Effect of high temperatures on seed germination and seedling survival in three pine species (*Pinus pinaster*, *P. sylvestris* and *P. nigra*)

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Abstract. In the present study, we analyse the germination and seedling growth of three *Pinus* species (*P. pinaster*, *P. sylvestris* and *P. nigra*) under laboratory conditions after thermal shocks simulating the temperature effects of fire. Temperatures up to 150°C and 5 min exposure show negative effects on the percentage germination of *P. pinaster* seeds. *P. sylvestris* and *P. nigra* cannot stand temperatures greater than 110°C and 5 min exposure. In all three species, thermal shocks delay the start of germination. In addition, seeds from *P. pinaster* germinate over a longer time range. Seedling aerial growth after germination is influenced by high temperatures in *P. sylvestris* and *P. nigra*, but not in *P. pinaster*. Finally, thermal shocks produce a reduction in root growth in comparison with aerial growth in *P. sylvestris*.

Additional keywords: dormancy, mean germination time, seedling growth, thermal shock, viability.

Introduction

Fire is a long-established ecological factor that has shaped the life-history traits of Mediterranean plant species (Trabaud 1983, 1987, 1991), and that plays a decisive role in the dynamics and structure of Mediterranean-type ecosystems (di Castri and Mooney 1973; Naveh 1975; Trabaud 1980; Gill *et al*. 1981). Nevertheless, in the last few years, the number and, especially, the surface burned by forest fires have increased considerably in the Mediterranean basin (Vélez 2004). These fires mainly affect pine forests (Daskalakou and Thanos 1996) owing, among other factors, to their high resin content, which favours the ignition (Elvira and Hernándo 1989) and propagation of fires (Vélez 2000).

Vegetation regeneration after fire can occur in two different ways (Thanos 1999; Moreno and Cruz 2000): by resprouting, as in *Quercus pyrenaica* (Calvo *et al*. 1991) and *Erica australis* (Calvo *et al*. 1998), or by germination when soil conditions are suitable, as occurs with *Pinus* or *Cistus* (Alonso *et al*. 1992; Valbuena *et al*. 1992; Tárrega *et al*. 1995).

Post-fire regeneration of pines, as with other non-sprouting woody plant species, depends on various factors, including the effects of temperatures reached during the fire, the availability of suitable microsites for germination, the presence of adequate microhabitats for seedling survival and growth (Keeley and Zedler 1978; St Pierre *et al*. 1992; Lloret *et al*. 1996), and the position of these seeds (cones *v*. soil bank) during the fire (Habrouk *et al*. 1999). Numerous studies have verified the influence of heat shock on seed germination in *Pinus* species (Thanos and Skordilis 1987; Castro *et al*. 1990; Thanos and Marcou 1991; Martínez-Sánchez *et al*. 1995; Reyes and Casal

1995, 2001, 2002*b*; Daskalakou and Thanos 1996; De las Heras *et al*. 1997; Escudero *et al*. 1997, 1999; Saracino *et al*. 1997; Skordilis and Thanos 1997; Habrouk *et al*. 1999; Núñez and Calvo 2000; Trabaud 2000; Álvarez *et al*. 2005). Furthermore, in all scenarios after a fire, the main factor for the regeneration of pine forests will be the availability of viable seeds in the burned area. Seeds may come from the soil seed bank, from serotinous cones, or from mature cones present on trees not killed by fire, both inside and on the margins of the burned area (Martínez-Sánchez *et al*. 1995). The position of the seeds, in the soil seed bank or in the canopy bank, is one of the characteristics that allows them to survive high temperatures reached during the fire. *Pinus pinaster* maintain a long-term permanent seed bank in the serotinous cones of the canopy, which open after the passage of fire (Daskalakou and Thanos 1996; Rodrigo *et al*. 2004) by differential shrinkage caused by desiccation of the different fibres constituting the cone scale (Harlow *et al*. 1964). The serotinous cones of *P. pinaster* allow it to tolerate higher temperatures (Torres Carretero 2002). *Pinus nigra* and *P. sylvestris* do not have serotinous cones (Lanner 1998), and show very low or nil regeneration in most areas affected by large summer wildfires (Trabaud and Campant 1991; Ibáñez and Retana 1997; Rodrigo *et al*. 2004). This is due to the fact that summer fires negatively affect the seeds that are either in the cones, as dissemination happens in winter (Tapias and Gil 2000), or in the soil seed bank.

