Establishment of *Pinus halepensis* Mill. saplings following fire: effects of competition with shrub species

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Abstract

An early study analysing the effects of competition from *Cistus monspeliensis*-dominated shrub canopy on *Pinus halepensis* saplings, both colonising a recently burnt area, has been extended in order to test initial predictions. Inter-specific competition effects on *P. halepensis* were experimentally analysed by a shrub thinning-out treatment carried out 1 year after fire. The extension of the recorded period confirmed (i) a significant increase in height, and (ii) the lack of variation in density of *P. halepensis* saplings when the shrub layer was removed. In contrast, the increase in relative growth rate in height (RGRh) and the decrease in mortality recorded during early post-fire stages for treated units did not persist in subsequent years. These two treatment-induced effects disappeared 1 year after the shrub clearing (29 months after fire). It is hypothesised that this time should represent a culminating point in the inter-specific competition established between *Cistus* and *Pinus* saplings simultaneously colonising recently disturbed areas and be a critical period for pine sapling survival. After this time, a reduction in relatively short-lived *Cistus* populations and an increase in *P. halepensis* abundance should be expected in the community. It is concluded that a shrub-clearing treatment could be recommendable if the initial post-fire pine sapling density is not high enough to successfully face the early critical competitive period. Consequences of early shrub competition on forest productivity during mature phases are also discussed. © 2002 Éditions scientifiques et médicales Elsevier SAS. All rights reserved.

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Nomenclature: for plant nomenclature see Tutin et al. (1964–1980).

1. Introduction

The crucial role that fire plays in the dynamics of many Mediterranean ecosystems has been repeatedly emphasised in the literature (Naveh, 1975; Trabaud, 1980; Espírito-Santo and Capelo, 1998; Martínez-Sánchez et al., 2000). Although fire is an ecological disturbance present in nearly all terrestrial ecosystems (Komarek, 1973), the dry summer conditions in regions with Mediterranean-type climates have resulted in recurrent wildfires, which have played a key role in the distribution, organisation, and evolution of ecosystems throughout their natural history (Keeley and Keeley, 1988; Singh et al., 1993; Trabaud, 1994). Trends in the secondary succession started after fire depend on several factors, such as species composition in the initial community (Hanes, 1971), fire severity (Trabaud and Valina, 1998), the season in which fire occurs (Martin, 1990; Davis, 1998), and the existence of a soil seed bank able to survive disturbances (Ferrandis et al., 1999a). The importance of fire in the natural history of Mediterranean ecosystems is evidenced by the development of a great number of adaptive plant responses, which have resulted in a widespread auto-succession phenomenon recorded throughout the Mediterranean regions (Hanes, 1997; Naveh, 1989; Trabaud, 1994).

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In southern Spain, *Pinus halepensis* Mill. is a dominant tree species, and by far the most abundant pine species. This dominance has been interpreted as a consequence of its high adaptation level to the low annual rainfall and the severe summer drought characterising the Mediterranean climate conditions in that region, in combination with fire (Gil et al., 1997). Indeed, *P. halepensis* has developed several adaptations in order to respond rapidly after fire, to the extent that many authors have considered fire as a key factor in explaining the expansion of this species (Trabaud et al., 1985; Quézel, 2000). Since *P. halepensis* is an obligate seeder, which often produces and accumulates serotinous cones (Tapias et al., 2001), it responds to fire on the basis of rapid seed dispersal, started even during fire and lasting for a few months after the disturbance (Saracino et al., 1993; Thanos et al., 1996; Herranz et al., 1997).

Inter-specific competition may strongly affect the population dynamics of competing plant species (Harper, 1977; Begon et al., 1999), water availability being particularly determinant in Mediterranean ecosystems (Trabaud, 1994). Studies on *P. halepensis* re-colonisation of recently burnt areas have revealed that inter-specific competition can greatly determine the success of pine re-establishment, with woody *Cistaceae* species being one of the most aggressive competitor taxa (Trabaud, 1995). In the Mediterranean basin, both *P. halepensis* (Martínez-Sánchez et al., 1999) and *Cistaceae* species (Arianoutsou and Margaris, 1981; Ferrandis et al., 1999b) concentrate their germination during the first post-fire stages (autumn and spring following the disturbance). Several authors have noted detrimental effects of some *Cistaceae* species such as *Cistus salvifolius* L. (Ne'eman et al., 1992; Ne'eman, 1994; Ne'eman et al., 1995) on *P. halepensis* saplings, while others have described some favourable interactions between pine and perennial species (e.g. *Brachypodium retusum* (Pers.) Beauv.) after fire (Trabaud et al., 1985). The effect of eliminating potential competitive shrub has been tested in *P. halepensis* in Israel (Ne'eman et al., 1992; Ne'eman, 1994; Ne'eman et al., 1995). Saplings without competition from *C. salvifolius* achieved a significantly greater height. In addition, a decrease in sapling mortality was also registered. This research also proved the importance of intra-specific competition in determining the success of *P. halepensis* establishment after fire.

