

Post-fire natural regeneration of a *Pinus pinaster* forest in NW Spain

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Abstract The aim of this study was to analyse the regeneration of *Pinus pinaster* after wildfire and the possible inter and intraspecific competition during the first 3 years after fire. The study area is located in a *P. pinaster* stand in León province (NW Spain). Three study sites (S1, S2 and S3) were established in an area burned in 1998. In each site, three permanent plots (20 × 1 m) were marked. A total of 20 quadrats of 1 m² were studied in each plot. The number and height of pine seedlings 1, 2 and 3 years after fire was recorded in each quadrat. The regeneration of understorey vegetation in the quadrats was analysed concurrently. The significance of linear correlations among the number and height of seedlings and understorey vegetation cover was tested by calculating Pearson correlation coefficients. Seed germination and seedling emergence took place massively during the first year after the fire and decreased through time. The height growth was constant over the 3 years at site S2, while a growth burst could be observed between years 2 and 3 at sites S1 and S2. Also, pines from site S2 reached shorter maximum heights in all years compared to pines from site S1 and S3. The understorey vegetation showed minimal regeneration during the first year but then increased greatly with time. Woody understorey cover and total vegetation

cover were negatively correlated with pine seedling density in sites with a high number of seedlings (e.g. S1 and S3). When woody cover, total cover and pine seedling density were low (e.g. S2), there were no correlations. There was a positive correlation between vegetation cover and the maximum height of *Pinus* seedlings in all study sites.

Keywords Wildfire · Maritime pine forest · Natural regeneration · Shrub species · Seedling density

Introduction

Fire is a natural factor of many Mediterranean landscapes and has an important influence on the biological productivity and composition of several ecosystems. Fire creates open areas, which favour the germination of species by removing established vegetation, and also has direct effects on germination and seedling survival (Hanley and Fenner 1998). The passage of fire may facilitate germination and the development of several species by changing the mineral nutrient content of the environment (Marcos 1997; Calvo et al. 2003, 2005). Trends in secondary succession beginning after a fire depend on several factors, including species composition in the initial community, fire severity, the season in which burning occurs (Dominguez et al. 2002) and the existence of either a soil or aerial seed bank able to survive disturbances (Ferrandis et al. 1996).

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In Spain, *Pinus pinaster* Ait. is one of the coniferous forest types most frequently subject to forest fires, which affect 33% of all coniferous forests (Pérez and Moreno 1998). Among the different *P. pinaster* populations distributed across Spain (Salvador et al. 2000), the population situated in the NW (León Province) is particularly subject to frequent fires. It is estimated that lightning starts two fires per year (Tapias et al. 1998). Likewise, in this zone, as in the rest of Europe, arson fires are very frequent. Owing to this high frequency, the *P. pinaster* population in this area has acquired a series of adaptive characteristics, including a high yield of serotinous cones, thicker bark and a significantly earlier flowering age than other Spanish populations (Tapias et al. 2004). *P. pinaster* is an obligate seeder that responds to fire through rapid seed dispersal, even beginning during a fire, and this continues for a few months after the disturbance; this is also a characteristic of other Mediterranean *Pinus* species, such as *Pinus halepensis* Mill. (Thanos et al. 1996; Herranz et al. 1997). For this reason, post-fire regeneration of this species depends on the canopy seed bank as a result of both the transient character of the soil seed bank for pine (Baskin and Baskin 1998) and the destruction of all seeds present on or near the soil surface during a fire. Seed germination and seedling recruitment are well adapted to exploiting post-fire conditions and promptly colonise open burned areas (Rego et al. 1991; Luis-Calabuig et al. 2002).