Percentage germination is not the only factor that controls the regeneration of *Pinus* species after fire: among other factors, seedling establishment is also very important. In addition, fire may also have direct effects on seedling survival (Hanley and

Fenner 1998). In some cases, the number of *Pinus* seedlings that appear in the field is lower than the number of seeds present in the soil seed bank (Valbuena and Calvo 1998; Torres Carretero 2002). This may be due to the effects of changes in temperature and humidity on initial seedling survival after fire (Valbuena and Trabaud 1993; Daskalakou and Thanos 1996).

Another factor that probably influences seedling establishment and growth is the pre-germination temperature to which seeds were subjected. Thermal shock produces an alteration in the embryo and so influences germination. However, larger seeds resist high temperatures better (Kandya and Ogino 1986; Escudero *et al.* 2000; Reyes and Casal 2001), and may also be able to emerge more successfully from deeper soil than smaller seeds (Hanley and Fenner 1998). In general, high temperatures modify proteins, the cell wall and cellular metabolism in seeds (Anderson 2004), and for these reasons, could affect the seedling growth (Bewley and Black 1994). There is a lack of knowledge about the effects of temperature on seedling survival and growth. In order to understand how post-fire patterns of seedling distribution are regulated, it is vital that the effects of heat shock on germination and seedling survival and growth are examined (Hanley and Fenner 1998).

The main goal of the present study was to simulate and analyse the effects of high temperatures produced during a fire on the germination of *P. pinaster*, *P. sylvestris* and *P. nigra* and on seedling survival and growth after thermal shock.

Materials and methods

Seed material

The biological materials used in the present study were seeds of *Pinus pinaster* Aiton, *Pinus sylvestris* L. and *Pinus nigra* Arn. The seeds were collected in three nearby stands in the Sierra del Teleno, SW León province (Universal Transversal Mercator-UTM coordinates 29TQG2984), at an altitude of approximately 1100 m. All three stands are characterised by acid brown soils of sandy textures with a very stony C horizon. The climate is Mediterranean with 2–3 months' summer dryness and annual precipitation that varies between 650 and 900 mm (Rivas Martínez 1987). The three stands were close to each other and shared similar soil conditions, climate, altitude and exposure.

Collection was carried out at the same time in three zones to avoid variations due to the annual variability of environmental conditions on seed characteristics (Molina *et al.* 1997). The *P. pinaster* cones were opened by placing them in a dry air oven at 45°C, whereas the *P. sylvestris* and *P. nigra* cones were opened by placing them in a dry air oven at 28°C. The temperature used to open the cones (45°C and 28°C respectively) has been shown not to affect the germination response of *P. pinaster*, *P. sylvestris* and *P. nigra* seeds (Reyes and Casal 2002*a*, 2002*b*; Álvarez 2003). The seeds were stored in open paper bags, which permitted ventilation, and at laboratory temperature in a dry place until they were used.

Germination tests

The *Pinus pinaster* seeds were subjected to the following combinations of temperature and exposure time using a dry air oven: 90, 110, 150 and 200°C for exposure times of 1 and 5 min. These temperatures were selected after Trabaud (1979), who showed that the heat in a fire acts 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 200°C. *Pinus sylvestris* and *P. nigra* seeds were only subjected to 90 and 110°C for 1 and 5 min, as several authors (Reyes and Casal 1995; Escudero *et al.* 1997; Núñez and Calvo 2000) indicate that the critical germination temperature of these two species is between 90 and 100°C. There were four replicates of 25 seeds for each treatment in each species.

A control sample was used for each species. Immediately after treatment, the seeds were sown in 8.5 cm-diameter Petri dishes on four layers of filter paper saturated with demineralised water. 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, and is comparable with other germination studies, where temperatures have varied between 20°C and 23°C (Trabaud and Oustric 1989). 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 duration was 70 days.

Before implementing these treatments, a viability test was carried out on a total of four replicates of 25 seeds for each species, i.e. a total of 100 seeds for each species, using the Tetrazolium test (Besnier Romero 1989).

When the seeds had germinated, 25 seedlings were randomly selected from each treatment and species and were transplanted into plastic pots. They were watered with demineralised water every week and were placed in a controlled temperature area. Seedling growth and survival were studied for 10 weeks. The length of both the aerial part of the stems and subterranean root length of every seedling was then measured (cm).

Statistical analysis

Total percentage viability was calculated for each species using the data obtained in the Tetrazolium test. The total germination percentages and the mean germination time were also calculated for each of the experimental treatments.

The mean germination time was estimated using the following expression:

$$t_m = \frac{N_1 T_1 + N_2 T_2 + \cdots + N_n T_n}{N_1 + N_2 + \cdots + N_n}$$

where N_1 is the number of seeds that have germinated during time T_1, N_2 the number of seeds that have germinated between time T_1 and time T_2, and so on (Côme 1970).