In southeastern Spain, *Cistus monspeliensis* L. plays an active role in the post-fire community dynamics, covering the bare soil rapidly after fire, particularly in calcareous terrain. Its high potential as a pioneering coloniser in such areas has been noted by Martínez-Sánchez et al. (1996). Indeed, large surfaces in southeastern Spain submitted to recurrent fires in recent decades are now covered by nearly pure *C. monspeliensis* stands (Ruiz de la Torre, 1981).

Since 1994, competition relationships between *C. monspeliensis* and *P. halepensis* saplings have been studied in a burnt stand in Albacete province (SE Spain) by comparison between *C. monspeliensis*-cleared and non-treated (control) plots. Results from records during the three first post-fire years were published by Martínez-Sánchez et al. (1998). Main findings were: (i) height and relative growth rate in height (RGRh) of *P. halepensis* saplings were enhanced by the shrub-clearing treatment, and (ii) 3 years after fire, mortality was reduced for those *P. halepensis* saplings growing in treated plots. However, the effects of competition interaction of perennials need long-term study to confirm predictions from early observations. It should be expected that the mortality of *P. halepensis* saplings in non-treated plots (and thus under natural conditions) is halted if these grow high enough to overcome the dominance in light and nutrient competition from *C. monspeliensis*. But, when does this happen? And, how many saplings do really survive? On the other hand, how long will saplings growing in cleared plots maintain a higher development rate than those in non-cleared ones? More general questions derived from those above are: To what extent does competition with *C. monspeliensis* during the first post-fire stages threaten the natural re-establishment of the pre-fire *P. halepensis* forest in the area? And, to what extent would an early post-fire shrub-clearing treatment be recommendable in a management context? Such forestry practice may induce a prompt *P. halepensis* re-colonisation by favouring sapling survival and development.

The general goal of this paper was to confirm predictions in the Martínez-Sánchez et al. (1998) study by extending the period of *P. halepensis* sapling-parameter records. More specifically, the aims were: (i) to determine if *P. halepensis* sapling mortality due to competition with *C. monspeliensis* stops upon reaching a certain sapling size, the time at which this takes place, as well as the final sapling survival; and (ii) to confirm whether the increase in the growth rate of *P. halepensis* saplings due to the *C. monspeliensis*-clearing treatment recorded during early post-fire stages persisted during the following years or not.

2. Materials and Methods

2.1. Study area

The study was carried out in the Tus Valley, located in the Segura mountain range (southwest [SW] Albacete province, southeast [SE] Spain). The dominant plant community type in the area was pine forest, mainly formed by *P. halepensis*, the dominant tree species in warm and moderately warm locations (average annual temperature from 14.6 to 15.8 °C; most of the territory) and, to a lesser extent, by *P. pinaster* Aiton, restricted to wetter and colder sites with higher altitudes (average annual temperature from 12 to 14 °C). In addition, there were relatively small areas covered by shrublands among pine forests. They were the result of ancient fires. Indeed, the recurrent fire history in the area has provided a somewhat tiled aspect to the landscape, with a mosaic of shrubland and large-forest areas. The high

amount of dry plant fuel accumulated on the ground as a consequence of the progressive abandonment of silvicultural practices in the area during the last two decades, in combination with the severe drought period registered in southern Spain from 1990 to 1994, resulted in highly fire-prone conditions. Thus, in August 1994, a large man-induced fire originating in the Tus Valley burnt the vegetation over a surface of 14,000 ha.

The substratum in the area is formed by carbonate materials, mainly limestone and dolomites (Rodríguez-Estrella, 1979). This substratum has led to a calcisol soil by leaching calcic carbonate from the upper layers.

Weather data recorded at the closest meteorological station (Yeste, 10 km away, altitude = 877 m) over a 32-year period revealed a typically Mediterranean climate in the area. The average annual rainfall was 550 mm, showing a pronounced summer drought from June to September (average monthly rainfall during this period = 23.3 mm). Inter-annual rain variability is wide, with fluctuations in the annual rainfall from 300 to 600 mm within 5–10 year periods. Mean annual temperature was 13.1 °C. The climate was markedly continental: during summer (June–September), mean maximum temperature was 33 °C (maximum absolute record = 42 °C), while in winter (December–February) mean minimum temperature was 2 °C (minimum absolute record = –13 °C).

