



Effects of overstorey canopy, plant–plant interactions and soil properties on Mediterranean maritime pine seedling dynamics

Encarna Rodríguez-García^{a,b,*}, Felipe Bravo^{a,b}, Thomas A. Spies^c

^a Departamento de Producción Vegetal y Recursos Forestales, E. T. S. Ingenierías Agrarias de Palencia, Universidad de Valladolid, UVA-INIA, Avenida Madrid 44, 34004 Palencia, Spain

^b Sustainable Forest Management Research Institute UVA-INIA, Avda. Madrid 44, 34004 Palencia, Spain

^c USDA, Forest Service, PNW Research Station, Forestry Sciences Lab, Corvallis, OR 97330, USA

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ABSTRACT

Seedling emergence, survival and early growth of the Mediterranean conifer *P. pinaster* were studied under closed canopy and open canopy (gaps) cover conditions in a Mediterranean forest of central Spain during two consecutive years (March 2008 to January 2010). Our main objective was to understand how overstorey structure, shrubs and soil properties influence recruitment in this species. Natural emergence and seedling survival were significantly better under closed canopy cover than under open canopy during the two consecutive years of the study; survival increased as radiation decreased. Proximity to shrubs under closed canopy cover was associated with lower mortality rates as well as a positive and apparently transitive effect on early growth. Amelioration of microclimatic conditions is hypothesized as the primary facilitation agent of those observed. Younger seedlings established during the spring of 2008 experienced higher mortality rates than older seedlings established before 2008, and soil properties affected seedling survival significantly. Water stress during summer appeared to be the main cause of seedling mortality in both years. Our study suggests that seedlings of shade-intolerant species may require overstorey cover to establish successfully, and that positive plant–plant interactions in forest communities may be more important than expected in the milder conditions provided by overstorey canopy cover.

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1. Introduction

Natural establishment in forest communities is influenced by multiple interacting factors and can be arranged into distinct and sequential stages (Matney and Hodges, 1991; Barnes et al., 1998a; Rebollo et al., 2001), with the seed and seedling phases recognized as the most critical and least stress-tolerant (Houle, 1996). One of the main abiotic factors limiting natural establishment of woody species in the Mediterranean region and in other Mediterranean ecosystems is summer drought (see Castro et al., 2004a and references inside). Several studies have indicated that pioneer shrubs can facilitate tree seedling survival and growth during natural establishment in Mediterranean forest communities, acting as nurse shrubs (Callaway, 1992; Castro et al., 2004b; Gómez-Aparicio et al., 2005b; Rodríguez-García et al., 2010a,b, 2011). This leads us to think that facilitation might be a common process in Mediterranean plant communities at early stages and in moisture-limited environments, which agrees with the theory of the stress-facilitation

relationship described by Bertness and Callaway (1994). Complex combinations of negative (competition and allelopathy) and positive (facilitation) interactions operating between plant species are common in most communities and biomes (Callaway, 1995). *Facilitation* and *competition* refer to the net effect of changes in the environment of a plant due to the presence of other plants, which includes aboveground and belowground components. Plants can modify temperature, moisture, and light beneath their canopies, thereby altering biological, physical and chemical soil properties. They may also act as seed traps or protect the seedlings of other species from herbivory (Callaway and Walker, 1997; Holmgren et al., 1997; García et al., 2000). The importance of plant–plant interactions appears to vary according to environmental heterogeneity (Hartgerink and Bazzaz, 1984; Kitzberger et al., 2000; Tielbörger and Kadmon, 2000; Beckage and Clark, 2003) and the intensity of abiotic stress experienced by the interacting species (Bertness and Callaway, 1994), as well as the life stages, size and physiologies of the interacting species (Callaway and Walker, 1997; Holmgren et al., 1997; Rodríguez-García et al., 2011).

Most “nurse shrub” studies have only considered the effect of shrubs on tree seedling performance in open areas, but not the effect of overstorey canopy on the shrub–tree seedling relationship (Rodríguez-García et al., 2011). Natural and human-induced disturbances produce openings in forest canopies. Light has been

* Corresponding author at: Departamento de Producción Vegetal y Recursos Forestales, E. T. S. Ingenierías Agrarias de Palencia, Universidad de Valladolid, UVA-INIA, Avenida Madrid 44, 34004 Palencia, Spain. Tel.: +34 979108427; fax: +34 979108440.

E-mail address: enkaro@hotmail.com (E. Rodríguez-García).

the focus of most research on forest dynamics. The specific dependence of different species on gaps for regeneration is associated with a range of shade tolerant physiologies (Catovsky and Bazzaz, 2002). However, seedling responses to light might be determined by belowground resource availability and could vary along soil fertility and seasonal drought gradients (Coomes and Grubb, 2000). Alternatively, this response may be dependent on adjacent vegetation. In forest communities, tree seedlings generally grow mixed in the same space with groups of different ages, sizes or development stages. Thus the plant–plant interactions would be transitive, or determined by their relative sizes. Where perennial woody plants are competing for light, small differences in seedling stature can have a critical effect on survival. Grime (1979) hypothesized that plant habitat competition intensifies along an increasing gradient of primary productivity. Bertness and Callaway (1994), hypothesized that the importance of competition would increase when abiotic stress and consumer pressure were relatively low, but competition between plants can be expected in highly stress-tolerant species (Grime, 1979).