However, regardless of the high seed germination capacity of *P. pinaster* after a fire (Torres et al. 2006), its forest regeneration is dependent on post-fire environmental conditions, which affect seed germination and seedling establishment (Rodrigo et al. 2004). Seedling growth and competitive interactions between neighbouring seedlings or sprouting understorey vegetation may be of critical importance in determining plant composition in the post-fire community (Hanley and Fenner 1998). Regeneration patterns in different understorey vegetation types affect the success of pine re-establishment through inter-specific competition (Elliott and White 1987; De las Heras et al. 2002), mainly for water or light. Some studies have shown that the re-colonisation of *P. halepensis* after fire is hampered by competitive effects from obligate seeders in the understorey (such as Cistaceae), which are favoured by fire (De las

Heras et al. 2002; Nathan and Ne'eman 2004). However, other studies have described favourable interactions between pine seedlings and perennial herbs after fire (Trabaud et al. 1985).

In addition, competitive effects on the establishment of *P. pinaster* seedlings can also be expected in forests where the dominant understorey species consist mostly of woody and herbaceous resprouters (Calvo et al. 2003). Several studies have highlighted rapid post-fire regeneration in resprouter species such as *Erica australis* (Willk.), *Arctostaphylos uva-ursi* (L.) Sprengel and *Chamaespartium tridentatum*, (L.) P. Gibbs, (Calvo et al. 2002, 2005), all of which are typical of the understorey in this type of *P. pinaster* forest (Luis-Calabuig et al. 2002).

Possible beneficial and harmful interactions between understorey species and pine establishment occur mostly during early recruitment processes (Nathan and Ne'eman 2004) and knowledge of these effects is important in designing forest management strategies for burned areas.

The main goal of this study was to analyse the regeneration of a *P. pinaster* community after fire and also to study the relations with understorey vegetation and the establishment of *P. pinaster* seedlings during the first three years after wildfire.

Materials and methods

Study area

The study area is located in a *P. pinaster* stand in the Sierra del Teleno, León province (NW Spain), at an approximate altitude of 1,100 m. This is a *P. pinaster* stand with the total size of the original wood being 11,500 ha. In this area, 3,000 ha were burned by a wildfire in September 1998 that destroyed most of aerial biomass. The vegetation present in the area before the fire was dominated by *P. pinaster* aged 60–85 years, with 95% cover, and a density of 500–900 trees/ha (García p.c.). The species in the under-ground layer were: *E. australis* (33%), *Calluna vulgaris* (7.8%), *C. tridentatum* (3.6%), *Halimium alyssoides* and *Genista florida* with less than 1% (Santalla et al. 2001).

In the burned area, we select three sites: S1, S2 and, S3. Site S1 was characterised by a gentle slope (<10%) and north-facing aspect (42°16'16" N;

6°11'52" W); site S2 was situated on a gentle slope (<10%), facing S–W (42°15'30" N; 6°11'24" W) and site S3 was situated on a gentle slope (<10%) facing N–W (42°15'10" N; 6°11'03" W). In each site three permanent transects of 20 × 1 m were placed perpendicularly to the slope. The first transect was placed at random and the following separated 3 metres from each other. The burned pines remained in the sites during the three-year study period.

The climate is Mediterranean with 2–3 months dryness in summer and an annual precipitation of 650–900 mm (Ministerio de Agricultura 1980). An interesting feature of the local climate is the frequency of dry storms together with very low precipitation in spring and summer, which often produces crown fires (Tapias 1998). Rainfall was extremely low in the year of the fire (355 mm). In the following year, 1999, there were three periods of drought, one during the summer and the other two in February and November, each of which affected the regeneration process.

The soil is classified as a Cambisol (Junta de Castilla y León 1987). According to granulometric analysis, the soils in this area are classified as very sandy and acidic (pH = 5.5) with low organic matter and nitrogen content.

Sampling data

In each transect, 20 sampling units of 1 m² were marked and studied during the first, second and third years after the wildfire. In each sampling unit, the number and height of each pine seedlings were recorded. Similarly, in each sampling unit, the percentage cover of all the species present (herbaceous and woody) was visually estimated always by the same research team. Cover percentage higher than 100% was due to the species overlapped.