The study was carried out in a pure burnt *P. halepensis* stand (38°22' N, 2°24' W) with the following characteristics: (a) homogeneous pine population in relation to age, size, and degree of affectation by fire, (b) altitude equal to 897 m, (c) slope about 5%, and (d) south aspect (dominant in the burnt area). Before fire, a mature 70-year-old *P. halepensis* forest occupied the selected stand. Tree density was 425–450 individuals ha^{-1}. Main species in the understorey were *C. monspeliensis*, *Cistus albidus* L., *Rosmarinus officinalis* L., *Quercus rotundifolia* Lam., *Juniperus oxycedrus* L., *Pistacia lentiscus* L., and *Dorycnium pentaphyllum* Scop. Species of secondary importance were *Daphne gnidium* L., *Psoralea bituminosa* L., *Argyrolobium zanonii* (Turra) P.W. Ball, *Linum suffruticosum* L., and *Dactylis glomerata* L. The understorey was totally consumed by fire. No pine survived in the study zone.

2.2. Experimental design

In the selected stand, a 2500 m^2 surface was fenced in order to prevent the passage of animals, particularly herbivores likely to disturb or predate the post-fire plant recovery by sprout and seedling. Within the fenced area, ten permanent plots of 20 m^2 (10 m × 2 m) were randomly placed 16 months after fire (January 1996) (Martínez-Sánchez et al., 1998). At the beginning of the study, the percentage of shrub cover was visually estimated in each plot and all seedlings, saplings and sprouts of woody species were counted. In addition, all *P. halepensis* seedlings and saplings were labelled, and sapling height was measured with a 1 cm

Table 1
Average sapling density (saplings m^{-2}; SD between brackets) for *C. monspeliensis* and *P. halepensis* at the beginning of the experiment (January 1996). Average cover (in percentage; SD between brackets) for *C. monspeliensis* and sapling height (in cm; SD between brackets) for *P. halepensis* are also shown. t_9= statistical contrast between control and cleared subplots by a paired sample *t*-test (associated *P* values are shown between brackets)

	Cistus monspeliensis		*Pinus halepensis*	
	Density	Cover	Density	Height
Control	43.0 (34.7)	23.2 (13.4)	5.1 (1.6)	8.1 (3.4)
Cleared	42.0 (29.1)	19.8 (6.6)	4.8 (2.2)	8.4 (3.8)
t_9=	0.71 (0.41)	1.03 (0.29)	0.34 (0.73)	1.26 (0.23)

precision. Each plot was divided into two equal parts (subplots), according to a paired block design. In each plot, all shrub saplings were removed from one randomly selected subplot by clearing with shears. Sprouts were also eliminated. The other subplot was left as a control. After the treatment was carried out, heights of *P. halepensis* saplings were measured every six months from January 1996 to June 1998, and last in July 1999, for a total of seven samplings. In each survey, sapling mortality was estimated by counting dead saplings, which had previously been labelled. Seedlings and saplings which appeared between successive surveys were also labelled. The total sample size of pine saplings labelled throughout the study was 507 and 486 in treated and control subplots, respectively.

2.3. Pre-experimental vegetation features

At the time of the clearing treatment, 95% of the shrub saplings growing in plots belonged to *C. monspeliensis*. The others belonged to *C. albidus* or *R. officinalis*. No significant difference was detected when comparing the shrub cover or density (individuals m^{-2}) between control subplots and those assigned to the treatment (Table 1). The average density and the average height of *P. halepensis* saplings did not show significant differences between subplot groups (Table 1). More detailed information on initial vegetation features in the experiment can be found in Martínez-Sánchez et al. (1998).

2.4. Statistical analysis

The *P. halepensis* sapling parameters analysed were those considered in Martínez-Sánchez et al. (1998): mortality, density, height, and RGRh [expressed as (height in t_i – height in t_{i-1})/height in t_{i-1}, t_i being the date of sampling]. They were compared between treated and control subplots by a paired sample comparison *t*-test at 0.05 significance level. In all cases, normality and homogeneity of variance were previously checked with the Kolmogorov–Smirnov and Cochran tests, respectively. Mortality and growth data, in percentages, were previously submitted to an arcsine transformation for normal distribution adjustment. Correlations between height, density and time elapsed after fire
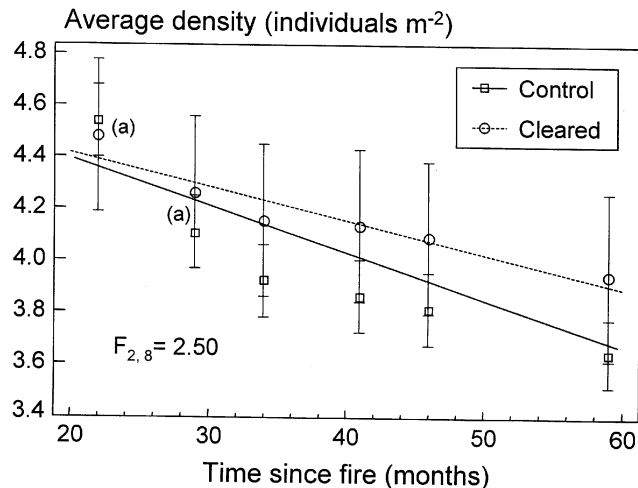
Average density (individuals m⁻²)