Maritime pine (*Pinus pinaster* Ait.) is a Mediterranean conifer whose main dispersal and germination seasons are autumn and spring (Gil et al., 1990). It is an early-successional, high-light-demanding species (Awada et al., 2003) that invades sites after disturbance and can grow quickly, competing with other plant forms (Richardson, 1998). Previous studies on *P. pinaster* natural regeneration indicate that canopy openness and light have a significant influence on seed germination, early seedling development (Ruano et al., 2009) and post-disturbance seedling density (González-Alday et al., 2008). However, studies of light effects on natural establishment of this species are scarce, and there is little information about how variation in overstorey characteristics affects natural establishment and early growth in Mediterranean forests. There are some examples of greater seedling densities in open canopy sites than in closed canopy sites (Fernández et al., 2001; Rodríguez et al., 2008), which confirm the shade-intolerant nature of this species. However, other findings indicate the need for overstorey cover to ameliorate abiotic conditions, mainly during water stress seasons (Rodríguez et al., 2008). The results of Ruano et al. (2009) corroborate this and results provided by Martínez and Tapias (2005) suggest that foliar distribution and overstorey structure may be very important for classification (Steinberg et al., 1995). They recommend characterizing species as shade-tolerant or not according to factors such as efficiency of water use, evapotranspiration, needle xeromorphology, mineral nutrition and other plant characteristics.

Our understanding of the role of shrubs in this process is also quite limited. Given the current and predicted climatic trends (IPCC, 2007), shrublands are likely to expand in Mediterranean systems because pioneer shrubs, for example *Cistus* spp., are physiologically well adapted to dry conditions and recurrent fires (Werner et al., 1998). In this study we examined *P. pinaster* based on its ability to rapidly colonize open areas. This study is an extension of a previous study (Rodríguez-García et al., 2011) and provides new results about the natural establishment of *Pinus pinaster*. The prior study focused on the effects of shrub and canopy cover on the relative growth rate of different-sized *Pinus pinaster* saplings (growth in the late establishment dynamic). The present study focuses on processes of survival and growth in the early establishment dynamics of young seedlings. Our main objectives were to better understand natural recruitment in this species, to test the influence of overstorey canopy on seedling dynamics, to identify the most important factors affecting seedling survival and to determine whether adjacent shrubs affect seedling survival positively or otherwise. We expected that: (1) natural seedling emergence would be higher under open canopy due to greater wind-dispersal of seeds in open areas and the shade-intolerant nature of the species; (2) establish-

ment would be limited (lower survival and growth rate) at more stressful sites, for example where open canopy with high light levels could produce photoinhibition and thermal fluctuations; (3) seedling survival and early growth would be influenced by shrub; (4) the intensity and the sign of the shrub–seedling interactions would vary depending on the overstorey canopy, with stronger and positive interactions at more stressful sites; (5) conversely, a negative or null effect would be expected under closed canopy conditions with greater availability of resources (soil water and air moisture); (6) overstorey–understorey vegetation and soil properties would affect seedling dynamics.

2. Methods

2.1. Site description

P. pinaster seedling dynamics were studied from early March 2008 through January 2010. The study was conducted in a mature *P. pinaster* forest located at 1050 m.a.s.l., in Las Navas del Marqués, Ávila (40°33'N and 4°20'W), in the Central Mountain System of peninsular Spain. The understorey vegetation is composed of the shrub *Cistus ladanifer* L. The climate in the study area is typically Mediterranean, with most rainfall distributed in autumn and spring, average annual precipitation of 738 mm, and an average annual temperature of 10 °C. Summer precipitation is usually scarce, with minimum annual values in July and August. The soil is siliceous and classified as an Entisol. The experimental site (~25 ha) was partially harvested in 1996 and 1997 using a shelterwood method that varied overstorey retention densities and created canopy gaps. The site had been fenced to keep out livestock and it was still fenced when the study started.

2.2. Study design and environmental factors

The study was carried out in a set of circular plots that were established in 2008 for an experiment about shrub effects on the relative growth of *P. pinaster* saplings of different sizes (Rodríguez-García et al., 2011). This set was composed of three circular plots (15 m radius) established in each of two types of canopy cover: open canopy (gaps), with an average density of 56.59 trees ha⁻¹ and closed canopy, with an average of 146.19 trees ha⁻¹. Forest structure and light parameters differed between canopy types (Table 1). The LAI was two times higher, while total, direct and diffuse transmittance were almost 20% lower in closed canopy plots than in open canopy plots (Rodríguez-García et al., 2011). Within the 15 m plots, four circular subplots with radii 2.5 m were established at each of the four cardinal points, and 7.5 m from the plot centre (Fig. 1). These subplots were used to characterize microclimate and soil conditions representative of growth conditions at random locations within three shrub-free and three shrub-shaded microsites under both types of canopy cover (Rodríguez-García et al., 2011). Soil samples were taken from the upper 20 cm in July 2008, while microclimatic conditions were recorded on six summer days, July 24–31, 2008. The average daily soil temperature and the soil temperature at noon were significantly lower under closed canopy than the average noon value of 39 °C in shrub-free microsites under open canopy (Table 2). The soil nitrogen and calcium content and air temperature were significantly lower under closed canopy, while relative air humidity, soil volumetric water content and phosphorous levels were significantly higher. Microsites with and without shrub presence did not show significant differences in textural and chemical soil properties, soil nutrients or soil VWC contents. However, under both canopy types, shrub-shaded microsites had higher relative air humidity and lower soil temperature at noon compared to shrub-free sites.

Table 1
Main overstorey–understorey characteristics of closed and open canopy plots in the study site (mean \pm SE).

