



Interaction between *Stipa tenacissima* and *Pinus halepensis*: consequences for reforestation and the dynamics of grass steppes in semi-arid Mediterranean areas

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Abstract

Alpha or esparto grass (*Stipa tenacissima*) is a perennial tussock grass that coexists with Aleppo pines (*Pinus halepensis*) in semi-arid areas of southeast Spain and northern Africa where the pine is the tree most widely used in reforestation projects. Several authors have proposed that the improvement of soil characteristics by *S. tenacissima* in semi-arid slopes might be brought about in restoration programs by the introduction of shrubs and trees in these areas. In this paper we analyse the role of *S. tenacissima* as a nurse plant of *P. halepensis* and the consequences of pine canopy development on the performance of *S. tenacissima*. We hypothesised that an interaction between both species exists in alfa steppes, so that *S. tenacissima* facilitates the establishment of *P. halepensis*, which then negatively affects *S. tenacissima*. Our results show that in steep slopes the presence of *P. halepensis* individuals was heavily associated with the terracettes formed by the accumulation of sediments upslope of the tussocks of *S. tenacissima*. Even though the surface occupied by the terracettes was a third of the total, 72.9% of *P. halepensis* individuals occurred in this environment. Significant differences were also found in seedling emergence ($P = 0.001$) and establishment ($P = 0.002$) of *P. halepensis*. Both were higher in terracettes than on the bare ground among the tussocks, although no seedlings survived after the drought season. *P. halepensis* interferes negatively on the performance of *S. tenacissima* in some but not all of its life stages. The number of spikes per tussock was higher in steppes without pines and was also dependent on the tussock size ($P < 0.0001$). Significant differences between both environments were also found in emergence ($P = 0.037$) and survival ($P < 0.001$) of seedlings of *S. tenacissima*. Seedlings that emerged in the sun also developed a higher number of leaves and root biomass ($P = 0.041$ and 0.015 , respectively). Pollination rates did not differ between the sites with pine cover and those without pine cover. These relationships may have important consequences for the dynamics and management of these plant communities.

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1. Introduction

In temperate environments where there is surplus water, the spatial proximity between plant species frequently results in a net negative effect as a consequence of competition for resources, mainly for

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light or nutrients (Tilman, 1988; Valladares, 2003). Therefore, the techniques of reforestation consider the pre-existing shrubby or herbaceous vegetation as a source of competition for the planted trees. Existing vegetation is eliminated or cleared before reforestation and trees are planted as far away as possible from competitors (Savill et al., 1997). On the contrary, in temperate water-limited environments, the combination of high irradiance, high temperatures and low rainfall can stress plants. In such circumstances, facilitation plays an important role. Shade from neighbours can protect plants from photo-inhibition and extreme temperatures reducing plant transpiration and improving the water status of the understory species (Soriano and Sala, 1986; Franco and Nobel, 1989; Pugnaire et al., 1996; but see Valladares and Percy, 2002). Additionally, nurse plants can enhance water availability via hydraulic lift (Dawson, 1993; Horton and Hart, 1998; Peñuelas and Fillela, 2003).

Facilitation studies have often emphasised the positive effects of the nurse plants on the performance of the facilitated plants, without considering that facilitation is a bi-directional process (Holzapfel and Mahall, 1999). So, the influence of the facilitated plants on their nurses should also be measured to ensure that negative effects do not appear in the interaction. On the other hand, the balance between positive and negative forces may change temporally throughout the life of the nurse and the facilitated plant (Rousset and Lepart, 2000; Tielbörger and Kadmon, 2000), and the few studies that have evaluated the sign of the interaction in long-lived plants have shown that facilitation becomes competition at later life stages, the facilitated plant increases its performance in detriment to that of the nurse species (McAuliffe, 1984; Valiente-Banuet et al., 1991; Flores-Martínez et al., 1994).

Because of facilitative interactions, the use of shrubs and perennial tussock grasses as nurse plants has been proposed as a reforestation technique that offers both economic and ecological advantages for restoring degraded semi-arid ecosystems (Maestre et al., 2001, 2003; Castro et al., 2002). In order to evaluate the use of these techniques in arid and semi-arid ecosystems, it is necessary to understand the effects of the planted trees on the nurse plants, which may have important consequences for the dynamics of these ecosystems. In water-limited environments facilitation and competition have been observed to drive plant succession by

the expansion and coalescence of vegetated patches around pioneer nurse plants (Yarranton and Morrison, 1974; Archer et al., 1988; Verdú and García-Fayos, 1996; Pugnaire et al., 1996), by the competitive displacement of the facilitator by the beneficiary (McAuliffe, 1984; Valiente-Banuet et al., 1991), and eventually by the re-colonisation of the nurse species once the beneficiary species die (Yeaton, 1978).

