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Influence of high temperatures on seed germination of a special *Pinus pinaster* stand adapted to frequent fires

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Abstract

This study examines the effect of fire on the germination of *Pinus pinaster* seeds from a population with special adaptations to this type of disturbance, due to the high frequency of fires to which they have been subjected. The action of fire was simulated in the laboratory using thermal shocks. Temperatures of 60, 90, 120, 200 and 300 °C were used for exposure times of 1 and 5 min. The viability of seeds of this species from the soil seed bank of a population subjected to a wildfire was also evaluated. The results show that germination is not increase by a thermal treatment. The effect is negative at temperatures above 90 °C and exposure times of 1 min with a significant decrease in, or even no, germination. Therefore the seeds cannot stand high temperatures and reproductive effort is placed on serotinous cone development and the production of high numbers of seeds. The high viability of the seeds from the area burned by wildfire, immediately after the fire and 1 year later, show the high potential of the soil seed bank to contribute to the regeneration of the burned area.

Introduction

Recurring fires are the most significant disturbances which the vegetation in the Mediterranean region is subjected to (Tárrega and Luis 1992). Over the last few decades more than 200,000 ha, 41.2% of which were woods, have been burned annually by fires in Spain (Pérez and Moreno 1998). Two factors characterize the strength of a fire: the duration of the burn and the temperature reached (Reyes and Casal 1995).

Pinus pinaster stands are amongst the communities which frequently suffer the effects of fire. According to Trabaud and Campant (1991) pine communities are more inflammable than isolated specimens of this species. The litter of these communities is usually inflammable during dry periods, producing flames which can reach the upper vegetation strata. The effects of the fires on coniferous forest ecosystems have been widely studied by various authors (Naveh 1974; Archibold 1989; Castro et al. 1990; Thanos and Marcou 1991; Trabaud and Campant 1991; Martínez Sánchez 1994; Pérez and Moreno 1998).

The recovery rate and the post-fire composition of the burned communities are determined by the nature of the original cover and by the type and intensity of the fire, because these factors determine the size and vigour of the residual flora (Archibold 1979). According to Fenner (1995), in order to carry out an appropriate management of the resources, it has become more and more necessary to model and predict the regeneration processes (Red et al. 1998)

In the case of *Pinus pinaster*, as in many other pine species, the only possibility of regeneration is from seed (Martínez Sánchez 1994). The advantage of germination is that it increases the genetic variability and stability of the populations (Baskin and Baskin 1998). However, obligate seeders are rare and present disadvantages in comparison with species that can resprout vegetatively and so occupy the area more quickly (Naveh 1975; Trabaud 1987; Valbuena 1995). In obligate seeders, the seedlings reappearing after a fire come from the soil seed bank, by dispersion from neighbouring areas or from seeds held within cones in the canopy (serotiny) (Lamont et al. 1991). Many studies verify the influence of fire on seed germination in *Pinus* species (Castro et al. 1990; Martínez-Sánchez et al. 1995; Reyes and Casal 1995; Thanos and Marcou 1999).

The population studied is in an area (Tabuyo, located in Sierra del Teleno, NW Spain), which suffered from frequent fires. Tapias et al. (1998) indicate that in this mountain region, 30 fires were caused by lightning between 1978 and 1998. The magnitude of the problem, and the historical importance and frequency of fires are evident from a summary of the most significant fires, which occurred in 1922 (8000 ha were burnt), 1949 (400 ha), 1979 (2000 ha), 1991 (2000 ha), 1993 (400 ha), 1994 (700 ha), 1997 (400 ha) and 1998 (3000 ha). The latter was classed as a large fire because more than 3000 ha burned. It is estimated that two fires per year are started by lightning in this area. Because of these frequent fires, the mass of *Pinus pinaster* in this area has acquired a series of morphological and physiological characteristics that are absent from the nearest populations (150 km away) (Tapias et al. 1998). The characteristics which distinguish this group from other *P. pinaster* populations in the Iberian Peninsula include high serotiny (more than 80% of cones are serotinous) (Tapias et al. 1998, 2004). Likewise, Tapias et al. (2004) point out that this *P. pinaster* population is included in the Atlantic genetic group (highly serotinous provenance) and in general high levels of this trait are found in locations with a high frequency of lighting fire (>1 fires 100 km^{-2} $year^{-1}$), as occurs in the area where this study was carried out. These serotinous cones accumulate in the crown of the trees and only open as a result of thermal increases (temperatures above 45 °C) (Tapias et al. 2001). Another important and distinctive characteristic of this population is early flower production, which can begin in 4 year old trees, although the production of fertile seeds starts between 10 and 15 years (Sanchez 1999). In addition, *Pinus pinaster* has a characteristic aerial seed bank, and is capable of storing fertile seeds in closed cones for up to 50 years (Tapias et al. 1998).