Variable	Canopy	
	Closed	Open
Overstorey structure		
CC-d (%)	32.14 \pm 0.55	5.10 \pm 0.57
Tree-D (N ha ⁻¹)	146.19 \pm 15.37	56.59 \pm 5.32
BA (m ² ha ⁻¹)	16.66 \pm 0.79	7.50 \pm 0.69
H0 (m)	18.16 \pm 0.07	14.95 \pm 0.48
Dbh (cm)	32.14 \pm 0.55	35.92 \pm 1.17
Light		
CO	47.8 \pm 5.0	61.6 \pm 2.4
LAI	0.6 \pm 0.1	0.3 \pm 0.04
(%)Trans-Dir	59.4 \pm 5.3	76.3 \pm 7.3
(%)Trans-Dif	57.7 \pm 5.3	76.7 \pm 3.1
(%)Trans-Tot	58.5 \pm 4.4	76.5 \pm 4.6
Understorey		
Shr-C (%)	50.54 \pm 5.21	63.94 \pm 1.63
Shr-h (cm)	135.73 \pm 6.88	128.75 \pm 4.26
Shr-d (cm)	32.40 \pm 4.68	28.07 \pm 4.63
Sapling-D (N ha ⁻¹)	6237 \pm 1192	3861 \pm 742

Overstorey structure: CC-d: canopy cover measured with spherical densiometer; Tree D: tree density; BA: tree basal area; H0: tree dominant height (Assman); Dbh: tree diameter at breast height (1.30 m); *Light:* CO, canopy openness (%); LAI*, leaf area index (m² m⁻²). *Note that variable LAI provided by GLA software may be considered as plant area index or vegetation area index, because of the inclusion of some trunks and tree branches in the captured image; (%Trans-Dir, (%Trans-Dif, (%Trans-Tot, direct, diffuse and total radiation transmitted (%). *Understorey:* Shr-C: shrub canopy cover; Shr-h: shrub height; Shr-d: distance of seedling to the nearest shrub; Sapling-D: sapling density. The stand structure was characterized in a previous study (Rodríguez-García et al., 2011).

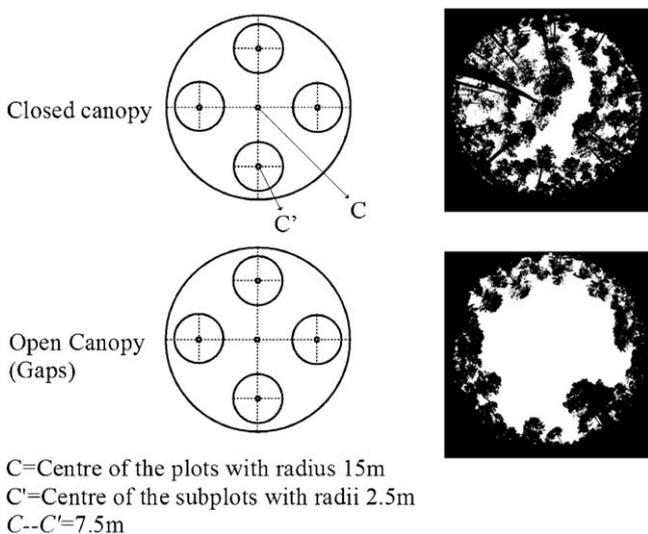


Fig. 1. Layout of the plots and experimental design.

2.3. Pattern of establishment and seedling initial growth

In early March 2008, circular plots (1 m radius) were established within each 2.5 m subplot per canopy cover, in order to observe the natural pattern of seedling establishment from the soil seeds bank (Fig. 1). Seedlings established before March 2008, likely not older than 1 year (<6 cm height and presence of dry cotyledons in many seedlings) were measured and grouped into the Previous to Spring 2008 group (*Seed<08*). Seedlings that sprouted between March 2008 and August 2008 (first growth season) were labeled and classified as the Spring 2008 group (*Seed08*). Seedlings that sprouted between February and August 2009 (second growth season) were labeled and classified as the Spring 2009 group (*Seed09*). Natural emergence and survival were surveyed monthly during

Table 2
Values of the microclimatic conditions and soil properties measured in July 2008 at shrub-shaded and shrub-free sampling points (mean \pm SE). Different letters indicate significant differences ($p < 0.001$).

	Overstorey canopy			
	Closed		Open	
	Shrub-free	Shrub-shaded	Shrub-free	Shrub-shaded
Microclimate				
T ^s	27.92 \pm 0.87a	26.60 \pm 1.00a	31.67 \pm 0.45b	30.01 \pm 0.57b
T ^{sn}	33.37 \pm 0.79a	27.77 \pm 0.87b	39.36 \pm 0.71c	33.03 \pm 0.82a
T ^a	23.17 \pm 0.21a	22.55 \pm 0.47a	25.17 \pm 0.55b	23.69 \pm 0.53b
RH ^a	40.50 \pm 0.55a	42.95 \pm 0.34b	38.03 \pm 0.64c	39.92 \pm 0.54a
Soil				
VWC	2.55 \pm 0.40a	2.86 \pm 0.23a	1.93 \pm 0.16b	2.19 \pm 0.17b
pH	5.94 \pm 0.04a	5.84 \pm 0.03a	5.86 \pm 0.10a	5.84 \pm 0.08a
EC	0.03 \pm 0.00a	0.04 \pm 0.00a	0.07 \pm 0.03a	0.05 \pm 0.00a
Sand	84.13 \pm 0.94a	83.24 \pm 0.73a	83.04 \pm 0.63a	83.00 \pm 0.70a
Clay	9.38 \pm 0.48a	9.82 \pm 0.31a	10.26 \pm 0.25a	9.86 \pm 0.38a
Silt	6.49 \pm 0.62a	6.66 \pm 0.42a	6.43 \pm 0.038a	7.14 \pm 0.49a
N	0.09 \pm 0.01a	0.11 \pm 0.13a	0.12 \pm 0.14b	0.13 \pm 0.18b
P	26.38 \pm 2.64a	27.66 \pm 2.64a	19.60 \pm 2.28b	19.33 \pm 2.12b
K	106.1 \pm 4.63a	113.57 \pm 4.06a	106.97 \pm 7.29a	120.28 \pm 7.28a
Ca	3.77 \pm 0.35a	4.01 \pm 0.35a	4.55 \pm 0.52b	4.75 \pm 0.42b
Mg	0.93 \pm 0.10a	1.08 \pm 0.10a	0.90 \pm 0.08a	0.95 \pm 0.09a
Na	0.04 \pm 0.00a	0.03 \pm 0.00a	0.04 \pm 0.00a	0.04 \pm 0.00a
OM	3.46 \pm 0.35a	4.15 \pm 0.34a	4.26 \pm 0.04a	4.30 \pm 0.431a