Stipa tenacissima L. (Poaceae) (esparto grass) is a perennial tussock grass, which is widely distributed in semi-arid ecosystems of the southwestern Mediterranean Basin. Esparto grass may establish virtually monospecific steppes or co-occur with shrubs and low trees such as *Juniperus phoenicea* L., *Pinus halepensis* Miller, *Tetraclinis articulata* (Vahl) Masters and *Quercus ilex* subsp. *ballota* (Desf.) Samp. As they age, the inner part of the tussocks senesce. Perturbations such as fire, drought or grazing can fragment the tussocks, but these fragments can then resprout and clonally propagate the species (Sánchez and Puigdefábregas, 1994). On slopes, the tussock or tussock fragments act as a trap for water and sediments running down the slope (Puigdefábregas and Sánchez, 1996; Cerdà, 1997; Cammeraat and Imeson, 1999). The sediment accumulation above the tussock forms a terracette, which is richer in nutrients and water than the soil among tussocks (Puigdefábregas and Sánchez, 1996; Bochet et al., 1998). Additionally, microclimate conditions can be ameliorated under and near the canopy of *S. tenacissima* (Valladares and Pugnaire, 1999). The favourable conditions of these terracettes have the potential to improve the establishment and development of other plants (García-Fayos and Gasque, 2002), which is the basis of the reforestation technique proposed by Maestre et al. (2001).

Le Houérou (1969, 1986, 2001) suggested that the great extension occupied by the steppes of *S. tenacissima* in northern Africa is the result of the regressive succession from open forest (dominated mainly by *P. halepensis*). The main mechanism of this regressive succession is the increasing anthropogenic pressure (fibre harvesting, grazing and hunting) periodically worsened by recurrent climatic droughts and forest fires (Puigdefábregas and Mendizábal, 1998; Le Houérou, 2001). In southeast Spain, the administrative authorities encouraged the elimination of *P. halepensis* in the esparto grass steppes to favour the expansion of the esparto grass during the second half of the last

century (Servicio del Esparto, 1953). However, no mechanism has been proposed for the progressive succession from these steppes towards the original forest. There was only the evidence of experimental long-term exclusions and the successful plantations of the original forest trees (Le Houérou, 2001).

We hypothesised that the mechanism in the progressive succession from steppes of *S. tenacissima* to *P. halepensis* forests on steep slopes may be due to facilitation by the terracettes formed by tussocks grass. We also hypothesised that once a canopy of *P. halepensis* has been established (spontaneously or via reforestation) it may negatively interact with the regeneration of *S. tenacissima* populations being the cause of their competitive displacement.

The objective of this paper is to analyse the positive and negative interactions between *S. tenacissima* and *P. halepensis* in an area where both species coexist and discuss them in the context of the natural dynamics of Mediterranean steppes and the use of *S. tenacissima* as a nurse plant in reforestation.

To accomplish this objective, we analyse the degree of spatial association of the adults of *P. halepensis* to the terracettes of *S. tenacissima* and the effects of the terracettes on seedling establishment of *P. halepensis*. The consequences of the *P. halepensis* overstory on the regeneration of the *S. tenacissima* populations were analysed through the comparison of the flower and seed production, and seedling establishment, growth and survival between populations of *S. tenacissima* with and without a *P. halepensis* canopy.

2. Methods

2.1. Study area

The study was carried out in several areas in the southeast of Spain (Table 1). All of the sites are

S. tenacissima steppes or open *P. halepensis* forests. In all cases there were also some individuals of woody shrubs as *Fumana laevipes*, *F. thymifolia*, *Helianthemum pilosum*, *Rosmarinus officinalis*, *Sedum sediforme*, *Teucrium polium*, *Thymus vulgaris* L., *Th. longiflorus*, etc.

The climate is typical Mediterranean semi-arid, with hot summers, mild winters and a dry season that lasts for over 3 months. In all cases, calcareous marls constitutes the substratum. The history of land use is also similar in this region and the main activities are fibre harvesting and grazing. However, the former is at present in full decline because it has been replaced by synthetic fibres.

