.

Although small and slow-growing, *P. halepensis* individuals were able to increase soil organic matter beneath them. Our results agree with Bautista (1999) and with other studies describing an increase in soil organic matter accumulation with plant growth on afforestations (Romanyà et al., 2000). However, the magnitude of the differences between pine and open microsites was rather meagre, and in the Xirau site they were not significant. Values of total nitrogen content followed the same tendency. The small changes in organic carbon and total nitrogen content may be related to low productivity and low above-ground and belowground inputs of these afforestations. The low C:N ratios also reflected the relatively

small effect of *P. halepensis* individuals on soil properties and were lower than values obtained in natural forests and afforestations with similar environmental conditions (C:N between 13 and 16, Herrero and Rubio, 1994; De la Torre and Alías, 1996). Soil data obtained in this study suggest that, for the time being, the introduction of *P. halepensis* under semi-arid climate has not substantially improved soil conditions, probably because of low tree productivity and growth associated with climatic constraints.

Pinus halepensis individuals intercepted substantial amounts of water during autumn rainfalls. But there were no significant differences in soil moisture content between the two microsites during most of the year, despite the trend towards higher water availability under *P. halepensis*, especially after winter rainfalls. This difference could have been mediated by pine-crown water funneling processes (Bellot and Escarré, 1991) or by reduced evaporation caused by shade.

Pinus halepensis substantially reduced incoming radiation. Despite this, we did not observe any improvement in the PSII status of these seedlings as compared with those planted in the open microsites. Maximum photochemical efficiency of PSII (F_v/F_m) was in all cases below the optimal value that characterizes unstressed plants (0.83, Mohammed et al., 1995), indicating that the seedlings were subjected to stress. We measured F_v/F_m values ranging from 0.53 to 0.64, similar to those reported by Maestre et al. (2001) for seedlings of the same species introduced in *Stipa tenacissima* steppes close to the study sites. The low F_v/F_m values found are probably related to partly irreversible or long-term photoinhibition (Long et al., 1994). The lack of differences between predawn and midday measurements of F_v/F_m , and between microsites in the effective quantum yield of PSII, despite the dramatic reduction in PAR radiation in the pine microsites, supports this hypothesis. The absence of differences in soil moisture during spring is also reflected in the observed water potentials. Any improvement in microclimatic conditions in the pine microsite due to shade, which has an important bearing on evapotranspiration and plant water status (Joffre and Rambal, 1993), can be overcome by the combination of water interception by the pine canopy and water uptake by pine and herbaceous understorey roots.

It is interesting to note the low survival values obtained in all species, regardless of the microsite considered. The low precipitation recorded during the study period, with a dry spring and an extremely dry summer, may explain this high mortality rate. In arid and semi-arid environments, seedling survival is primarily a function of moisture availability (Harrington, 1991), and a positive relationship between seedling survival and length of summer drought have been found in Mediterranean afforestations (Alloza and Vallejo, 1999).

It has been suggested that the importance of facilitation increases with respect to abiotic stress (Bertness and Callaway, 1994). However, we observed a clear negative effect of *P. halepensis* on seedling establishment. This is in contrast with the facilitation observed between adult individuals of this species and oak seedlings (Lookingbill and Zavala, 2000), and with neutral effects of *P. halepensis* on the performance of introduced seedlings of woody species (Vilagrosa et al., 1997) in more mesic areas of the Iberian Peninsula. This variability may reflect the dynamics of the net balance between negative and positive interactions, which may shift depending on small variations in climate, soil and topography (Greenlee and Callaway, 1996; Pugnaire and Luque, 2001). We suggest three hypotheses for future investigation that could explain the negative interaction observed in this study: (1) competition between introduced seedlings and *P. halepensis*, (2) competition between introduced seedlings and herbaceous understorey, and (3) allelopathic effects of pine litter and/or root exudates.

Despite being less documented than the interactions between trees and grasses, competition between trees and shrubs in semi-arid areas has been reported (Callaway et al., 1996; De Luis et al., 1998; Barnes and Archer, 1999). If *P. halepensis* is able to access water from the upper soil horizons, it may outcompete introduced shrubs, whose root systems are mostly limited to exploiting the soil within the plantation hole during the first months after planting (Fonseca, 1999). However, data obtained in S France under Mediterranean dry–subhumid conditions suggest that adult *P. halepensis* individuals have only a negligible impact on the water balance in the upper soil layer (0–15 cm, Koechlin et al., 1986).

We observed patches of the perennial grass *B. retusum* beneath the canopy of almost all pines, in a way similar to that reported in natural *P. halepensis* forests close to the study area (Bautista, 1999). The exploitation of spatially and/or temporally different soil moisture areas by plants in semi-arid environments permits the coexistence of different life forms (Noy-Meir, 1973). Differential water uptake patterns between *B. retusum* and *P. halepensis* may explain the improved status of *B. retusum* under the canopy of the latter. *Brachypodium retusum* has an extensive below-ground rhizome that is mainly developed at a depth of 5–10 cm (Caturla et al., 2000), but root profiles reveal the presence of *B. retusum* roots in plantation holes at a depth of 15–20 cm (F.T. Maestre, unpublished data). Thus, it may be possible that *P. halepensis* has a negative indirect effect (sensu Miller, 1994) on introduced shrubs by facilitating the development of *B. retusum*, which competes with the shrubs.

Competition mediated by allelopathic factors has been thoroughly described in the literature (Schenk et al., 1999) and can be especially important in semi-arid areas due to the low activity of microorganisms, which favors the accumulation of allelochemicals (Friedman, 1987). It is well known that allelopathic interactions are present in *P. halepensis* forests after a fire, mainly mediated by changes in soil pH induced by pine ash (Néman, 2000). In the absence of fire, studies evaluating allelopathic interactions between *P. halepensis* and other species are scarce. In a greenhouse experiment, Broncano et al. (1998) showed no effect of *P. halepensis* litter on the emergence and growth of the late-successional *Q. ilex*.

In the presence of disturbances such as fire, stands of *P. halepensis* may exhibit autosuccessional loops that lead to their regeneration, instead of being the starting point of secondary succession (Trabaud, 1994; Barbéro et al., 2000). In the absence of fire, forests of *P. halepensis* may be replaced by *Q. ilex* or *Quercus pubescens* Willd. under dry, subhumid conditions (Pausas, 1999; Barbéro et al., 2000). Our data shows that, under the conditions of our study, *P. halepensis* did not facilitate the establishment of late-successional shrubs under semi-arid conditions. In the last 50 years, large areas of natural shrublands throughout the Mediterranean Basin have been replaced by *P. halepensis* plantations. These large-scale changes in vegetation cover may have substantially altered nat-

ural succession. The limitations to native shrub colonization may be enhanced by the high fire frequency that characterizes *P. halepensis* forests and the auto-successional trajectories taking place after fire. Further manipulative experiments are needed to clarify the mechanisms involved in the negative interaction observed and to explore its consequences for community composition and dynamics in both afforestations and natural stands.

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