The aim of this study is to analyse the effect of the high temperatures produced during a fire on the germination of *Pinus pinaster* seeds belonging to a population with special adaptations to recurring fires. This study includes an analysis of the viability of the seeds present in the soil seed bank after a wildfire.

Materials and methods

The biological materials used in this study were seeds of *Pinus pinaster* Aiton. The seeds were collected in a natural *Pinus pinaster* stand situated in the Sierra del Teleno, SW León province (M.T.U.29TQG2984), at an approximate altitude of 1100 m. The climate is Mediterranean with 2–3 months' summer dryness and annual precipitation of 650–900 mm (Ministerio de Agricultura 1980). An interesting feature of the local climate is the frequency of dry storms and very low precipitation in spring (mean annual spring precipitation is 180 mm) and summer (mean annual summer precipitation is 14.65 mm), which often produces crown fires (Sanchez 1999).

Seeds were collected in July 2000, coinciding with the natural dispersal period of this species. The cones were collected from different specimens throughout the stand of *Pinus pinaster*. The pine cones were opened by placing them in a dry air oven at 45 °C. This temperature was chosen in accordance with the bibliographical information on the opening of *Pinus pinaster* serotine cones (Tapias and Gil 2000; Tapias et al. 2001; Reyes and Casal 2002a). The temperature used to open the cones (45 °C) has been shown not to affect the germination response of *Pinus pinaster* seeds (Reyes and Casal 2002b, c). The resin sealing the scale joints melts at this temperature, thus releasing the seeds. The seeds were stored in open paper bags, which permitted ventilation, and at laboratory temperature in a dry place until they were used.

In order to determine the effect of fire on germination, a method widely used by various authors (Trabaud and Casal 1989; Tárrega et al. 1992) was employed. This method consists of exposing non-selected seeds to high temperatures for short periods of time in order to simulate the action of fire under conditions as natural as possible. According to Trabaud (1979), the heat in a fire operates on a concrete point for only a short period of time (between 5 and 15 min) and the temperatures reached at 2.5 cm below the soil surface vary between 44 and 150 °C. Based on these facts and on the information obtained in field experiments (Valbuena 1995), in which temperatures reached in the soil surface during fire were 300 °C, in soils with a high quantity of stones, as the soils of study area (unpublished data), we selected the following combinations of temperature and exposure times: 60, 90, 120, 200 and 300 °C for 1 and 5 min; the seeds were heated in a hot air chamber.

Immediately after treatment the seeds were sown in 8.5 cm diameter Petri dishes on four layers of filter paper saturated with demineralized water. There were 6 replicates of 15 seeds for each treatment. These treatments were compared with another group of 6 replicates, which was not subjected to thermal shock. The dishes were placed in a controlled environment cabinet at a temperature of 20 °C ± 1 °C with photoperiods of 15 h light/9 h dark. A temperature of 20 °C was used, following other germination studies where the temperature between 20 and 23 °C (Trabaud and Oustric 1989). Fungus attacks were avoided by using a fungicide (Benlate) at a very low concentration of 0.5 g/l, which has been proven to have no effect on seed germination.

The seeds were examined every week. A seed was considered to have germinated when the radicle could be seen with the naked eye (Côme 1970). The experiment was continued in this way for 17 weeks.

The average time for germination was also estimated using the expression:

$$t_m = \frac{N_1 T_1 + N_2 + \cdots + N_n T_n}{N_1 + N_2 + \cdots + N_n}$$

where N_1 is the number of seeds which have germinated between time T_1 and T_2, and so on (Côme 1970).

In order to identify the viability of the *Pinus pinaster* seeds present in the soil seed bank, which have suffered a wildfire, and maintenance of this viability over time, three plots (B1, B2 and B3) of 30×10 m were established in the area affected by the 1998 fire. A control plot was established in an unburned area. Ten 20×25 cm soil samples were randomly collected to a depth of 5 cm in each plot (B1, B2, B3 and control). Sampling was carried out immediately after the fire (1 month), before the first rains and 1 year later in order to examine the maintenance of viability over time. The direct method was used to obtain the seeds from the soil seed bank (Roberst 1981). The Tetrazolium test (Benister Romero 1989) was used to assess the viability of the seeds collected from the plots.

Data analysis

Data on percentage germination in each treatment in time was compared by a two-way (treatment and time, repeated measure) ANOVA. The significance of the results was assessed using Scheffe's test (1959). Prior to this, we checked sampling normality following David et al. (1954) and the homogeneity of the variances following Cochran (1941).