Fig. 1. Changes in *P. halepensis* sapling density (mean ± standard error) throughout the study period in treated and control subplots. Regression lines: treatment scores: $y = 4.67 - 0.01 \times$ ($P = 0.004$; $r^2 = 0.89$); control scores: $y = 4.98 - 0.02 \times$ ($P = 0.026$; $r^2 = 0.75$). Anova *F* ratio from comparison of line slopes ($F_{2,8}$) is also shown. Letter *a* indicates data from Martínez-Sánchez et al. (1998). Values of paired sample *t*-test (d.f. = 9): June 1996: 1.03; January 1997: 0.40; June 1997: 0.40; January 1998: 0.48; June 1998: 0.49; July 1999: 0.44 (not significant in all cases).

were calculated. A linear regression model was chosen by considering the best adjustment. For density and height, slopes of treatment and control regression lines were compared in order to detect differences in temporal change patterns. General suggestions in Zar (1984) were taken into account for the performance of statistics.

3. Results

3.1. Pine sapling density

P. halepensis sapling density did not vary significantly with the clearing treatment in any sampling (Fig. 1). However, a significant decrease in sapling density was detected throughout the study period in both subplot groups (Fig. 1), although final values were high (3.94 ± 2.37, and 3.64 ± 1.55 saplings/m² in treated and control subplots, respectively, 5 years after fire). Slopes of regression lines did not statistically differ (Fig. 1).

3.2. Pine sapling mortality

Significant differences in pine sapling mortality due to the thinning-out of shrubs were manifested 1 year after treatment (January 1997; Fig. 2): average mortality value registered in the control subplots was higher than that obtained in the treated ones. After this time, mortality gradually decreased in both treated and untreated subplots, with significant differences between treatments disappearing in subsequent samplings (Fig. 2). Sapling mortality
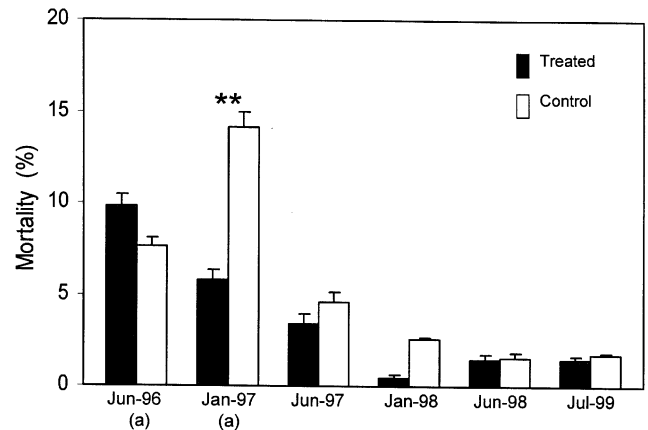

Fig. 2. *P. halepensis* sapling mortality (in percentage) recorded in treated and control subplots throughout the study period. Bars on columns indicate standard error. Letter *a* indicates data from Martínez-Sánchez et al. (1998). Values of paired sample *t*-test (d.f. = 9): June 1996: 1.15; January 1997: 2.83; June 1997: 0.61; January 1998: 0.94; June 1998: 0.19; July 1999: 0.26. Significance level (** $P < 0.01$) is shown in the figure.

values recorded at the end of the study were low (<2%) in both control and treated subplots (Fig. 2).

3.3. Pine sapling height and growth

Average height of pine saplings increased significantly with the removal of shrubs; such differences in height were detected in all post-treatment samplings (Fig. 3). Pine sapling height increased with time in both treated and control subplots; slopes of regression lines, however, did not significantly differ (Fig. 3).

Relative growth rate in height (RGRh) of *P. halepensis* saplings was sensitive to the shrub-clearing treatment dur-
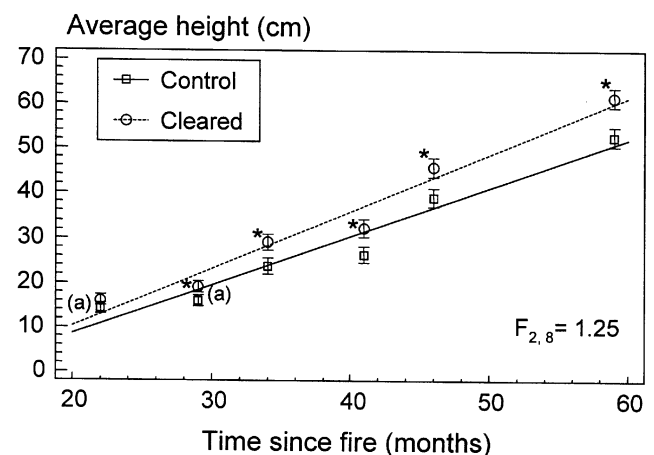
Average height (cm)