2.2. Experimental design

2.2.1. Effects of *S. tenacissima* on the establishment of *P. halepensis*

To determine the degree of spatial association between the individuals of *P. halepensis* and the terracettes of *S. tenacissima*, a plot of 150 m × 10 m (south-facing and with a 30° slope) was established perpendicular to the middle-slope of a representative hill in the Zarzilla de Ramos study area. The relative importance of bare soil and terracettes were determined with 75 linear transects 1 m apart and perpendicular to the slope. In each linear transect we counted all the individuals of *P. halepensis* and the soil category (terracette or bare soil) was noted. Pines more than 15 years (i.e., pines with 5 or more fully developed cones) were not considered in the analysis because pines had been harvested in this area 15 years previously and then, the spatial pattern of the pine individuals remnants of this age class may be biased by this effect. The null hypothesis that the number of pines in each site category is related to the relative area covered by each site category was

Table 1
Location and environmental characteristics of the study areas

Site	Geographic coordinates	Altitude (m.a.s.l.)	Mean annual <i>T</i> (°C)	Annual rainfall (mm)
Porta-Coeli (Valencia)	39°40'N, 0°29'W	200	16.7	386
Finestrat (Alicante)	37°33'N, 0°11'W	106	19.6	293
Zarcilla de Ramos (Murcia)	38°21'N, 1°30'W	700	16.8	275
Caravaca (Murcia)	38°18'N, 1°28'W	625	16.0	367
Cancarix (Albacete)	37°58'N, 1°58'W	560	14.9	316
Venta del Olivo (Murcia)	37°50'N, 1°53'W	560	14.9	316

tested using Chi-square tests with continuity correction (Zar, 1996).

An experiment was designed to determine whether pine seedling emergence and establishment differed between the terracettes and the bare soil among the tussocks. The experiment was performed on a south-facing hillside with a 35° angle slope at the Finestrat study area, where pines were absent within a radius of 1 km. A total of 180 terracette and bare soil sites with the same dimensions and soil surface characteristics were marked. We then randomly selected 30 sites from each category and four seeds of *P. halepensis* were sown in each site in September 1996. Emergence (the total number of seedlings emerging), establishment (the number of seedlings at the end of the first growth season, 6 months after sowing), and survival (the number of seedlings surviving after the first dry season, 10 months after sowing) of the pines was monitored. The effect of site on the frequency of emergence and establishment of seedlings was analysed using generalised log-linear analysis. The height of the established seedlings in each soil category was measured and then compared with a *t*-test.

2.2.2. Effects of *P. halepensis* on the regeneration of *S. tenacissima*

We divided the regeneration niche of *S. tenacissima* into five separate phases, flower production, seed production, seedling emergence, seedling growth and seedling survival. All these steps were compared between populations of *S. tenacissima* with and without a *P. halepensis* canopy.

To compare flower production, 20 reproductive individuals from each of these two environments were selected in the Porta-Coeli study area in the spring of 1996. In these plants, the number of spikes as well as the tussock size were determined. As this species is a reputed mast species (Haase et al., 1995), we repeated the observations of the number of spikes per tussock on 38 individuals per treatment in the spring of 2000, a year of mast production. We did not consider the number of flowers per spike as a working variable because of its high variability within and among individuals (Haase et al., 1995; Gasque, 1999). An analysis of covariance using the general linear model procedure was performed considering the number of spikes per tussock (square root transformed) as a dependent variable, the environment (with vs. without

a pine canopy) as fixed factor and the tussock size (square root transformed) as covariate.

Assuming that seed production is controlled by pollination efficiency and that, for wind-pollinated plants, the tree canopy can influence pollination, we analysed the fruit set in both environments. We selected nine plots in steppes with a canopy of *P. halepensis* and 16 plots in steppes without pines, in the Finestrat, Cancarix, Porta-Coeli, Venta del Olivo and Zarcilla de Ramos study areas. Pine densities in the areas in which plots were selected were similar, averaging 428.6 ± 138 pines ha⁻¹ (throughout the paper values are presented as mean \pm 1 S.D.). Plot sizes of 10 m \times 10 m were selected because they proved to have a high predictability of pollination rate of spikes (Gasque, 1999). In each plot, we determined the spike density and collected a total of 20 ripe spikes. For each plot, the mean number of flowers per spike and the mean number of filled seeds per spike were determined; the fruit set or mean rate of filled seeds per spike was then considered as an estimate of the pollination rate of the spikes in the plot. An analysis of covariance using the general linear model procedure was performed using the pollination rate as a dependent variable, the environment (with vs. without pines) as fixed factor and spike density in the plot as a covariate.