Similarly, we calculated the average aerial stem/subterranean length ratio and percentage seedling survival.

Data from mean germination time, percentage germination, seedling survival and the growth of aerial and subterranean parts of each species were analysed by a two-way ANOVA (temperature and exposure time). In order to compare the differences between species after common treatments (control, 90°C – 1 min, 90°C – 5 min, 110°C – 1 min and 110°C – 5 min), a two-way analysis of variance (treatments and different species) was carried out to check for the existence of significant differences in mean germination time, percentage germination, seedling survival and the growth of aerial and subterranean parts. To indicate differences between the control and treatments, the control data

were included in all the analyses. The Tukey test was performed to determine the significance of the differences. All statistical analyses were carried out using the statistical package Stastistica '98 (Statsoft, Tulsa, OK, USA). Before analysis, sampling normality was checked using the David test (David *et al*. 1954) and homogeneity of variance was assessed using the Cochran test (Cochran 1941). For statistical analyses, data expressed as percentage germination were arcsine-transformed prior to analysis and the average germination time and aerial and subterranean length data were log-transformed.

Results

Percentage germination and mean germination time

Percentage germination in the control (Table 1) was high and did not show any significant differences between the three *Pinus* species ($F = 1.381$; $P > 0.05$). However, percentages for common thermal shock treatment (90°C – 1 min; 100°C – 1 min; 100°C – 5 min) were significantly higher in *P. pinaster* and in *P. sylvestris* ($F = 29.439$; $P < 0.05$) than in *P. nigra*.

Pinus pinaster seed germination after thermal shock (Table 1) showed significant differences as regards temperature ($F = 159.384$; $P < 0.05$) and exposure time ($F = 465.511$; $P < 0.05$), because germination was nil at temperatures equal to or above 150°C and exposure times of 5 min. There were no significant differences in comparison with the control in this species when the temperatures or exposure times were low (less than 150°C – 1 min and 200°C – 1 min).

Pinus sylvestris and *P. nigra* seeds were negatively affected by high temperatures and exposure time relative to the control (Table 1). At a temperature of 110°C for 5 min, percentage germination was significantly reduced, falling to 4% in *P. sylvestris* ($F = 990.125$; $P < 0.05$) and to 15% in *P. nigra* ($F = 1128.125$; $P < 0.05$).

The mean germination time was significantly greater in the seeds of *P. pinaster* (between 21 and 28 days) than in *P. sylvestris* and *P. nigra* (4 days, Fig. 1) in the common treatments (control, 90°C – 1 min, 90°C – 5 min, 110°C – 1 min
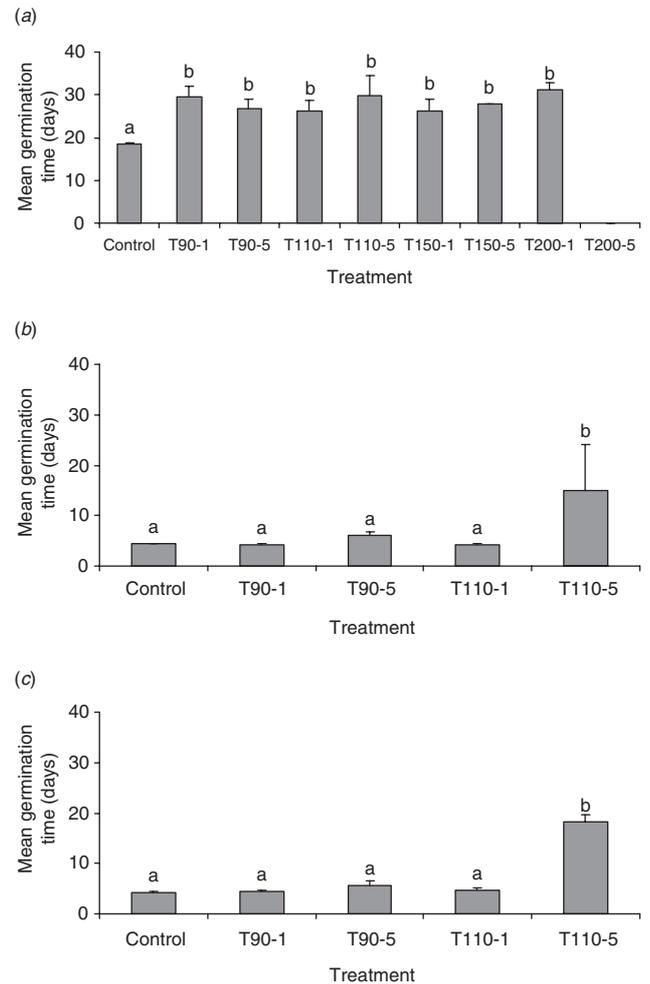

Fig. 1. Mean germination time (days) and standard deviation (s.d.) for *Pinus pinaster* (*a*), *Pinus sylvestris* (*b*) and *Pinus nigra* (*c*) seeds for each treatment. Different letters indicate significant differences between treatments at 95% ($P < 0.05$) in each species.