Fig. 3. Changes in *P. halepensis* sapling height (mean ± standard error) throughout the study period in treated and control subplots. Regression lines: treatment scores: $y = 15.41 + 1.28 \times$ ($P = 0.000$; $r^2 = 0.97$); control scores: $y = -13.39 + 1.09 \times$ ($P = 0.000$; $r^2 = 0.95$). Anova *F* ratio from comparison of line slopes ($F_{2,8}$) is also shown. Letter *a* indicates data from Martínez-Sánchez et al. (1998). Values of paired sample *t*-test (d.f. = 9): June 1996: 1.93; January 1997: 2.61; June 1997: 2.58; January 1998: 2.67; June 1998: 2.28; July 1999: 2.47. Significance level (* $P < 0.05$) is shown in the figure.
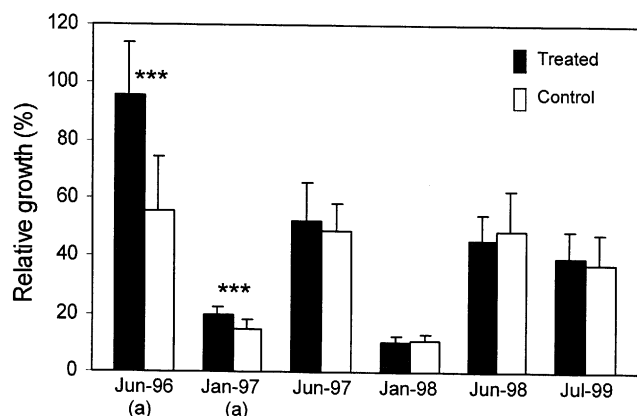
Fig. 4. Relative growth rate in height (RGRh) of *P. halepensis* saplings (in percentage) recorded in treated and control subplots throughout the study period. Bars on columns indicate standard error. Letter *a* indicates data from Martínez-Sánchez et al. (1998). Values of paired sample *t*-test (d.f. = 9): June 1996: 7.14; January 1997: 5.69; June 1997: 0.64; January 1998: 0.52; June 1998: 0.17; July 1999: 0.85. Significance level (***$P < 0.001$) is shown in the figure.

ing the subsequent year, as revealed by the significant increase in the growth rate registered in the first two samplings after treatment in the cleared subplots. However, this parameter was not significantly different between treated and control subplots from that time to the end of the study (Fig. 4).

Spring growth was greater than that registered in the autumn period in both treated and non-treated pine saplings. The average values of RGRh in spring were around 50%, whereas autumn ones never exceeded 20% (Fig. 4).

4. Discussion

Martínez-Sánchez et al. (1998) showed that an early shrub-clearing treatment enhanced height and RGRh and reduced mortality of *P. halepensis* saplings colonising a recently burnt stand in the first 3 post-fire years. In the present study, the record period is expanded from three to five years, confirming that shrub removal produces (i) a significant increase of *P. halepensis* sapling height and (ii) no differences in density of *P. halepensis* saplings. In contrast, the increase in RGRh and the decrease in mortality due to the thinning-out shrub treatment, which was recorded in the early stages, did not persist in subsequent years. These two treatment-induced effects disappeared 1 year after the shrub clearing, which was 29 months after fire.

This moment should represent a culminating point in the inter-specific competition established between *Cistus* and *Pinus* saplings, which colonise recently disturbed areas. A similar temporal pattern in pine sapling survival changes was described by Ne'eman et al. (1992) and Ne'eman (1994) in a *P. halepensis* forest stand submitted to a post-fire *C. salvifolius* thinning-out treatment. The reduction in pine sapling mortality from the third post-fire year shown in the present study was also described in south-eastern France

(Trabaud, 1988) from the fourth post-fire year and in Greece (Thanos et al., 1996) from the second. Ne'eman et al. (1992), Ne'eman (1994), and Ne'eman et al. (1995) proved the detrimental effect of inter- and intra-specific competition on pine sapling relative growth in height when studying a mixed *P. halepensis* and *C. salvifolius* stand. As detected in the present study, such an effect was restricted to the second post-fire year.

This critical period may be determined by the attainment of the maximum growth rate in relatively rapid-development *Cistaceae* shrub species, which may impose severe inter-specific competition intensity. Both *Cistus* (Arianoutsou and Margaris, 1981; Ferrandis et al., 1999b) and *Pinus* (Skordilis and Thanos, 1995; Herranz et al., 1997; Martínez-Sánchez et al., 1998; Martínez-Sánchez et al., 1999) species usually concentrate their post-fire seed germination in short time intervals after the disturbance, coinciding with the first rainy season. Twenty-nine months after fire, the competitive dominance of a well-developed dense *Cistus* shrub canopy on moderately low-developed pine saplings would become dramatic for the latter. The average height of control *P. halepensis* saplings at this time was 15.5 cm, with individuals shorter than 10 cm displaying the strongest mortality effects (Martínez-Sánchez et al., 1998). Therefore, this figure could be considered as a minimum height threshold: those individuals which surpassed this above-ground sapling size would greatly enhance their survival probability.