The soil characteristics one year after wildfire were analysed in each selected site by collecting five soil samples to a depth of 5 cm, as this is the horizon most affected by fires and where the main changes occur (Marcos 1997). The soil samples were air-dried and passed through a 2-mm mesh sieve. The following elements were determined: pH in water (1: 2.5), organic matter, total N, available P and Ca, Mg, K, and Na.

Statistical analysis

A two-way repeated measures analysis of variance was carried out to compare the results obtained relating to the number of seedlings/m² and maximum height in different sites over time, using the 3 years of study as the repeated measure and sites as fixed factor. The same procedure was used to compare woody, perennial and annual herbaceous cover and total vegetation cover values over time. Data expressed as percentage cover were arcsine-square root transformed prior to analysis. Data on density and height were log transformed to obtain the normal distributions required to perform the analysis. The results obtained for the different physical and chemical parameters of the soil were compared using a one-way analysis of variance to determine whether statistically significant differences exist between sites. The Tukey test was used to assess whether differences were significant. The David et al. (1954) test was used to check normality and the Cochran (1941) test was used to check homoscedasticity.

Pearson correlation coefficients were calculated to assess the significance of linear correlations between cover values for perennial herbs, annual herbs, woody species and total understorey vegetation with the number and maximum height of *Pinus* seedlings along the 3 years after fire. The maximum height was calculated based on the tallest seedling in each sampling unit. Plant nomenclature follows Tutin et al. 1964–1980.

Results

In the study of the soil characteristics one year after wildfire (Table 1), there were significant differences between S2 compared with S1 and S3 in terms of pH ($F_{2,12} = 7.30$; $P < 0.05$), soil organic matter ($F_{2,12} = 23.26$, $P < 0.05$), total nitrogen ($F_{2,12} = 27.39$; $P < 0.05$) and available K ($F_{2,12} = 7.08$; $P < 0.05$). These differences in soil characteristics could help explain changes in the density and height of the pine seedlings and in the regeneration of the vegetation community during the first year. No differences in the content of P, Mg, Ca and assimilable Na were observed amongst the sites.

The density of seedlings in the field (Table 2) indicated great heterogeneity in the response of the

Table 1 Mean values and standard errors (in brackets) of the soil characteristics in the burned sites one year after the fire

	S1	S2	S3	
pH	4.53 (0.07)	4.95 (0.12)	4.60 (0.02)	*
O.M. (%)	7.46 (0.28)	5.31 (0.44)	9.31 (0.49)	*
N (%)	0.15 (0.01)	0.09 (0.01)	0.20 (0.01)	*
P (mg kg ⁻¹)	16.50 (3.95)	37.50 (7.70)	14.40 (4.42)	n.s.
Mg ²⁺ (cmol _c kg ⁻¹)	0.22 (0.03)	0.29 (0.06)	0.28 (0.01)	n.s.
Ca ²⁺ (cmol _c kg ⁻¹)	0.47 (0.05)	0.79 (0.17)	0.64 (0.11)	n.s.
Na ⁺ (cmol _c kg ⁻¹)	0.22 (0.03)	0.16 (0.01)	0.17 (0.01)	n.s.
K ⁺ (cmol _c kg ⁻¹)	0.20 (0.01)	0.13 (0.01)	0.21 (0.01)	*

* $P < 0.05$ and n.s.=not significant. O.M.=Organic Matter (%)

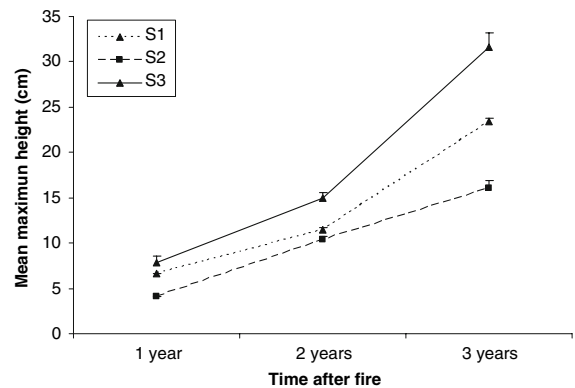
Table 2 Mean number of *Pinus pinaster* seedlings/m² and standard errors 1, 2 and 3 years after the wildfire.