Results

The germination results for the *Pinus pinaster* seeds allow three treatment groups to be differentiated (Figure 1) with significant differences among them ($p < 0.0001$). The first one consists of the control, with 86.58% germination, 60 °C for 1 and 5 min treatment and, lastly, the 90 °C-1 min treatment with a recorded maximum of 88.82% germination. There were no significant differences between these treatments. A second group includes the 90 °C-5 min treatment as an intermediate situation with 24.44% germination. The third group is formed by the highest temperature treatments: 120, 200 and 300 °C and exposure times of 1 and 5 min. Independent of the exposure time, percentage germination in this group falls more markedly or is even zero. No significant differences are recorded among them.

In general, *Pinus pinaster* germination is not significantly affected by temperatures from 60 to

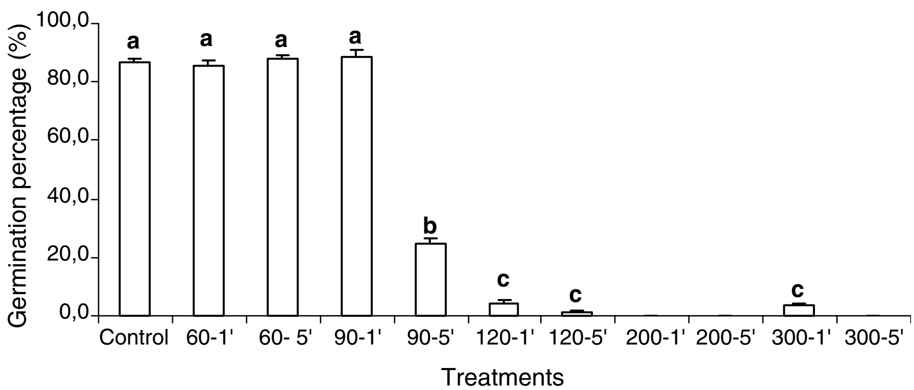

Figure 1. Percentage germination of *Pinus pinaster* seeds in the original situation and after thermal shock treatments: 60, 90, 120, 200, 300 °C and exposure times of 1 and 5 min; different letters indicate significant differences between treatments.