From that time and during the following successional stages, *P. halepensis* should be expected to increase its relative cover in relation to *C. monspeliensis*. The response of obligate-seeded woody *Cistaceae* species to fire is based on massive seed germination during the early post-fire stages from large persistent physically dormant soil seed banks (Thanos et al., 1992; Ferrandis et al., 1999b, 1999c), which are promoted to germinate by the thermal shock registered in the upper soil layers during fire (Thanos and Georghiou, 1988; Ferrandis et al., 1999b). However, they are relatively short-lived species, so a prompt decline in their populations can be expected. There is little information in the literature referring to this topic, but indeed Roy and Sonie (Roy and Sonie, 1992) described a *C. monspeliensis* and *C. salvifolius* ageing-induced population decline 15 years after fire. Conversely, long-lived *P. halepensis* individuals that survived the critical inter-specific competition period will increase their relative abundance (and dominance) in the plant community. This prediction for the community studied has been confirmed in other studies on *Pinus* and *Cistus* post-fire population dynamics in the Mediterranean basin (Trabaud et al., 1985; Moravec, 1990).

The significant effect of the *C. monspeliensis* clearing treatment on the RGRh of pine saplings recorded in the early study disappeared 29 months after fire. This result is consistent with the absence of differences in the regression line slopes for height (Fig. 3), which denotes similar temporal change patterns in pine sapling growth, regardless

of shrub removal treatment. In contrast, the significant effect on sapling height persisted to the end of the study period (at this point, control pines were 14% shorter than those treated), which may be essential for pine size in subsequent (and even final) successional stages. This observation should be taken into account in any post-fire pine forest management programme.

Another relevant consideration that should be stressed is the high pine sapling density recorded in the initial stage of post-fire plant recovery in our study zone. *P. halepensis* re-establishment is not always guaranteed. Studies in SE Spain have shown that the density of *P. halepensis* seedlings emerged after fire can vary in a wide range, from no regeneration at all to over 40,000 trees/ha (Herranz et al., 1997; Martínez-Sánchez et al., 1997, 1999; Ferrandis et al., 2001). *P. halepensis* colonisation ability depends on fire traits (Ouadah et al., 2001), pre-fire pine population (Martínez-Sánchez et al., 1997), post-fire climate factors (Trabaud et al., 1985; Trabaud, 1988), and predation of seeds (Saracino and Leone, 1993). In the present study, initial seedling density was high enough (ca. 50,000 saplings ha^{-1}) to ensure the re-establishment of *P. halepensis* in the area. In fact, no difference was recorded in pine sapling density due to the shrub-clearing treatment, and the final value (5 years after fire) was also very high in untreated subplots (nearly 40,000 saplings ha^{-1}). However, the mortality recorded during the early period of intense competition with *C. monspeliensis* could have dramatic effects on *P. halepensis* colonisation ability if initial density is not so high.

5. Conclusion

The expansion of the study period confirms that an early post-fire shrub-clearing treatment significantly increases the height of *P. halepensis* saplings, at least during the first five years of the succession. Research for a longer period is needed to determine the final effect on pine size. In contrast, the increase of the relative growth rate in height and the survival of *P. halepensis* saplings recorded in the early study, are restricted to the initial phases of re-colonisation (29 months after fire). In the study area, density was high enough to guarantee *P. halepensis* re-establishment, in spite of sapling mortality due to competition with shrub canopy. Additional studies in different situations of initial pine sapling density, also characterising *P. halepensis* natural post-fire recovery, would be recommendable to determine the profitability of such forestry practice.

Acknowledgements

References

Arianoutsou, M., Margaris, N.S., 1981. Early stages of regeneration after fire in a phryganic ecosystem (east Mediterranean). I. Regeneration by seed germination. Biol. Ecol. Méditer. 8, 119–128.

Begon, M., Harper, J.L., Townsend, C.K., 1999. Ecology, Individuals, Populations and Communities. 3rd ed. Blackwell Scientific Publications, Oxford.

Davis, G., 1998. Landscapes and biodiversity in Mediterranean-type ecosystems: the role of changing fire regimes. In: Moreno, J.M. (Ed.), Large Forest Fires. Backhuys Publishers, Leiden, pp. 109–131.

Espírito-Santo, M., Capelo, J., 1998. Ten years of observations after wildfire on permanent plots in central Mediterranean Portugal. In: Trabaud, L. (Ed.), Fire Management and Landscape Ecology. International Association of Wildland Fire, Washington, pp. 87–102.

Ferrandis, P., de las Heras, J., Herranz, J.M., Martínez-Sánchez, J.J., 2001. Influence of a low-intensity fire on a *Pinus halepensis* Mill. forest seed bank and its consequences on the early stages of plant succession. Isr. J. Plant Sci. 49, 105–114.