Microclimate: T^s, daily average soil temperature (°C); T^{sn}, Soil temperature (°C) at noon (12–5 pm); T^a, average air temperature (°C) at soil surface level; RH^a, average relative air humidity at soil surface level (%); *Soil:* VWC, soil volumetric water content (%); pH, soil pH; EC, electrical conductivity (dSm m⁻¹); Sand, clay and silt, percentage of soil particles by size (%); N, nitrogen content (%); P, phosphorous content (mg kg⁻¹); K, potassium content (mg kg⁻¹); Ca, calcium content (mg kg⁻¹); Mg, magnesium content (mg kg⁻¹); Na, sodium content (mg kg⁻¹); OM, organic matter (%). The microclimatic conditions and soil properties were characterized in a previous study (Rodríguez-García et al., 2011).

both years; from March 2008 to August 2008, and from February 2009 to January 2010, respectively.

The relative growth rates in height (cm) of the surviving seedlings at the end of the first and second growth seasons (RHG₁ and RHG₂, respectively) were calculated as the fraction of height increment observed in one growth season:

$$RHG = \frac{\ln h_1 - \ln h_0}{\ln h_0} \quad (1)$$

where h_1 and h_0 are the final and initial height (cm), measured above ground in the corresponding growth season. Initial height was measured in March 2008 in established seedlings (*Seed<08*), and in the month in which seedlings were sprouted and recorded (throughout the 2008-growing season in *Seed08*, and throughout the 2009-growing season in *Seed09*). Final seedling height measurements were recorded in February 2009 (RHG₁ in *Seed<08* and *Seed08*) and in January 2010 (RHG₁ in *Seed09*, and RHG₂ in *Seed<08* and *Seed08*). The distance to the geometrical centre of the nearest shrub was measured when seedlings were recorded, and seedlings were classified as being either inside (0–30 cm) or outside (>30 cm) the shrub canopy.

2.4. Factors conditioning seedling survival

The relationship between seedling survival probability in summer conditions and site factors was examined. We included variables defining the overstorey–understorey structure, light and soil properties (the average values between shrub-free and shrub-shaded sampling microsites per 2.5 m subplot), distance to the nearest shrub and seedling group. We only evaluated seedling survival after the first growth season due to the very low number of seedlings found alive after the second season.

Table 3

Number of emerged seedlings per shrub-microhabitat and canopy cover type, and number of seedlings surviving after the first (Feb-09) and second growth season (Jan-2010).

		No of emerged seedlings per microhabitat				No of seedlings surviving per microhabitat (Feb-09)			
		Closed		Open		Closed		Open	
		0–30 cm	>30 cm	0–30 cm	>30 cm	0–30 cm	>30 cm	0–30 cm	>30 cm
Seedling class	IOE								
Seed < 08	B2008	96	63	7	3	72	34	4	1
Seed08	March-08	0	0	0	0	–	–	–	–
	April-08	0	0	0	0	–	–	–	–
	May-08	0	0	0	0	–	–	–	–
	June-08	117	81	38	26	19	7	0	0
	July-08	4	1	3	1	1	0	0	0
	August-08	0	0	0	0	–	–	–	–
		No of emerged seedlings per microhabitat				No of seedlings surviving per microhabitat (Jan-2010)			
		Closed		Open		Closed		Open	
		0–30 cm	>30 cm	0–30 cm	>30 cm	0–30 cm	>30 cm	0–30 cm	>30 cm
Seedling class	IOE								
Seed < 08	B2008	–	–	–	–	34	17	0	0
Seed08	June-08	–	–	–	–	10	2	0	0
Seed09	Feb-09	0	0	0	0	–	–	–	–
	March-09	0	3	0	0	–	0	–	–
	May-09	12	5	1	0	0	0	0	–
	June-09	11	4	0	0	0	0	–	–
	July-09	1	0	0	0	0	–	–	–
	August-09	0	0	0	0	–	–	–	–

Shrub-d, distance to the nearest shrub; IOE, interval of establishment; B2008, before spring 2008.

2.5. Statistical analysis

Differences in seedling emergence between years 2008 and 2009 as well as canopy cover type were analyzed with a split-plot GLM design (plot nested in canopy treatment). Differences in seedling relative height growth between canopy cover types were analyzed using the seedling group and distance from shrub as categorical factors. The variables RHG₁ and RHG₂ were transformed to their natural logarithm.

Seedling survival probability was analyzed using generalized linear models (GLZ; McCullagh and Nelder, 1989). The 'survival of summer conditions' response variable was fitted to a binomial distribution with the Logit link function. Categorical factors included the seedling group, listed as Spring 2008 (*Seed08*) and Previous to Spring 2008 (*Seed<08*), along with two categories for seedling distance from the nearest shrub (0–30 cm and >30 cm). Due to the fact that most of the Spring 2008 seedlings emerged in June, we decided to compare differences in seedling survival probability between seedlings established previous to spring of 2008 and in spring of 2008, rather than looking at seedling groups based on month of emergence within the Spring 2008 group. Overstorey structure, light and soil properties were included as continuous independent variables. Prior to that, a principal component analysis (PCA) was conducted to reduce the dimension of the observations and search for combinations of environmental variables that explained the largest variation in the data (Hårdle and Simar, 2007). The PCA was based on the correlation matrix and the components were rotated according to the *varimax* method. The eigenvalues and explained variance shown in the text are from the initial values matrix. The PCA variables with a correlation to the principal components that was higher than 0.75 were selected to describe the environmental gradients indicated by the principal factors and were included in the survival probability model. Several models were tested and the final one was chosen based on its goodness of fit with Akaike information criterion (AIC) and statistical stability evaluated by the ratios of deviance to the respective degrees of freedom. The models were fitted using Statistica 6.0®.