	Years after wildfire		
	1	2	3
S1	46.73 (2.28) a	7.42 (0.98) b	11.53 (0.88) b
S2	16.63 (1.18) a	5.30 (0.85) b	7.25 (0.64) b
S3	12.38 (0.97) a	5.42 (0.81) b	6.53 (0.51) b

Different letters indicate statistically significant differences using the Tukey test ($P < 0.05$) for each site and time

three sites, with significant differences between sites through time ($F_{4,354} = 136.4$, $P < 0.05$). For this reason, they were independently analysed. However, although the interaction is statistically significant ($F_{4,54} = 138.9$, $P < 0.05$), the seedlings showed common trends through time in all three sites except that the decrease in the density of seedlings between the first and second years is much greater in S1. In general, the highest number of seedlings appeared in the first year in all three sites. There was a significant decrease in the number of seedlings from the first year after fire to the second and third years (S1— $F_{2,118} = 211.91$, $P < 0.05$; S2— $F_{2,118} = 10.57$; $P < 0.05$ and S3— $F_{2,118} = 28.9$; $P < 0.05$). However, these differences disappeared between the second and the third year in all the sites. In general, very high natural regeneration was observed in the dominant species, *P. pinaster*. A mean of 25.25 seedlings/m² was recorded in the first year, although this density was lower in the second (6.04 seedlings/m²) and third years (8.44 seedlings /m²) after wildfire.

The height growth (Fig. 1) was constant over the 3 years at site S2, while a growth burst could be observed between years 2 and 3 at sites S1 and S2. Also, pines from site S2 reached significant shorter ($F_{2,162} = 40.92$, $P < 0.05$) maximum heights in all

**Fig. 1** Mean values and standard error of maximum heights of *Pinus pinaster* seedlings in each site during the study period

years compared to pines from site S1 and S3. Seedling height patterns showed similar behaviour in all three sites from 1 to 3 years after the fire and there was a significant increase in height over time ($F_{2,312} = 424.2$, $P < 0.05$). However, there was a significant interaction between sites and height over time ($F_{4,312} = 16.4$, $P < 0.05$), as growth in S2 was similar between years 1–2 and years 2–3, whereas in S1 and S3 the increase was greater from the second to the third year.

The correlation analysis between mean number of *Pinus* seedlings and mean maximum seedling height (Fig. 2) showed a significant negative correlation only in S1 ($r = -0.41$, $P < 0.05$). This site had the highest number of seedlings so when height increased there was strong intraspecific competition which resulted in a decrease in the number of *Pinus* seedlings. In S2 and S3 there was no significant trend or intraspecific competition due to lower seedling density.

An analysis of changes in the plant community in terms of vegetation cover through time (Table 3)