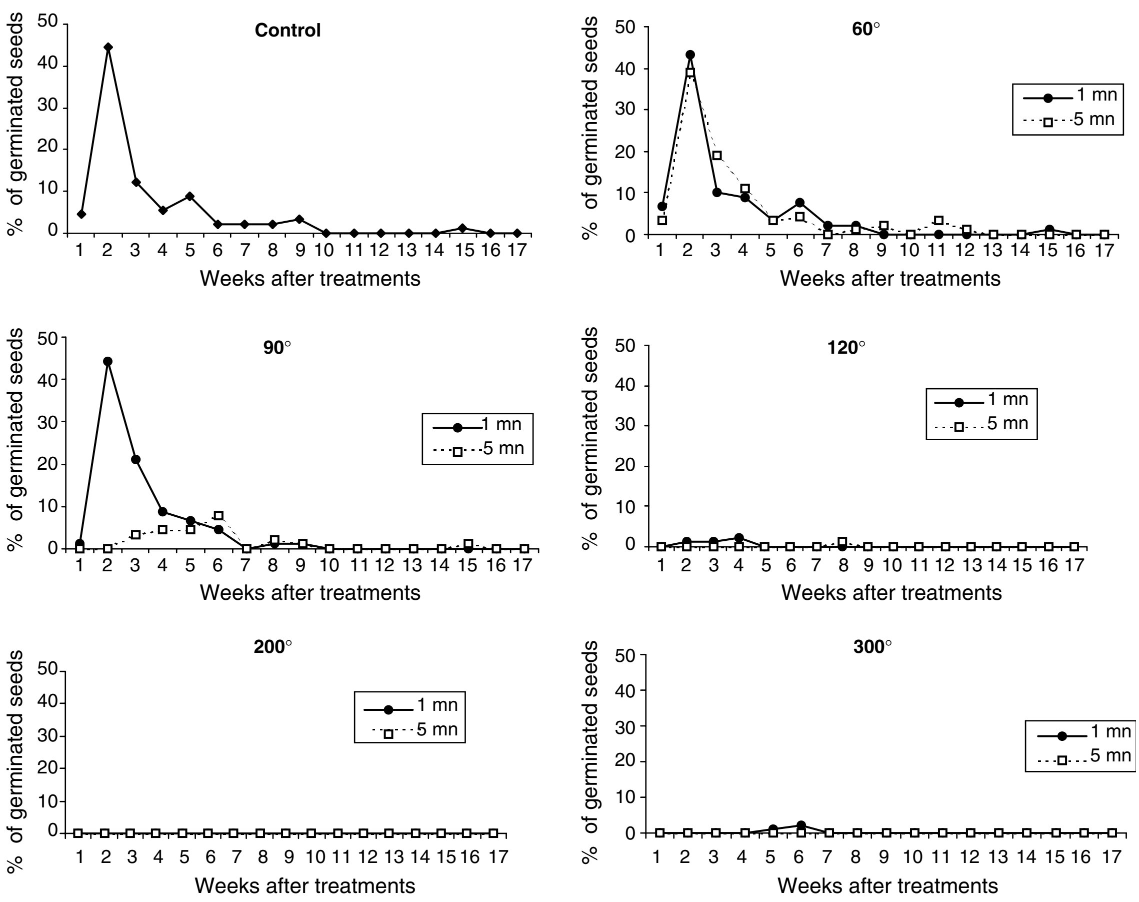

Figure 2. Distribution of germination times of *Pinus pinaster* according temperatures (°C) and times (minutes).

90 °C. However, when temperatures are higher than 90 °C and exposures times are elevated, it has a significant negative influence on germination.

The temporal distribution of germination (Figure 2) after each thermal treatment shows that the control, 60 °C-1 min, 60 °C-5 min and 90 °C-

Table 1. Germination average time (weeks).

	Control	60°-1 min	60°-5 min	90°-1 min	90°-5 min	120°-1 min	120°-5 min	200°-1 min	200°-5 min	300°-1 min	300°-5 min
Germination average time (weeks)	3.35	3.18	3.47	3.01	5.77	3.25	8	0	0	5.67	0

Table 2. Percentage viability of seeds from the burnt plots (B1, B2 and B3) and the number of seeds found per square metre.

	B1	B2	B3
Time 0			
After fire	85.39%	77.58%	84.78%
Seeds/m^2	246 ± 31.13	202 ± 32.58	188 ± 30.32
Time 1			
1 year after fire	88.23%	27.77%	50%
Seeds/m^2	432 ± 79.12	158 ± 24.49	136 ± 23.63

1 min attain germination peak (approximately 40%) in the second week. From this point on there is a significant ($p < 0.0001$) decrease in germination. However, when either temperature or exposure time increase there are a delay in the germination peak (until the sixth week).

Most treatments: control, 60 °C-1 min–5 min; 90 °C-1 min and 120 °C-1 min, show an average germination time (Table 1) of approximately 3 weeks. However, 90 °C-5 min, 120 °C-5 min and 300 °C-1 min attain the highest average germination times at more than 5 weeks.

The information provided by these results can be completed with that concerning what happens in the soil after a wildfire; this depends on the viability of the seeds which come from the aerial seed bank. For this reason, we studied the viability of seeds collected from the soil seed bank after a wildfire. Immediately after a fire, the percentage viability of the seeds from this *Pinus pinaster* stand is very high, exceeding 77% in the plots B1, B2 and B3 (Table 2). As regards the control zone, the number of seeds found is very small (four seeds), as this species maintains a persistent aerial seed bank and therefore does not need to invest much energy in maintaining a soil seed bank. These viability percentages decrease 1 year after the fire in the plots B2 and B3, since some seeds in the seed bank had already germinated, others are eaten by herbivores and there is no new addition from the aerial seed bank. In contrast, in plot B1 the number of seeds increased and viability was very high 1 year after the fire presumably because of new seeds which were deposited by trees surviving a fire (personal observation) and which were viable.

Discussion

It is well established that the fire regime has important implications for plant community composition within ecosystems (Williams et al. 1994). As indicated by Hanley and Fenner (1998), the growth responses of seedlings from seeds that have been subjected to thermal treatment may provide some clues as to how fire-adapted regeneration strategies influence the patterns of recruitment observed in post-fire plant communities. It this study area, no significant differences were observed between the germination of seeds which were not subjected to heat treatment and those which received up to 90 °C-1 min, but higher temperatures damage the embryo and germination falls sharply. Therefore the temperature increase did not produce an increase in percentage germination. Similar results have been obtained in other populations of the same species (Martínez-Sanchez et al. 1995; Escudero et al. 1999) and in other species of the genus *Pinus* (*P. halepensis* and *P. sylvestris*) from nearby areas (Nuñez and Calvo 2000). However, other authors, such as Reyes and Casal (1995), working with a *P. pinaster* population in Galicia (NW Spain), recorded differences between percentage germination in the control (58%) and in thermally treated seeds (approximately 35 %). However, the percentages reached in the Galician study are very far from the 90% attained in our study.