In order to compare the seedling emergence rate under the pine canopy to that outside of the pine canopy, a set of 100 seeds were sown in each of the two environments. Seeds were arranged in pairs and introduced into the cells of 50-cell seedbed trays, which contained a mixture of soil and compost. These trays were placed under the canopy of a small *P. halepensis* forest in the research centre which has similar climate characteristics than the Porta-Coeli area. One of the trays was placed under the shade of pines and the other was placed in the sun. The only water received in both trays during the experiment was from rainfall; they were not watered. Photosynthetic active radiation (PAR) and the R/FR ratio, both under the shade of the pine, and in the sun, were measured with a radiometer (Skye Instruments Ltd., Llandrindod Wells, Powys, Wales) three times during the experiment in the months of January and February (values in Table 2). The seeds were sown on 2 September 1997 and then removed on 27 April 1998 after verifying that no new emergence had occurred since the 20 February 1998. Emergence was recorded every 1–3 days. Data

Table 2

PAR ($\mu\text{mol m}^{-2} \text{s}^{-1}$), and red to far red (R:FR) ratio (660/730), under the pine canopy and in full sun on sites where experiments on seedling emergence and development of *S. tenacissima* were run

	Date	Solar hour	Pine canopy	Full sun	Remarks
PAR	29 January 1998	12:30	54–56	70–77	Very cloudy day
R:FR			1.14–1.15	1.17	
PAR	20 February 1998	12:15	250–270	740	High clouds and gaps
R:FR			1.19–1.17	1.11	
PAR	24 February 1998	13:30	120–150	1180	Cloudless, wind
R:FR			0.98–1.05	1.14	

were analysed with generalised log-linear analysis with the environment as a factor and the frequency of seedling emergence per cell as a dependent variable.

An experiment was designed to compare the growth of seedlings of *S. tenacissima* in the sun and under the shade of the pines. Thirty flowerpots per treatment were sowed with one seed of *S. tenacissima* in each pot and then placed in the garden of the research centre in the same sites than the experiment of seedling emergence (see above). The flowerpots contained 1 l of a mixture of soil and compost and were regularly watered to synchronise germination and to prevent seedling desiccation. The seeds were sown on 10 October 1997, and the emergence date of each seedling was recorded. The experiment was concluded on 24 April 1998; the total number of leaves produced was then counted and the longest leaf of each seedling was measured. Likewise, both aerial (hereafter referred as shoot) and root fractions were separated, dried at 60 °C for 48 h, and then weighed. We used *t*-tests to compare the mean values of the parameters measured in the seedlings of both environments.

To compare seedling survival of *S. tenacissima* on steppes with and without pines, two plots of nearly 50 m² per treatment were selected in the Porta-Coeli study area. In these four plots, all the *S. tenacissima* seedlings that emerged during the favourable season (from autumn to early spring) of 1994–1995 and 1995–1996 were recorded and a small coloured pin with a number was placed close to each seedling in order to facilitate its identification during subsequent samplings. Seedling censuses were performed after every autumn and winter rainfall event and at the end of the summer until 1997. In each census, both the survival of previously emerged seedlings and the recruitment of new ones were recorded. The analysis

of seedling survival was carried out using the Kaplan–Meier method.

If seed production and seedling emergence and performance were different on sites with a pine canopy from those without it, then this may have consequences on the age structure of *S. tenacissima* populations. Therefore, we performed a comparative analysis of the densities of *S. tenacissima* by age class on sites with and without pine with *t*-tests. In order to carry out this analysis, twenty-five 10 m × 10 m plots were selected in 1996 in the Cancarix, Caravaca, and Porta-Coeli sites. At the Caravaca and Porta-Coeli sites, we selected the same number of plots with pine canopies and without pine-trees. At Cancarix, there was one extra plot without pine. In each plot, the number of reproductive, non-reproductive, and seedling individuals of *S. tenacissima* were counted. The presence of spikes or some other previous signs of reproduction and the size of the tussocks were used to assign each individual to one of the three age classes. Previously, the absence of statistical differences in the covering of *S. tenacissima*, in either of the three areas as a whole and in each separate site, was verified to control for the effect of possible differences in the esparto grass dominance among plots with and without pine (data not shown). All statistical analyses were performed using the SPSS v. 8–10 package (SPSS Inc., Chicago, IL).