Ferrandis, P., Herranz, J.M., Martínez-Sánchez, J.J., 1999a. Fire impact on a maquis soil seed bank in Cabañeros National Park (Central Spain. Isr. J. Plant Sci. 47, 17–26.

Ferrandis, P., Herranz, J.M., Martínez-Sánchez, J.J., 1999b. Effect of fire on hard-coated Cistaceae seed banks and its influence on techniques for quantifying seed banks. Plant Ecol. 144, 103–114.

Ferrandis, P., Martínez-Sánchez, J.J., Agudo, A., Cano, A.L., Gallar, J.J., Herranz, J.M., 1999c. Presencia de especies del género *Cistus* L. (Cistaceae) en el pastizal de la raña del Parque Nacional de Cabañeros. Invest. Agr.: Sist. Recur. For. 8, 361–376.

Gil, L., Díaz-Fernández, P.M., Jiménez, M.P., Roldán, M., Alia, R., Agúndez, D., et al., 1997. Regiones de Procedencia de *Pinus halepensis* Mill., DGCN (Ministerio de Medio Ambiente), Madrid. .

Hanes, T.L., 1971. Succession after fire in the chaparral of southeastern California. Ecol. Monogr. 41, 27–52.

Harper, J., 1977. Population Biology of Plants. Academic Press, London.

Herranz, J.M., Martínez-Sánchez, J.J., Marín, A., Ferrandis, P., 1997. Post fire regeneration of *Pinus halepensis* Miller in a semi arid area in Albacete province (southeastern Spain). Écoscience 4, 86–90.

Keeley, J.E., Keeley, S.C., 1988. Chaparral. In: Barbour, M.G., Billings, W.D. (Eds.), North American Terrestrial Vegetation. Cambridge University Press, New York, pp. 165–207.

Komarek, E.V., 1973. Ancient fires. Proc. Annu. Tall Timbers Fire Ecol. Conf. 12, 219–240.

Martin, R.E., 1990. Goals, methods, and elements of prescribed burnings. In: Walstad, J.D., Radosevich, S.R., Sandberg, D.V. (Eds.), Natural and Prescribed Fire in Pacific Northwest Forests. Oregon State University Press, Corvallis, Oregon, pp. 55–66.

Martínez-Sánchez, J.J., Ferrandis, P., de las Heras, J., Herranz, J.M., 1998. Influence of *C. monspeliensis* on the early stages of development of *Pinus halepensis* seedlings after fire in Tus Valley (SE Spain). In: Trabaud, L. (Ed.), Fire Management and Landscape Ecology. International Association of Wildland Fire, Washington, pp. 205–211.

Martínez-Sánchez, J.J., Ferrandis, P., de las Heras, J., Herranz, J.M., 1999. Effect of burnt wood removal on the natural regeneration of *Pinus halepensis* after fire in a pine forest in Tus valley (SE Spain). Forest Ecol. Manag. 123, 1–10.

Martínez-Sánchez, J.J., Ferrandis, P., de las Heras, J., Herranz, J.M., 2000. Functioning and dynamics of plant communities in central and southern Spain. In: Trabaud, L. (Ed.), Life and Environment in the Mediterranean. WIT Press, Southampton, pp. 87–128.

Martínez-Sánchez, J.J., Herranz, J.M., Guerra, J., Trabaud, L., 1996. Natural re-colonisation of *Pinus halepensis* Mill. and *Pinus pinaster* Aiton in burnt forests of the Sierra de Alcaraz-Segura mountain system (SE Spain). Ecol. Mediter. 22, 7–24.

Martínez-Sánchez, J.J., Herranz, J.M., Guerra, J., Trabaud, L., 1997. Influence of fire on plant regeneration in a *Stipa tenacissima* L. community in the Sierra Larga mountain range (SE Spain. Isr. J. Plant Sci. 45, 309–316.

Moravec, J., 1990. Regeneration of NW Africa *Pinus halepensis* forests following fire. Vegetatio 87, 29–36.

Naveh, Z., 1975. The evolutionary significance of fire in the Mediterranean region. Vegetatio 29, 199–208.

Naveh, Z., 1989. Fire in Mediterranean landscape, an ecological perspective. Fire in Ecosystems Dynamics. SPB Academic, The Hague, pp. 1–20.

Ne'eman, G., 1994. The effect of thinning-out on the survival and development of *Pinus* and *Cistus* seedlings after fire on Mt Carmel, Israel. In: Domingos, X. (Ed.), Proceedings of the 2nd International Conference on Forest Fire Research. University of Coimbra, Coimbra, pp. 1021–1031.

Ne'eman, G.H., Lahav, H., Izhaki, I., 1992. Spatial pattern of seedlings one year after fire in a Mediterranean pine forest. Oecologia 91, 365–370.

Ne'eman, G.H., Lahav, H., Izhaki, I., 1995. Recovery of vegetation in a natural east Mediterranean pine forest on Mount Carmel, Israel, as affected by management strategies. Forest Ecol. Manag. 75, 17–26.