Martínez-Sanchez et al. (1995) state that *Pinus pinaster* seeds from populations situated in the south of Spain are unlikely to be significantly affected at temperatures of up to 150 °C-1 min, and even register germination at 200 °C-1 min. Escudero et al. (1999) obtained identical results with seeds from the south of Spain. Reyes and Casal (1995) used seeds collected in the north of the peninsula and obtained germination at temperatures of up to 150 °C. In contrast, in the *Pinus pinaster* stand studied here the temperature limit for germination was reduced to 90 °C-1 min; that is, these seeds had greater sensitivity to higher temperatures than any other population of the same species, despite having been subjected to frequent fires. Perhaps this population has adopted another strategy to adapt to the fires which consists of producing an abundant quantity of serotinous cones that remain closed in the tree, thus maintaining viability and ensuring the survival of the species. Serotinous cones provide efficient insulation against the effects of high temperatures reached during the fire (Hanley and Fenner 1998; Reyes and Casal 2002a). Consequently, the seeds, as our results show, cannot stand high temperatures, and reproductive effort goes into either cone serotiny or a high seed yield.

As regards the time required for germination to start, germination was observed in this population from the first week after the thermal shock in those treatments which have no harmful effect on the seeds. At temperatures above 90 °C the time taken to start germination was longer. Similar results were observed by other authors (Reyes and Casal 1995; Escudero et al. 1999), but with the difference that all the seeds began to germinate at the same time independent of the thermal ranges. This supports the idea that this population is more sensitive to the thermal impacts.

The mean germination time was 3 weeks and was considered intermediate in comparison with those obtained by other authors: less than 3 weeks (Reyes and Casal 1995; Escudero et al. 1999) and longer periods in the studies carried out by Martínez Sanchez et al. (1995).

The heat to which seeds, either present in the soil or aerial bank, were subjected in the natural fire did not exceed 90 °C. This conclusion was arrived at by comparing the viability of seeds from the area burned by natural fires and the results of experimental thermal shock.

If the seeds were in the soil this is possible, as bibliographical data given by Trabaud (1979) and Marcos (1997) show that the soil temperature does not exceed 70 °C during a fire. If the seeds were in the aerial bank, the serotinous cones protected the pine seeds from high temperatures. The protective value of coniferous cones was demonstrated by Fravers (1994). In studies carried out in *Pinus pinaster* populations from Galicia (NW Spain), Reyes and Casal (2002a) found that high temperatures during the fire favoured the opening of cones and released the seeds, with minimal effects on their viability. Higher temperatures also occur during maximum summer and spring temperatures in these latitudes, when natural dissemination occurs (Loisel 1966; Francelet 1970; Vega 1977; Abbas et al. 1984; Catalan 1985). *Pinus pinaster* does not need excessively high temperatures for most of its cones to open their bracts and disperse the seeds from inside: an estimated temperature of about 45 °C may be sufficient (Tapias et al. 1998; Reyes and Casal 2002a).

The population in the Sierra del Teleno exhibits some morphological and physiological adaptations that could have arisen from the particular environmental conditions which occur in the area, namely the frequent recurrence of fires. Among these adaptations, the most remarkable may be the existence of serotinous cones (Tapias et al. 2004), which protect the seeds from the devastating effects of fire. This, together with the fact that a high percentage of germination occurs very early in the life of the trees (Sanchez 1999), allows us to predict that natural regeneration in this area will not suffer the problems found by Castro et al. (1990) in Portugal or by Escudero et al. (1999) in south of Spain. As a result of these special adaptations, this population can withstand lower temperatures than other populations in the Iberian peninsula. Another special adaptation presented in this population is the appearance of fertile cones 8 years after the fire (unpublished data). This is not unique, since other researchers have recorded flowering in trees in less than 6 years, but in conditions of reduced intraspecific or interspecific competition from shrubs (Tapias et al. 2001).

In conclusion, the seeds of the *Pinus pinaster* stand studied show greater sensitivity to high temperatures than any other population of the same species. This population may have adopted an alternative strategy to adapt to fires, which involves producing an abundant quantity of serotinous cones that remain closed in the tree, so maintaining viability and ensuring the survival of the species. As a result of this adaptation, post-fire regeneration will be conditioned more by the presence of viable seeds that are deposited in the soil seed bank from the aerial seed bank than by the high temperatures; that is to say, the cones which open as a result of temperatures reached during the fire. The density of viable seeds present in the soil was sufficient to ensure natural regeneration in this area during the first months after a fire. One year after the fire, the presence of seedlings is only possible if burnt trees in the area continue to contribute viable seeds to the ground.

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