3. Results

3.1. Pine facilitation

P. halepensis individuals were significantly linked to the terracettes of *S. tenacissima*. The percentage of surface occupied by the terracettes was 28.7%, three

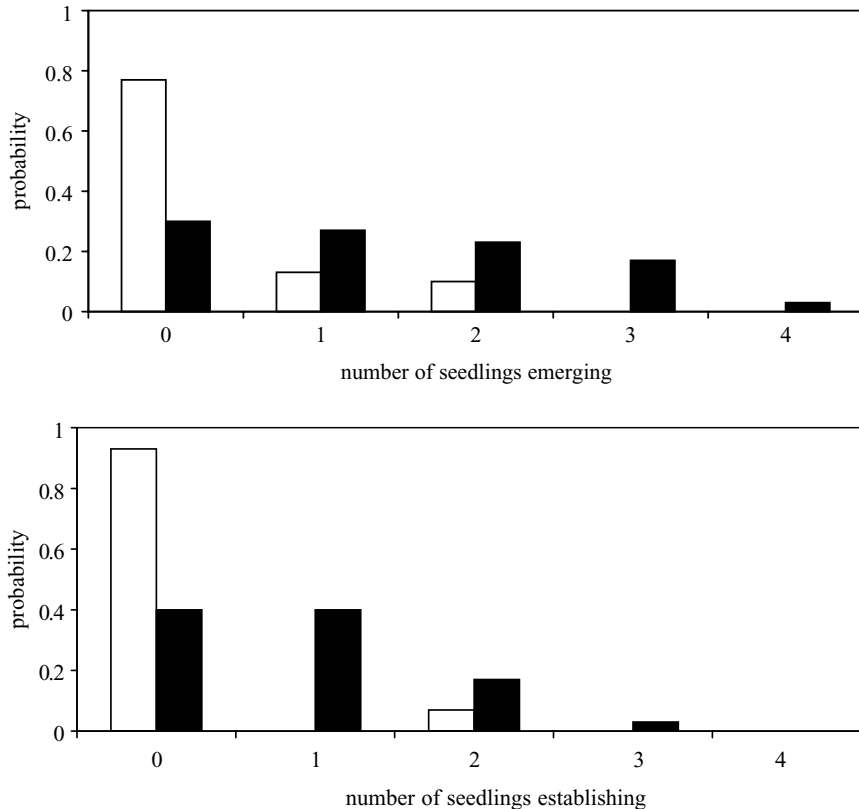


Fig. 1. Probability of emergence and establishment of *P. halepensis* on bare soil sites among tussocks of *S. tenacissima* (blank bars) and on the terracettes formed by the tussocks (dark bars).

times smaller than the surface occupied by the bare ground category (71.3%), but 72.9% of the individuals of *P. halepensis* occurred in the terracettes ($n = 27$) ($\chi^2 = 33.31$, d.f. = 1, $P < 0.001$).

In the 6 months after the emergence, both seedling emergence and seedling establishment were more favourable on terracettes than on bare soil, 51 vs. 10 seedlings emerging and 23 vs. 4 seedlings establishing, respectively (Fig. 1). Also, the analysis of data shows that site category (terraces vs. bare soil) significantly

influenced the distribution of frequencies of emergence and establishment ($G^2 = 17.66$, d.f. = 4, $P = 0.001$ and $G^2 = 14.15$, d.f. = 4, $P = 0.002$, respectively). Despite seedling emergence differences there were no seedlings surviving on the plots after the dry season.

3.2. Spike production and pollination rate

In the spring of 1996, the percentage of variance explained by the model (covariant + factor) had a very

Table 3

Size of the tussocks, number of spikes per individual, and number of flowers per spike in the areas with and without a pine canopy for the years 1996 and 2000 (values are mean \pm 1 S.D.)

	With pines		Without pines	
	1996	2000	1996	2000
Tussock surface (m ²)	0.362 \pm 0.192	0.316 \pm 0.256	0.338 \pm 0.147	0.348 \pm 0.277
Spikes per individual	12.7 \pm 9.6	31.2 \pm 26.4	11.9 \pm 7.9	96.1 \pm 69.5

low value ($R^2 = 0.008$) and neither the environment nor the surface of the tussock had any effect on the number of spikes per individual ($F_{2,37} = 0.146$, $P = 0.865$) (Table 3). However, in the spring of 2000, the average number of spikes per tussock in the areas without pines was threefold the number of spikes of the tussocks under a pine canopy and was also strongly dependent on the tussock size ($R^2 = 0.627$, $F_{2,73} = 63.951$, $P < 0.0001$).