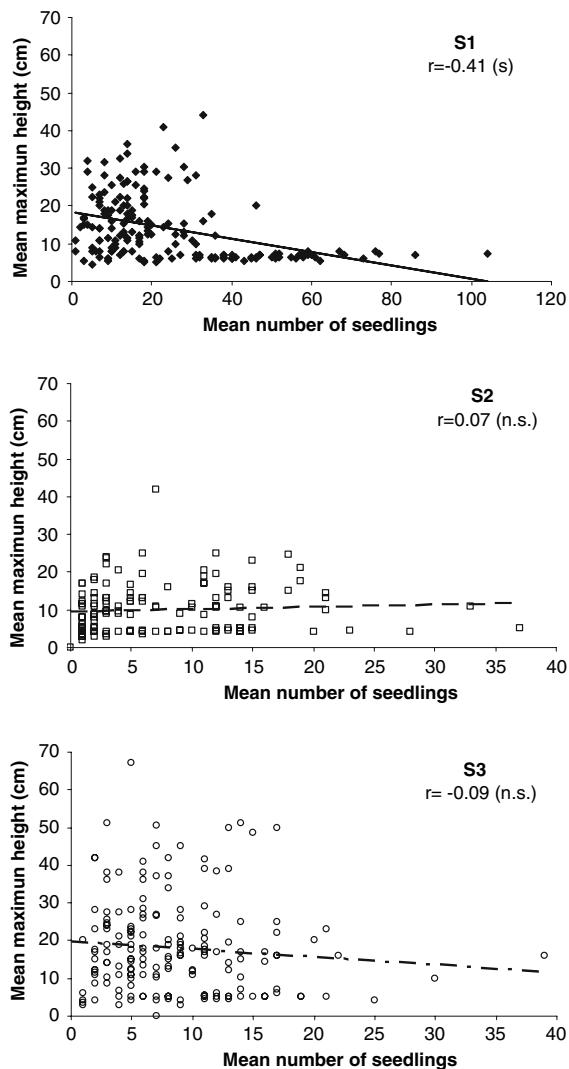


Fig. 2 Linear correlation between mean number and maximum height of *Pinus* seedlings in the three study sites. r = correlation coefficient; s = significant correlation ($P < 0.05$); n.s. = no significant correlation

showed that regeneration started 1 year after the fire, mainly with the recovery of typical woody resprouter species like *C. tridentatum* and *E. australis*, and seeders like *H. alyssoides* (Lam.) C. Koch. The recovery of woody species in the first year was significantly lower ($F_{2,177} = 11.52$, $P < 0.01$) in S2 than S1 and S3. The same differences were found in the second ($F_{2,177} = 43.46$, $P < 0.01$) and third years ($F_{2,177} = 31.85$, $P < 0.01$). This was most marked for the perennial woody species, *Hypochoeris radicata* L. and *Ornithogalum umbellatum* L. The recovery of perennial woody species was significantly lower in

S1 ($F_{2,177} = 8.04$, $P < 0.01$) than in S2 and S3. However, after the second year, no differences were observed between sites. Annual herbaceous species in the three sites appeared in the second year, with consistently lower values in S2. Both woody species and herbaceous (annual and perennial) species generally increased their cover values through time, although woody species showed the greatest increases and were dominant throughout the study period.

The total cover values showed a significant increase in time in the three sites. Significant differences were also found in S2, with lower values ($F_{2,177} = 39.09$, $P < 0.01$), compared with S1 and S3.

After the wildfire, there was an increase in percentage cover for woody and herbaceous (annual and perennial) species (Table 3), a decrease in the number of *Pinus* seedlings (Table 2) and an increase in maximum seedling height (Fig. 1) in the three sites. As a result, significant negative correlations were found (Table 4) between the number of pines and woody species cover in the sites where pine density and woody species cover was higher, that is, in S1 ($r = -0.56$) and in S3 ($r = -0.27$). This was also observed in the correlation of the number of pines and total understorey vegetation cover in S1 ($r = -0.56$) and S3 ($r = -0.27$). By contrast, in S2, where the density of pines was lower from the first year (Table 2) and values for woody species cover and total understorey cover were low (Table 3), no competitive effects were observed. There were significant negative effects between herbaceous (perennial and annual) species cover and the number of pines in S1. No significant influence was observed in the other two sites.

The increase in woody, annual and perennial herbaceous cover and in total cover through time showed a significant positive correlation with the maximum height of the *Pinus* seedlings (Table 4) in the study sites. The values for woody species cover and total cover showed the highest correlations with maximum *Pinus* seedling height in all sites.