2.6. Intensity of the seedling–shrub interaction

An index of interaction intensity was used to synthesize the net effect of seedling–shrub interaction and to determine the impact of facilitation on cumulative seedling survival after the first and second growing season, (end of the study), independently from the impact of other factors such as abiotic stress (Brooker et al., 2005). We modified the relative neighbour effect index (RNE) of Callaway et al. (2002), so that

$$RNE = \frac{X_c - X_t}{x} \quad (2)$$

where X is an estimate of plant performance (survival) in the presence (c) or absence (t) of neighbours, and x is the highest value of the pair X_c , X_t . The modified index varies from -1 to 1 , with positive values indicating facilitation and negative values indicating competition. We used cumulative seedling survival at the end of the first growing season and at the end of the study (January 2010). The RNE index was calculated for each seedling class and year of observation, as the difference between the seedlings established under shrub canopy (0–30 cm) and seedlings established further than 30 cm from shrub. Note that due to the shrub height (Table 1), 'shrub absence' should apply to seedlings growing further than 30 cm from shrubs, even though there is a likely shelter effect. In the horizontal plane, the presence or absence of the neighbour shrub can be nuanced and interpreted as seedling proximity to the shrub, or as being inside or outside the shrub's canopy.

3. Results

3.1. Natural patterns of establishment and early seedling growth

Initial densities of *Pinus pinaster* seedlings in March 2008 (*Seed<08*) were much higher under closed canopies (average of 16.7 seedlings m²) than under open canopies (average of 1 seedling m²). Seedling emergence from the soil seed bank during the spring of 2008 (*Seed08*) was higher under closed canopies and occurred mainly in June in all plots and for both canopy types. After

the first growth season (August 2008), the *Seed<08* density had decreased to an average of 11 seedlings m^2 under closed canopy, and a total of 5 seedlings under open canopy cover (Table 3).

In the case of *Seed08*, only 27 out of a total of 271 established seedlings under closed canopy survived the summer, and none of the 68 seedlings established under open canopy cover survived the first summer (Table 3). Seedling emergence during the second year, 2009, began in March and continued through July, where June corresponded with the peak month. The number of seedlings emerged was low (Table 3), and 100% of the seedlings had died by August 2009 under both canopy types. At the end of the study in January 2010, only closed canopy plots contained live seedlings. Seedling emergence was significantly higher under closed canopy than under open canopy during both years, and was significantly higher during 2008 ($F=23.98$; $p<0.001$). Dead seedlings were found to be desiccated at the time of recording, without symptoms of insect or fungus damage. Water stress during summer appeared to be the main cause of seedling mortality in both years.

Due to the low number of survivors under open canopy, comparisons of relative growth rates between seedling groups and growth seasons were limited to seedlings under closed canopy cover. Only seedlings from the *Seed08* and *Seed<08* groups were still alive at the end of the study; there were no survivors from *Seed09*. The relative growth rate in height during the 2008 growth season (RHG_1) was significantly influenced by the distance to the nearest shrub ($F=6.33$; $p<0.001$), and by the seedling group ($F=23.74$; $p=0.013$). Within a distance of 0–30 cm from the nearest shrub, there was a difference in relative growth between the seedling groups (Fig. 2). However, the *Seed08* RHG_1 did not differ from the *Seed<08* RHG_1 for seedlings established further than 30 cm from shrub. These differences in RHG disappeared during the 2009 growth season (RHG_2), when neither the distance to the shrub ($Id\text{-shrub}$; $F=0.34$; $p=0.564$), nor the seedling group ($F=3.74$; $p=0.057$) had a significant effect on the relative height growth.

3.2. Factors conditioning seedling survival

The first three principal components of the PCA explained 69.46% of the total variance. The eigenvalues, percentage variation of each factor and interpretation (with factor-variable correlations) are provided in Table 4. The first and most important factor described a 'shade effect' positively related to overstorey canopy cover, LAI, basal area and tree density and negatively related to canopy openness and transmittance. The second factor described soil textural properties along with soil water and Ca and Mg availability. The third factor described the soil chemical properties and explained only 9.03% of the variation. The role of sapling density and shrub cover was scarcely perceptible (Table 4), but seedling distance to the nearest shrub ($Shr\text{-}d$) was negatively correlated with the third factor ($r=-0.395$).

We tested several different environmental variable sets in GLZ mortality models. Many combinations using the LAI variable led to models that did not converge. Since BA is a measure of the overstorey density and structure, we selected it and the percentage of total radiation transmitted (% $Trans\text{-}Tot$), as the primary explanatory variables from the group of the variables related to the canopy gradient. However, canopy cover, tree density and canopy openness were also tested. All these variables represent the two extremes of the gradient, so they were tested separately in the models, as were soil textural properties, sand and clay. Soil water content, pH and the most important nutrients (Mg and Ca) were included in all models. Ten models were tested, combining the categorical factors of seedling group and distance to the nearest shrub with different continuous predictors (Table 5 and Appendix). All models presented ratios of close to 1 for deviance to the respective degrees