The analysis of the covariance showed that spike density, at the scale of $10\text{ m} \times 10\text{ m}$, is a good predictor of the rate of pollinated flowers per spike in *S. tenacissima* ($F_{1,22} = 15.788$, $P = 0.001$). However, we did not find any effect of the pine canopy on pollination rates ($F_{1,22} = 0.125$, $P = 0.728$).

3.3. Seedling emergence and growth

A total of 73 seedlings emerged in the seedling tray placed out of the pine canopy and 56 emerged in the tray placed under the pines (Fig. 2). Likewise, the distribution of frequencies of seedling emergence per cell was different and more favourable outside the pine canopy than under it (Fig. 2) ($G^2 = 6.54$, d.f. = 2, $P = 0.037$).

The total amount of seedlings that emerged in the sun was 27 while 26 emerged under the shade of the pine. Seedlings that emerged out of the pine canopy had a significantly higher number of leaves, though these leaves were smaller than those from seedlings that developed under the pine canopy (Table 4). Nevertheless, no significant differences in biomass of leaves were found. Root biomass was almost twice

Table 4

Number of leaves, leaf size, seedling biomass, biomass of leaves (aerial biomass), root biomass and root–shoot ratio of seedlings living under the pine canopy and seedlings living in the sun

	Without a pine canopy	With a pine canopy	P^a
Number of leaves	29.1 ± 9.6	24.0 ± 8.2	0.041
Leaf size (mm)	120.8 ± 16.6	143.6 ± 19.7	<0.001
Seedling biomass (g)	0.425 ± 0.187	0.326 ± 0.134	0.032
Leaves biomass (g)	0.221 ± 0.085	0.187 ± 0.071	0.129
Root biomass (g)	0.204 ± 0.115	0.139 ± 0.068	0.015
Root–shoot	0.914 ± 0.399	0.727 ± 0.181	0.033

^a The P -values of the t -test are also given.

in seedlings developing out of the pine canopy than in seedlings under this canopy. As a result of this, seedlings developed in areas without trees had a greater biomass than those developed in areas with a pine canopy as did the root–shoot ratio.

3.4. Seedling survival

During the first year of sampling (1994/1995), seedling densities of *S. tenacissima* in the four plots were significantly higher than those of the following year, but the dynamics of seedlings of both cohorts showed a similar tendency in all plots during the study (Table 5). The greatest mortality rate occurred in the first year after the emergence and was higher in plots with a pine canopy than in plots without pines (87.9–98.6% and 30.8–78.8%, respectively). After the first year, a tendency towards the stabilisation of mortality could be noted. However, seedling survival

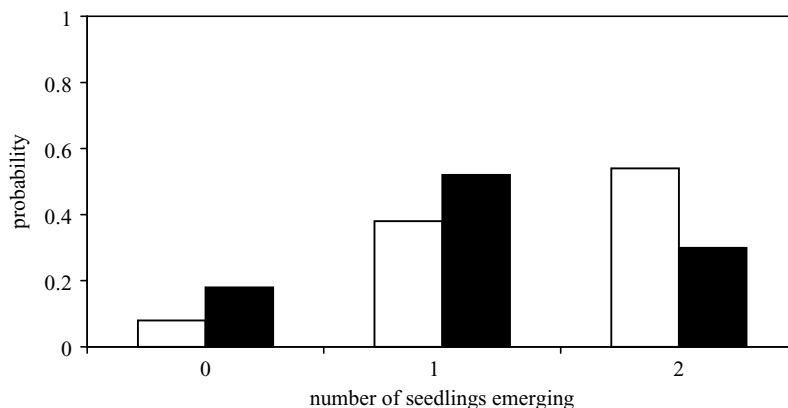


Fig. 2. Probability of emergence of *S. tenacissima* out of the canopy (blank bars) and under the canopy of *P. halepensis* (dark bars).

Table 5
Initial density and seedling survival after 1, 2 and 3 years (seedlings m^{-2})

Treatment	Plot	Initial density	Survival		
			First year	Second year	Third year
Cohort 1994/1995					
Without pines	P1	3.569	0.755	0.446	0.172
Without pines	P2	1.044	0.723	0.455	0.241
With pines	P3	1.394	0.020	0.000	0.000
With pines	P4	0.887	0.108	0.027	0.000
Cohort 1995/1996					
Without pines	P1	0.100	0.040	0.020	
Without pines	P2	0.080	0.040	0.020	
With pines	P3	0.042	0.021	0.000	
With pines	P4	0.041	0.020	0.020	

was null during the second and third years in plots with a pine canopy, while there were still some surviving seedlings after the third year in the plots placed in areas without pines (Table 5). The contrast of the survival functions indicates that life expectancy of seedlings of *S. tenacissima* out of the pine canopy is higher than under the pine canopy ($\log\text{-rank } \chi^2 = 69.71$, d.f. = 1, $P < 0.001$).