Discussion

The post-fire regeneration of *P. pinaster* stands depends mainly on the effects of fire on pine seeds, which may be present in the soil seed bank or in the

Table 3 Mean percentage cover and standard error (in brackets) of woody species, perennial herbs, annual herbs and total understorey vegetation cover in the three sites (S1, S2, S3) situated in the *Pinus pinaster* area for each year after the wildfire: 1, 2, 3

	S1 years after fire			S2 years after fire			S3 years after fire		
	1	2	3	1	2	3	1	2	3
<i>Pinus pinaster</i>	1.22 (0.05)	7.33 (0.61)	15.13 (1.02)	0.03 (0.03)	5.05 (0.64)	9.56 (1.1)	1.00 (0)	8.58 (1.12)	14.17 (1.63)
<i>Chamaespartium tridentatum</i>	1.18 (0.05)	24.25 (2.18)	45.16 (3.47)	0.83 (0.13)	10.48 (1.26)	21.8 (2.1)	0.92 (0.07)	12.8 (0.96)	17.03 (1.34)
<i>Erica australis</i>	0.12 (0.02)	3.58 (0.96)	21.6 (3.77)		0.12 (0.08)	6.58 (0.7)	0.02 (0.02)	3.85 (1.2)	8.93 (1.45)
<i>Erica umbellata</i>						0.23 (0.12)			
<i>Halimium alyssoides</i>	0.15 (0.04)	6.93 (1.64)	12.92 (2.84)	0.21 (0.05)	2.4 (0.59)	8.05 (0.13)	0.86 (0.11)	21.76 (2.23)	39.83 (3.42)
<i>Halimium umbellatum</i>							0.02 (0.02)	3.88 (0.92)	6.26 (1.32)
<i>Helicrysum stoechas</i>		0.03 (0.03)	0.33 (0.26)						
<i>Polygala microphylla</i>		0.16 (0.11)	0.42 (0.34)						
Total woody cover	2.67 (0.08)	42.28 (2.90)	95.56 (6.47)	1.07 (0.12)	18.05 (1.62)	46.22 (3.27)	2.82 (0.14)	50.87 (2.90)	86.22 (3.95)
<i>Asphodelus albus</i>	0.03 (0.2)		0.33 (0.3)						
<i>Filipendula vulgaris</i>		0.53 (0.35)	0.37 (0.26)		0.17 (0.1)	0.02 (0.01)		0.08 (0.08)	0.01 (0.01)
<i>Hieracium pillosella</i>		0.02 (0.01)	0.25 (0.12)		0.07 (0.04)	0.25 (0.1)		0.25 (0.1)	0.25 (0.1)
<i>Hypochoeris radicata</i>		0.37 (0.09)	1.6 (0.4)	0.32 (0.1)	0.67 (0.2)	0.72 (0.2)		0.83 (0.28)	0.32 (0.1)
<i>Ornithogalum umbellatum</i>	0.03 (0.02)	0.25 (0.14)			1.22 (0.3)	1.38 (0.5)	0.35 (0.06)	1.3 (0.3)	0.58 (0.27)
<i>Rumex acetosella</i>							0.02 (0.01)		
<i>Sonchus arvensis</i>		0.08 (0.08)	0.33 (0.2)		0.05 (0.05)	0.55 (0.19)		0.33 (0.1)	0.85 (0.2)
Total perennial herbs	0.06 (0.04)	1.25 (0.48)	2.88 (0.6)	0.32 (0.1)	2.18 (0.36)	2.92 (0.6)	0.37 (0.01)	2.54 (0.48)	2.01 (0.47)
<i>Aira caryophyllea</i>			0.45 (0.3)			0.35 (0.1)		0.08 (0.1)	
<i>Andryala integrifolia</i>		0.17 (0.11)	0.27 (0.1)		0.17 (0.1)	0.18 (0.07)		0.43 (0.2)	0.1 (0.1)
<i>Senecio vulgaris</i>		2.33 (0.51)	12.5 (0.8)	1 (0.3)	6.38 (0.6)	6.91 (0.7)		3.21 (0.2)	2.92 (0.59)
Total annual herbs		2.5 (0.55)	13.22 (0.95)		1.17 (0.34)	6.91 (0.7)		3.64 (0.6)	3.1 (0.59)
Total understorey cover	2.73 (0.09)	46.03 (3.22)	111.66 (6.65)	1.39 (0.16)	21.4 (1.82)	56.05 (3.4)	3.19 (0.2)	57.05 (0.9)	91.33 (3.58)