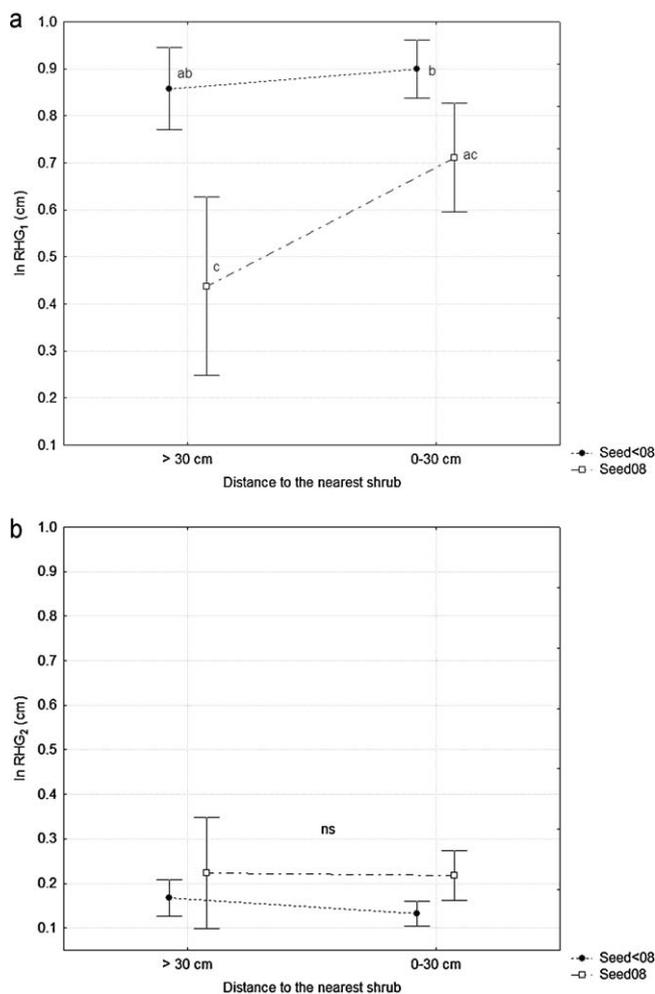


Fig. 2. Natural logarithm of the average relative height growth (RHG) of established seedlings of different cohorts under closed canopy cover, during the first growth season (a) and the second growth season (b), and at different distances to the nearest shrub. Different letters show significant differences ($p<0.05$) between treatments. Vertical bars denote 0.95 confidence interval.

of freedom. Thus, there was no evidence of overdispersion, indicating that the parameter estimate values for significant variables were appropriately scaled.

The ranking of competing models indicated by the AIC criterion is shown in Table 5. Models 1 and 9 appeared to be the best, but all models tested showed significant differences in mortality between seedling groups, with significantly higher probability of seedling mortality during the first summer for the younger, Spring 2008 seedlings (positive parameter estimate for the effect level, $Id\text{-seed}=0$) than for the seedlings established prior to Spring 2008. The probability of seedling mortality differed significantly between seedlings established under shrub canopy and those established further from the shrub canopy (>30 cm): seedlings established between 0 and 30 cm had a significantly lower probability of mortality during summer (negative parameter estimate for the effect level, $Id\text{-shrub}=1$), than seedlings established further from the shrub canopy (Table 5). The influence of the overstorey canopy appeared to be very important, and all models tested showed that lower radiation resulted in higher survival of summer conditions. Greater canopy openness and total transmitted radiation increased the probability of seedling mortality, while higher basal area, tree density or canopy cover significantly decreased this probability during summer. Soil pH, Ca and Mg content were significant in all models but had opposite effects. Ca was associated with a decrease

Table 4

Principal factors and explained variance obtained from the PCA carried out with overstorey and structure variables and soil properties. Factor loadings higher than 0.75 are in bold.

Variable	Factor 1	Factor 2	Factor 3
%Trans-Tot	-0.967	0.120	0.006
%Trans-Dif	-0.935	0.167	0.118
CO	-0.908	0.277	0.100
%Trans-Dir	-0.905	0.062	-0.108
Ca	-0.325	0.763	0.158
Silt	-0.269	0.739	0.032
EC	-0.264	0.114	0.763
Na	-0.253	-0.062	0.374
Shr-C	-0.243	-0.008	0.041
K	-0.204	0.518	0.334
Clay	-0.184	0.848	0.109
pH	-0.103	-0.223	-0.913
OM	-0.092	0.722	0.639
Sapling-D	0.133	-0.010	-0.062
Shr-d	0.229	-0.025	-0.395
Sand	0.250	-0.913	-0.129
Dbh	0.256	0.112	0.227
Mg	0.258	0.901	-0.013
N	0.377	0.659	0.535
VWC	0.487	0.755	0.099
H0	0.543	0.059	0.030
P	0.568	0.488	-0.140
Tree-D	0.895	0.151	-0.221
LAI	0.903	-0.208	-0.107
CC	0.908	-0.277	-0.100
BA	0.910	0.145	-0.127

Factor	Eig.	% V	% AV
1	9.67	37.21	37.21
2	6.04	23.23	60.43
3	2.35	9.03	69.46

% Trans-Tot: total radiation transmitted through the canopy; %Trans-Dif: diffuse radiation transmitted through the canopy; CO: canopy openness; %Trans-Dir: direct radiation transmitted through the canopy; Ca: calcium; Silt: percentage of silt; EC: electrical conductivity; Na: sodium; Shrub-C: shrub coverage; K: potassium; Clay: percentage of clay; pH: soil pH; OM, organic matter; Sapling-D: sapling density; Shr-d: distance of seedling to the nearest shrub; Sand: percentage of sand; Dbh: tree diameter at breast height (1.30 m); Mg: magnesium; N: nitrogen; VWC: soil volumetric water content; H0: tree Assman dominant height; P: phosphorous; Tree-D: tree density; LAI: leaf area index (see Table 1); CC: canopy cover; BA: basal area. Eig.: eigenvalues; %V: explained variance; %AV: accumulated explained variance.

in the probability of seedling mortality, while Mg was associated with an increase. The percentage of clay in the soil was not significant, but the percentage of sand was significant in two models and was associated with increased mortality. The soil volumetric water content variable had a significant effect on decreasing the probability of seedling mortality when it was included with BA, CC, CO and

Table 5

GLZ models of mortality probability during the first summer of different *P. pinaster* seedling groups (1d-seed) established at different distances from shrub (1d-shrub).