3.5. Age structure in esparto grass populations

With regards to the density of the three age groups of *S. tenacissima*, neither mean density of reproductive nor non-reproductive individuals showed variation

with dependence on the environment, but seedling density was significantly greater in plots without pine-trees than in plots with pine cover (Fig. 3) ($t\text{-test} = 2.625$, d.f. = 17.5, $P = 0.015$).

4. Discussion

The association between individuals of *P. halepensis* and terracettes formed by sediment accumulation upslope of the tussocks of *S. tenacissima* supports the hypothesis that *S. tenacissima* facilitates the colonisation of *P. halepensis* in steep slopes. This association is coherent with the results of a more extensive survey on positive association between the terracettes of *S. tenacissima* and many other woody plants (García-Fayos and Gasque, 2002; Maestre et al., 2001) or lichens and mosses (Martínez-Sánchez et al., 1994; Maestre, 2003). Moreover, the sowing experiment shows that *P. halepensis* emerged and established more frequently on the terracettes than on the bare soil among the tussocks of the esparto grass, but survival was zero at the end of the summer in both environments. Hence, this facilitative effect, whatever the mechanisms involved, would be the driving force in the progressive succession from grass steppes to open forests in North Africa and southeast Spain.

On the other hand, the canopy of *P. halepensis* negatively affected the reproduction, emergence, growth and survival of the seedlings of *S. tenacissima* supporting the hypothesis of negative interaction.

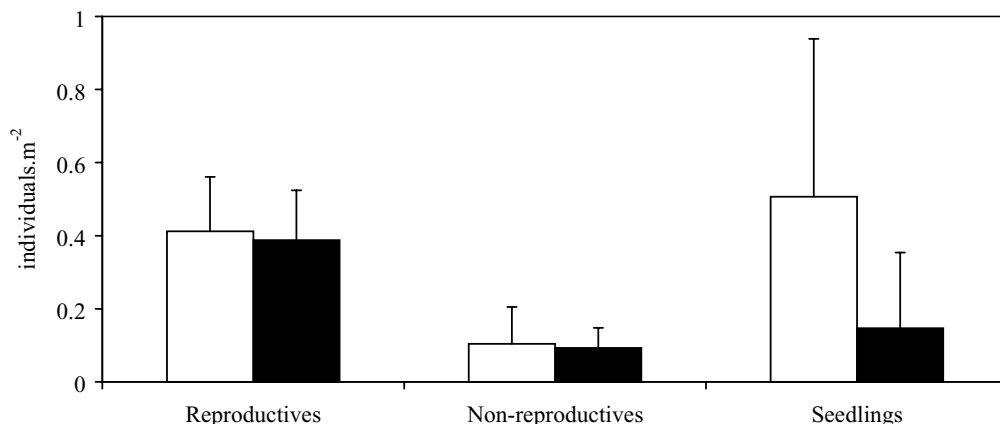


Fig. 3. Density of seedlings, reproductive and non-reproductive adults of *S. tenacissima* in plots without a pine canopy (blank bars) and with a pine-tree canopy (dark bars).

The reproductive effort of the tussocks of *S. tenacissima*, measured as the number of spikes per individual, was strongly related to their size only in the mast year. In addition, the number of spikes per tussock was negatively related to the presence of a pine canopy only in the mast year. Moreover, the pollination rate of *S. tenacissima* was dependent on the spike density as expected by its anemophyllous character, but the presence of a pine canopy did not interfere in the pollination success, possibly because pollen deposition in wind-pollinated species seems to be tightly centred around the parent (Willson, 1983). If we assume that offspring in mast years is more successful than in inter-mast years, as mast theories predict (Norton and Kelly, 1988; Silvertown, 1980), then *P. halepensis* would negatively affect the reproduction of *S. tenacissima* these years by producing a lower number of spikes per tussock.

Seedling emergence, survival and growth of *S. tenacissima* were higher outside of pine canopies than under them. The differences between environments on seedling emergence may be interpreted here as a consequence of rainfall interception by *P. halepensis*, since germination of seeds of *S. tenacissima* is not affected by the light regime (Gasque, 1999) and the experiment of seedling emergence controlled interspecific interference below ground. Several studies have shown that the canopy of *P. halepensis* intercepts up to 50% of the annual rainfall amount, and that rain events smaller than 10 mm are completely or almost completely intercepted (Belmonte and Romero-Díaz, 1994; Maestre et al., 2003). During the emergence experiment it rained 27 out of 37 days and precipitation of 10 mm or less amounted to 19.2% of the total precipitation.