Table 4 Pearson correlation analysis between number and mean maximum height of *Pinus* seedlings and woody, perennial herbs, annual herbs and total understorey vegetation cover in sites S1, S2 and S3

	No. <i>Pinus</i> seedlings	Height <i>Pinus</i> seedlings
<i>S1</i>		
Woody cover	−0.56*	0.73*
Perennial herbs cover	−0.22*	0.29*
Annual herbs cover	−0.44*	0.68*
Total understorey veg. cover	−0.56*	0.76*
<i>S2</i>		
Woody cover	0.06	0.66*
Perennial herb cover	−0.02	0.21*
Annual herb cover	0.01	0.46*
Total understorey veg. cover	0.05	0.65*
<i>S3</i>		
Woody cover	−0.27*	0.62*
Perennial herb cover	−0.05	0.25*
Annual herb cover	−0.13	0.22*
Total understorey veg. cover	−0.27*	0.63*

* marked correlations are significant at $P < 0.05$

aerial seed bank, or come from nearby populations that have not been affected by fire (Ferrandis et al. 1996; Daskalidou and Thanos 2004). This species, and in particular the Sierra del Teleno population, has a high percentage (82%) of serotinous cones (Velez 2000), that is, an aerial seed bank (Tapias et al. 1998), with high percentage viability (almost 100%) over long periods of time (Tapias et al. 2001, 2004). Furthermore, several laboratory studies (Martínez-Sánchez et al. 1995; Reyes and Casal 1995; Torres et al. 2006) have demonstrated that *P. pinaster* seeds can tolerate relatively high temperatures. These features could ensure good post-fire recovery. The presence of a high percentage of serotinous cones, which protect the seeds from high temperatures, may be the key characteristic that ensures good regeneration in the field (Rodrigo et al. 2004), as has been described for other species of *Pinus* (Habrouk et al. 1999). The importance of serotinous cones is reflected by the fact that other *P. pinaster* populations in southern Spain with a lower proportion of serotinous cones (Tapias et al. 2004) show little post-fire regeneration (Gallegos et al. 2003).

In the population studied, seed germination and seedling emergence occurred massively during the first year. The bulk of viable seeds (derived from the canopy seed bank) germinated after the rainy season during the following spring, and not in winter as occurs in other areas and species (Skordilis and Thanos 1995), since winters in this area are very

harsh. Therefore, it can be confirmed that pine seed germination and subsequent establishment occur early in the natural post-fire vegetation succession (Daskalidou and Thanos 2004). Conditions immediately after the fire, with reduced inter- and intraspecific competition and favourable microscale conditions, enhanced seed release, germination and seedling establishment (Izhaki and Ne'eman 2000). In the study area, high densities of *Pinus* seedlings were observed 1 year after the fire, similar to responses found in other parts of the Iberian Peninsula where the prolific regeneration of *P. pinaster* populations in S and SE Spain has been associated with the high amount of light reaching the area (Martínez Sánchez et al. 1996; Fernández Rebollo et al. 2001).

Although pine seedling regeneration is good across the study area, there is great heterogeneity in seedling density and height amongst the sites. This could be due to differences in exposure (as S2 was S–W exposure) and edaphic conditions (Luis-Calabuig et al. 2002), as site S2 has significantly less organic matter, nitrogen and potassium, as well as the fewest *Pinus* seedlings and least vegetation regeneration. Slight increases in pH values, and, above all, the higher amount of organic matter and nitrogen content after the fire favour the natural regeneration of this *P. pinaster* population, similar to that recorded by many other authors (e.g. Tsitsoni 1997). Similarly, variations in seedling regeneration between sites

could also be explained by differences in exposure. Thus, the sites with a northerly exposure (S1 and S3) have greater soil humidity and this is a condition required not only for germination, but also for seedling viability. Similarly, pine leaf content helps maintain site humidity, an aspect that differentiates S1 from S3 and S2 (Luis-Calabuig et al. 2002), as greater seedling density is recorded in the former.