Model	Continuous predictors													Categorical factors			AIC
	No	Interc	CC	BA	N ha ⁻¹	% Trans-Tot	CO	pH	Mg	Ca	VWC	Clay	Sand	Id-seed (=0)	Id-shrub (=1)	S × Sh	
1	**	-	(-) ^{***}	-	-	-	(-) ^{***}	(+) ^{***}	(-) ^{**}	(-) [*]	ns	-	(+) ^{***}	(-) ^{***}	ns	378	
2	*	-	(-) ^{***}	-	-	-	(-) ^{**}	(+) ^{***}	(-) ^{**}	(-) [*]	ns	ns	(+) ^{***}	(-) ^{***}	ns	378	
3	**	-	-	-	(+) ^{***}	-	(-) ^{***}	(+) ^{**}	(-) ^{**}	ns	ns	-	(+) ^{***}	(-) ^{***}	ns	381	
4	ns	-	-	-	(+) ^{***}	-	(-) ^{***}	(+) [*]	(-) ^{***}	ns	-	ns	(+) ^{***}	(-) ^{***}	ns	380	
5	**	(-) ^{***}	-	-	-	-	(-) ^{***}	(+) ^{***}	(-) ^{**}	(-) ^{***}	-	(+) [*]	(+) ^{***}	(-) ^{***}	ns	383	
6	***	(-) ^{***}	-	-	-	-	(-) ^{***}	(+) ^{***}	(-) ^{**}	(-) ^{***}	ns	-	(+) ^{***}	(-) ^{***}	ns	386	
7	ns	-	-	-	-	(+) ^{***}	(-) ^{***}	(+) ^{***}	(-) ^{**}	(-) ^{***}	-	(+) [*]	(+) ^{***}	(-) ^{***}	ns	383	
8	***	-	-	-	-	(+) ^{***}	(-) ^{***}	(+) ^{***}	(-) ^{**}	(-) ^{***}	ns	-	(+) ^{***}	(-) ^{***}	ns	386	
9	ns	-	-	(-) ^{***}	-	-	(-) ^{**}	(+) ^{***}	(-) ^{**}	(-) [*]	-	ns	(+) ^{***}	(-) ^{***}	ns	377	
10	**	-	-	(-) ^{***}	-	-	(-) ^{**}	(+) ^{***}	(-) ^{**}	ns	ns	-	(+) ^{***}	(-) ^{***}	ns	377	

Interc, intercept of the model; See name of continuous predictors in Table 4; (+/-) sign of the parameter estimate; ***($p < 0.001$); **($p < 0.01$); *($p < 0.05$) significant effects at different levels of confidence; ns, no significant effect; Id-seed = 0 indicates differences between the two categories of seedlings and that the probability of mortality for the level = 0 (Seed08) is higher than for the analysis reference level (1 = Seed<08); Id-shrub = 1, indicates differences between the two categories of distance to shrub and that the level for probability of mortality = 1 (distance between 0 and 30 cm) is lower than the reference level for the distance to shrub (2 => >30 cm); S × Sh, Id-seed × Id-Shrub interaction; AIC, Akaike index criterion.

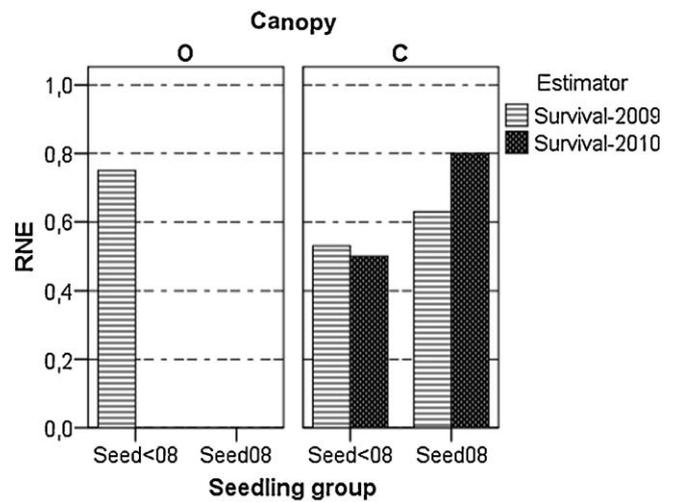


Fig. 3. Sign and strength of the shrub–tree seedling interactions using the relative neighbour effect (RNE). Positive values indicate facilitation. The RNE was calculated as the difference in seedling performance (survival) with shrubs (0–30 cm) and without (>30 cm), relative to the case with the greatest performance in the pair. RNE was calculated for survivors after one growing season (February 2009) and at the end of the experiment (January 2010): O, open canopy; C, closed canopy.

tree density in the models; but it did not show a significant effect when it was tested together with the % Trans-Tot variable (Table 5).

3.3. Intensity of the seedling–shrub interactions and plant performance estimators

The RNE index showed that the net effect of shrubs on cumulative survival after the first growing season (February 2009) and at the end of the study (January 2010) was strong and positive for all live seedlings and both canopy types (Fig. 3). In January 2010, after two growth seasons, no seedlings had been established under open canopy cover, so the RNE index was calculated only for seedlings established under closed canopy cover.

4. Discussion

The results of this study show that natural emergence and survival of *P. pinaster* seedlings were significantly better under closed canopy cover than under open canopy during two consecutive years. The establishment pattern varied between the first and second year of observation, which may indicate establishment pulses with year-to-year variation (Rodríguez-García et al., 2010a,

b). Solar radiation appeared to be an important environmental factor defining the regeneration niche of Mediterranean *P. pinaster* in the system studied: the lower the radiation, the higher the seedling survival. Therefore, we argue that the more stressful environmental conditions under open canopy may have impeded seed germination and emergence. Despite the shade-intolerant nature of *P. pinaster*, its establishment appeared to be better under canopy cover than in the open. The suite of organisms present in a given ecosystem is adapted to local conditions, and apparently minor deviations from optimal conditions can impose a large degree of stress (Holmgren and Scheffer, 2010). Fajardo et al. (2006) observed that ponderosa pine germinants could recruit throughout the stand wherever available seed fell on suitable seedbeds, but in dry sites survival was favored by the shade available in close proximity to overstorey trees. Ruano et al. (2009), compared germination of *P. pinaster* planted seeds in different basal area removal settings (0, 25, 50 and 100%) and reported higher germination and seedling survival rates with 75% basal area retention, implying around 54% average canopy openness. This is close to our study average of 49% under closed canopy. Canopy cover may have protected seedlings from photoinhibition (Valladares et al., 2005), and lowered transpiration demands and thermal stress as a result of higher relative air humidity and lower air and soil temperature.