Higher seedling growth in the high light environment is a consequence of the greater allocation to roots (see Table 4). Since root competition was controlled in the experiment and the flowerpots were regularly watered, then the lower biomass of the seedlings of *S. tenacissima* under the tree canopy may be only the result of a lower assimilation rate because of the light interception by tree canopy (see Table 2) (Fulbright et al., 1997; Canham et al., 1999). Otherwise, in conditions of root competition, a more negative effect of the pine canopy on seedling growth would be expected. Aguiar et al. (1992) found that root competition had a greater impact on seedlings of *Bromus*

setifolius when grown in the shade of vegetated patches than it did in the open areas in Patagonian steppes.

Greater root allocation results in higher root–shoot ratios that may allow seedlings of *S. tenacissima* to use water more efficiently and have higher survival probability under severe drought conditions (Hilbert and Canadell, 1995). Concurring with that prediction, seedling survival of *S. tenacissima* was more favourable on open sites than under the pine canopy, resulting in a higher seedling density without pines compared to areas covered with a pine canopy (Fig. 3). Lloret et al. (1999) also found a positive relationship between root–shoot ratios and survival in seedlings of a set of dominant species of Spanish Mediterranean shrublands. On the other hand, it is expected that pine cover may attenuate water stress caused by the direct effect of sun exposure (Breshears et al., 1998) and thus favour seedlings of *S. tenacissima*. But the long duration of the summer drought (usually more than 3 months) and the root competition caused by the more dense vegetation under pines may override this benefit. Studies of soil moisture dynamics in this ecosystem show that there were no differences in soil moisture throughout the year in the upper 20 cm between open sites and under the pine canopy (Maestre et al., 2003). These data about the negative effects of the canopy of *P. halepensis* on the reproduction and establishment of *S. tenacissima* do not support previous research. Le Houérou (1969, 1986) and White (1983) reported that the recruitment of *S. tenacissima* was greater under the shade of tree canopies than in more sunny habitats.

Despite the greater seed production and establishment and survival of seedlings of *S. tenacissima* in the areas without a pine canopy, there was no such relationship observed with adult plants. Adult densities of *S. tenacissima* with and without a pine canopy were the same and the variances in all cases were low. It can be interpreted that the greater recruitment of *S. tenacissima* in the areas without a pine-tree canopy could not have demographic consequences on the adult classes of the esparto grass in these areas. This lack of demographic consequences may be the consequence of an insufficient time for differences in seedling recruitment to manifest themselves at differences in adult community structure. This interpretation is supported by the history of these environments and the

biological characteristics of *S. tenacissima*. Aleppo pine invasion in alpha grass steppes is a very recent phenomenon in our study area (less than 35 years ago, Puigdefábregas and Mendizábal, 1998; Bonet et al., 2001) and the life span of *S. tenacissima* may be measured by centuries due his clonal propagation (Le Houérou, 1969; Sánchez and Puigdefábregas, 1994).

The facilitative role of *S. tenacissima* on *P. halepensis* supports the use of this tussock grass as a nurse species in reforestation of degraded semi-arid ecosystems in southwest Mediterranean areas (Maestre et al., 2001, 2003; Castro et al., 2002). Notwithstanding, once a canopy of *P. halepensis* has been established (spontaneously or via reforestation) it may negatively interact with the regeneration of *S. tenacissima* populations and then causes the competitive displacement of the nurse species, as it occurs in other associated species in some semi-arid areas (Yeaton, 1978; McAuliffe, 1984; Fowler, 1986; Archer et al., 1988; Valiente-Banuet et al., 1991; Holzapfel and Mahall, 1999).

In conclusion, *S. tenacissima* acts as a nurse plant providing a physical barrier to the water and sediment circulation downslope, which results in habitat amelioration for the establishment of *P. halepensis*. Once a canopy of pines develops, it negatively affects the *S. tenacissima* performance, mainly on seed production, seedling establishment, survival and development. The long-term consequences of these relationships are that *S. tenacissima* could be displaced by *P. halepensis* in the areas where both species coexist, but this pattern still remains to be shown because pine invasion in alpha grass steppes is a very recent phenomenon in our study area.

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