As occurs in the population dynamics of other species after fires, initially high seedling density decreases markedly after the first summer, due to great drought stress. Thus, high recruitment rates, as observed in S1, are generally accompanied by high rates of seedling mortality, while relatively low levels of seedling establishment (e.g. S2) are counterbalanced by low seedling mortality (Borchert et al. 2003). The slight increase in the third year in the three sites may be due to the input of new seeds from cones on the burned trees that remained in the area or could come from not burned pines of nearby stands.

Nevertheless, a further factor needs to be taken into account to explain the decrease in pine seedling density from the second year, namely interspecific competition (Hanley and Fenner 1998; Eshel et al. 2000) from typical woody understorey species. Numerous studies (Elliott and White 1987; De las Heras et al. 2002) emphasise that the regeneration of different types of understorey vegetation affects the success of pine re-establishment through inter-specific competition, mainly for water or light. Ne'eman (1997) found that the development of the pine trees may be severely retarded by intense competition with *Cistus* shrubs during the early stages of succession. In the study area, 2 years after the fire, very good regeneration was observed in woody species such as *E. australis* and *C. tridentatum*, both of which are typical resprouters (Calvo et al. 2002), and in seeders such as *H. alyssoides*. The cover values for these woody species increase significantly over time, a characteristic which has been widely documented in post-fire regeneration in shrublands with similar species composition (Calvo et al. 2002, 2005). Consequently, as described in other studies, an increase in woody species in the understorey is negatively correlated with pine seedling density in sites where density is very high (S1 and S3) and cover values for woody species are highest after 3 years (95% cover in S1 and 86% in S3). However, where the cover values for woody species are relatively low (57% after

3 years in S2) and *Pinus* seedling density is low; this competitive effect was not observed.

In the study area, despite the possible competitive effects from understorey vegetation on the number of pine seedlings, the density reached after three years (approximately 8 seedlings/m²) is considered high enough to ensure good natural regeneration (Luis-Calabuig et al. 2002). The density in mature stands (60–80 years old) was 500–900 trees/ha (Garcia p.c.) and in other studies carried out in the same area 8–9 years after other different wildfire the mean density was 4 trees/m² (Torres 2000), indicating a good survival rate of seedlings. This density is much higher than that recorded in *P. halepensis* stands in the south of Spain (3.3 seedlings/m²) (Simarro et al. 2001) or in *P. brutia* populations in Greece (2–6 seedlings/m²) (Spanos et al. 2000).

Generally, the competitive effects of understorey vegetation on pine seedlings are mostly evident from changes in maximum seedling height. Thus, in the three study sites, there is a positive correlation between an increase in vegetation cover and the maximum height reached by the seedlings. This could indicate that *Pinus* seedlings have a strategy for searching for light when they are in intense competition with shrubs. By contrast, in studies carried out on *P. halepensis* after fire, Kazanis and Arianoutsou (1996) state that pine seedlings achieve a competitive advantage over other plants only at a later stage, when they grow above the shrubs and interfere with their light interception. Probably, in our study referred to early stages, seedling growth could also be influenced by other factors, like soil characteristics and water conditions.

Therefore, the post-fire management of *P. pinaster* stands with good and rapid natural regeneration, must take into account pine seedling density, understorey vegetation recovery and the heterogeneity of the environment. It should also be noted that during the first 3 years, when *Pinus* seedling density is high, the elimination of understorey vegetation is not advisable as the final density of the seedlings, even after possible competitive effects, is high enough to ensure good natural regeneration in the area. In addition, understorey vegetation appears to have a positive influence on the height of *Pinus* seedlings. Other authors (De las Heras et al. 2004; Gonzalez-Ochoa et al. 2004) have discussed the different silviculture treatments effectiveness in the potential improvement in young pine stands.

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