Alternatively, canopy cover may have improved soil conditions for seedling growth and survival (significantly higher VWC and phosphorous in the soil under closed canopy). Despite the fact that significant differences in soil chemical properties and soil Mg content were not observed between canopy cover sites, the analysis suggested that these soil nutrient conditions could affect seedling survival. This is contrary to statements made by Goldberg and Novoplansky (1997), who argued that water variation is more likely to affect seedling survival than nutrient availability. They also suggested that the effects of competition on survival, but not on growth, would increase with productivity. Our results, which show strong facilitation effects, would give evidence of the opposite tendency. In our case, closed canopy cover plots may present greater productivity than open plots due to the greater content of soil water and phosphorous. The role of competition and facilitation along productivity gradients should be explored with greater attention to the conditions under which the findings of Goldberg and Novoplansky (1997) would be expected to apply in light of these two apparently contradictory hypotheses.

Soil pH, which was associated with decreased probability of seedling mortality, may influence both the supply of nutrients for plant growth by controlling the solubility of soil minerals, and the activity of soil microorganisms (Barnes et al., 1998b). Calcium was associated with decreased probability of seedling mortality and might be related to seedling growth. Unlike most nutrients, calcium is taken up almost exclusively by young root tips (Brady and Weil, 2002). The negative effect of Mg concentration on seedling survival might be connected to the photosynthesis process or to intra-specific competition for nutrients and light caused by the need to grow fast or increase shoot due to neighbour shade (Bloom et al., 1985). These relationships could be derived from other factors that drive both the mortality and the soil nutrient patterns, e.g. shrub litter effects on soil chemical properties. The negative effect of percentage of sand on seedling survival might be connected to soil temperature and/or water holding capacity (Barnes et al., 1998b).

The mortality rates of *P. pinaster* seedling groups varied; the younger seedlings were more likely to die during summer than seedlings established prior to spring 2008. These results differ from the results of Gobbi and Schlichter (1998), who found higher survival for conifer seedlings emerging later in the season (from mid-spring to mid-summer), but agree with results of Castro (2006a, 2006b), who found that early-emerging *P. sylvestris* seedlings had

greater chances of establishment in all microsites, even under pine canopies. Summer drought is one of the most important stress factors that affects natural establishment of tree seedlings in Mediterranean systems. We propose that these differences in mortality are likely related to seedling size as well as ability to withstand environmental stress and grow rapidly enough to capture resources during hot, dry periods (Holmgren et al., 1997; Cavender-Bares and Bazzaz, 2000). Mortality rates were also lower under shrub canopies. These results show the importance of temporal variation and spatial heterogeneity in establishment patterns. Seedlings below a certain height or beyond a certain radius from the target shrub species may be affected differently by shrubs (Rodríguez-García et al., 2011). For this reason, horizontal and vertical spatial dimensions should be considered in studies of this system.

The net effect of shrub on seedling survival was very strong and positive, while the intensity of the seedling–shrub interaction varied with the seedling group and growth season. The positive effect of shrub cover on survival may have been driven by increased moisture, resulting from the effects of shrub cover on soil temperature and relative air humidity (Holmgren et al., 1997). Previous studies on Mediterranean systems describe similar results for *P. sylvestris* and *P. nigra* seedlings (Castro et al., 2004b; Gómez-Aparicio et al., 2005a), and *P. halepensis* (Gómez-Aparicio et al., 2005a). Higher survival percentages were observed under the live shrub canopy of *Salvia lavandulifolia*, *Santolina canescens* and *Ulex parviflorus*, and under mimicked shrub-canopy (open interspaces without vegetation where seedlings were covered with cut branches) than in open spaces or where the shrub canopy had been clipped and removed. Positive effects of shrubs on pine seedling survival have also been observed in North American *P. ponderosa* forests in xeric systems (Keyes and Maguire, 2005) and other conifers such as *Austrocedrus chilensis* in Patagonian forests (Kitzberger et al., 2000; Letourneau et al., 2004). A positive effect of woody debris over the soil surface (especially branches) on post-fire regeneration was recently reported for *P. pinaster* (Castro et al., 2010). It seems to be related to the amelioration of microclimatic and edaphic conditions in areas shaded by fallen branches. The presence of these “nurse objects” may reduce solar radiation and soil temperature and favor increased relative humidity, thus reducing the risk of damage from water stress. Although we have not explored these establishment microsites, our observations at the experimental site and in other field conditions tend to corroborate these results.

5. Conclusions

Solar radiation appeared to be the most important environmental factor in determining survival and the regeneration niche of *P. pinaster* in the system studied, with low emergence and greater seedling mortality under open canopy conditions. Shrubs may act as nurse plants facilitating tree establishment and contribute to successional changes in *P. pinaster* Mediterranean forests, based on the overall positive and strong effect on seedling survival. Amelioration of microclimatic conditions by shade is hypothesized as the primary facilitation agent. Nutrient availability, soil moisture and chemical soil properties may significantly affect seedling survival. Further research is needed, but our study suggests that seedlings of shade-intolerant species may be unable to establish in larger gaps, and that positive plant–plant interactions may be more important in the more moderate conditions provided by overstorey canopy cover.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.foreco.2011.03.029.

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