Ouadah, N, Pausas, J.G., Ferran, A., Cortina, J., 2001. The role of fire severity in the regeneration of *Pinus halepensis* forests. Proceedings of the International Workshop "Fire and Biological Processes", Banyuls-Sur-Mer. pp. 22–26.

Quézel, P., 2000. Taxonomy and biogeography of Mediterranean pines (*Pinus halepensis* and *P. brutia*). In: Ne'eman, G., Trabaud, L. (Eds.), Ecology, Biogeography and Management of *Pinus halepensis* and *P. brutia* Forest Ecosystems in the Mediterranean Basin. Backhuys Publishers, Leiden, pp. 1–12.

Rodríguez-Estrella, T., 1979. Geología e Hidrología del Sector de Alcaraz-Liétor-Yeste (prov. Albacete), Síntesis Geológica de la Zona Prebética, Segunda Parte, IGME, Madrid. .

Roy, J., Sonie, L., 1992. Germination and population dynamics of *Cistus* species in relation to fire. J. App. Ecol. 29, 647–655.

Ruiz de la Torre, J., 1981. Matorrales. In: Ramos, J.L. (Ed.), Tratado del Medio Natural, UPM-CETONA-INIA-ICONA, Madrid. pp. 501–542.

Saracino, A., Leone, V., 1993. Ecological features and dynamics of seed dispersal after fire in a *Pinus halepensis* Miller forest. In: Trabaud, L., Prodon, R. (Eds.), Fire in Mediterranean Ecosystems. Commission of the European Communities, Brussels, pp. 151–159.

Saracino, A., Leone, V., De Natale, F., 1993. Permanent plots for the study on natural regeneration after fire of *Pinus halepensis* Miller in dunal environment. Annali Bot. 51, 209–217.

Singh, G., Kershaw, A.P., Clark, R., 1993. Quaternary vegetation and ire history in Australia. In: Gill, A.M., Groves, R.H., Noble, I.R. (Eds.), Fire and the Australian Biota. Australian Academy of Science, Camberra, pp. 23–54.

Skordilis, A., Thanos, C.A., 1995. Seed stratification and germination strategy in the Mediterranean pines *Pinus brutia* and *Pinus halepensis.*. Seed Sci. Res. 5, 151–160.

Tapias, R., Gil, L., Fuentes-Utrilla, P., Pardos, J.A., 2001. Canopy seed bank in Mediterranean pines of southeastern Spain: a comparison between *Pinus halepensis* Mill., *P. pinaster* Ait., *P. nigra* Arn. and *P. pinnea* L. J. Ecol. 89, 629–638.

Thanos, C.A., Daskalakou, E.N., Nikolaidou, S., 1996. Early postfire regeneration of a *Pinus halepensis* forest on Mount Párnais. Greece. J. Veg. Sci. 7, 273–280.

Thanos, C.A., Georghiou, K., 1988. Ecophysiology of fire-stimulated seed germination in *Cistus incanus* subsp. *creticus* (L.) Heywood and *C. salvifolius* L. Plant. Cell Environ. 11, 841–849.

Thanos, C.A., Georghiou, K., Kadis, C., Pantazi, C., 1992. Cistaceae: a plant family with hard seeds. Isr. J. Bot. 41, 251–263.

Trabaud, L., 1980. Impact Biologique et Écologique des Feux de Végétation sur l'Organisation, la Structure et l'Evolution de la Végétation des Garrigues du Bas-Languedoc. Thèse d'Etat, Univ. Sci. Tech. Languedoc, Montpellier.

Trabaud, L., 1988. Survie de jeunes plantules de pin d'Alep apparues après incendie. Studia Oecol. 5, 161–170.

Trabaud, L., 1994. Postfire plant community dynamics in the Mediterranean basin. In: Moreno, J.M., Oechel, C. (Eds.), The Role of Fire in Mediterranean-type ecosystems. Springer-Verlag, Berlin, pp. 1–15.

Trabaud, L., 1995. Modalités de germination des cistes et des pins méditerranées et colonisation des sites perturbées. Rev. Ecol. (Terre Vie) 50, 3–14.

Trabaud, L., Michels, C., Grosman, J., 1985. Recovery of burnt *Pinus halepensis* Mill. forests. II. Pine reconstitution after wildfire. Forest Ecol. Manag. 13, 167–179.

Trabaud, L., Valina, J., 1998. Importance of tree size in *Pinus halepensis* fire survival. In: Trabaud, L. (Ed.), Fire Management and Landscape Ecology. International Association of Wildland Fire, Washington, pp. 189–196.

Tutin, T.G., Heywood, V.H., Burges, N.A., Moore, D.M., Valiente, D.H., Walters, S.M., et al., 1964–1980. Flora Europea. Cambridge University Press, Cambridge.

Zar, J.H., 1984. Biostatistical Analysis. 2nd ed. Prentice-Hall, New Jersey.