Table 1. Percentage germination of *Pinus pinaster*, *Pinus sylvestris* and *Pinus nigra* seeds and standard deviation (s.d.) in the control and after different thermal shock treatments at 90, 110, 150 and 200°C (exposure times 1 and 5 min)

Treatment	*Pinus pinaster*		*Pinus sylvestris*		*Pinus nigra*	
	Germination (%)	s.d.	Germination (%)	s.d.	Germination (%)	s.d.
Control	97[a]	1.5	99[c]	0.5	91[e]	2.63
90°C – 1 min	86[a]	1.91	96[c]	0.82	94[e]	0.58
90°C – 5 min	91[a]	1.5	96[c]	0.82	91[e]	1.5
110°C – 1 min	87[a]	1.5	99[c]	0.5	84[e]	1.63
110°C – 5 min	92[a]	2.16	4[d]	0.82	15[f]	1.89
150°C – 1 min	94[a]	1.29	–	–	–	–
150°C – 5 min	1[b]	0.5	–	–	–	–
200°C – 1 min	88[a]	0.82	–	–	–	–
200°C – 5 min	0[b]	0	–	–	–	–

Significant differences between treatments in each species: [a,b] *P. Pinaster*; [c,d] *P. Sylvestris*; [e,f] *P. nigra*.

and 110°C – 5 min) ($F = 341.745$; $P < 0.05$). Mean germination time in the three species was significantly increased by both temperature ($F = 31.999$; $P < 0.05$) and exposure time ($F = 51.090$; $P < 0.05$) after all thermal treatments in comparison with the control.

Temporal distribution of germination

The temporal distribution of germination was concentrated during the second and third weeks for *Pinus pinaster* (Fig. 2). In contrast, the maximum germination peak appeared during the first week in *P. sylvestris* and *P. nigra* (Fig. 2). In general, thermal treatments delayed the onset of germination, mainly in *Pinus pinaster*, and in this species, seed germination occurred over a prolonged period.

Seedling survival and growth

Pinus pinaster seedling survival percentages (Fig. 3) were similar to the control after all thermal treatments. However, seedling survival of *P. sylvestris* (25% survival) and *P. nigra* (7%) were reduced at 110°C for 5 min relative to the control.

In the control samples, seedling aerial stem length for *P. sylvestris* was significantly lower ($F = 6.39$; $P < 0.05$) than in the other two pines (Table 2). However, after common thermal treatments (90°C – 1 min, 90°C – 5 min, 110°C – 1 min, 110°C – 5 min), aerial stem length in *P. pinaster* seedlings was significantly higher ($F = 16.646$; $P < 0.05$) than both *P. sylvestris* and *P. nigra* (Table 2).

Neither temperatures ($F = 0.524$; $P > 0.05$) nor exposure time ($F = 0.399$; $P > 0.05$) affected seedling growth in *P. pinaster*, which after 10 weeks had reached 9-cm aerial stem length for all the treatments (Table 2) without any significant differences relative to the control. By contrast, seedling aerial stem length in *P. nigra* decreased significantly with increased temperature ($F = 155.98$; $P < 0.05$) and exposure time ($F = 118.05$; $P < 0.05$) in relation to the control. In the case of *P. sylvestris*, seedling aerial stem length only decreased with drastic shock (110°C – 5 min).

Seedling root lengths showed significant differences between *Pinus* species ($F = 48.337$; $P < 0.05$) in the control, with the longest root growth in *P. nigra* and the shortest in *P. sylvestris*. Thermal treatments significantly reduced *P. sylvestris* root growth ($F = 45.14$; $P < 0.05$), whereas *P. pinaster* root length was only negatively affected by drastic shock (110°C – 5 min). In contrast, *P. nigra* seedling root length was significantly increased ($F = 29.93$; $P < 0.05$) following this drastic shock (110°C – 5 min).

The aerial stem/root length ratio was significantly higher ($F = 20.922$; $P < 0.05$) in *P. sylvestris* than in the other species in both control and thermal treatments (90°C and 110°C).

Discussion

The post-fire regeneration of *Pinus* species depends not only on the removal of established vegetation, which favours
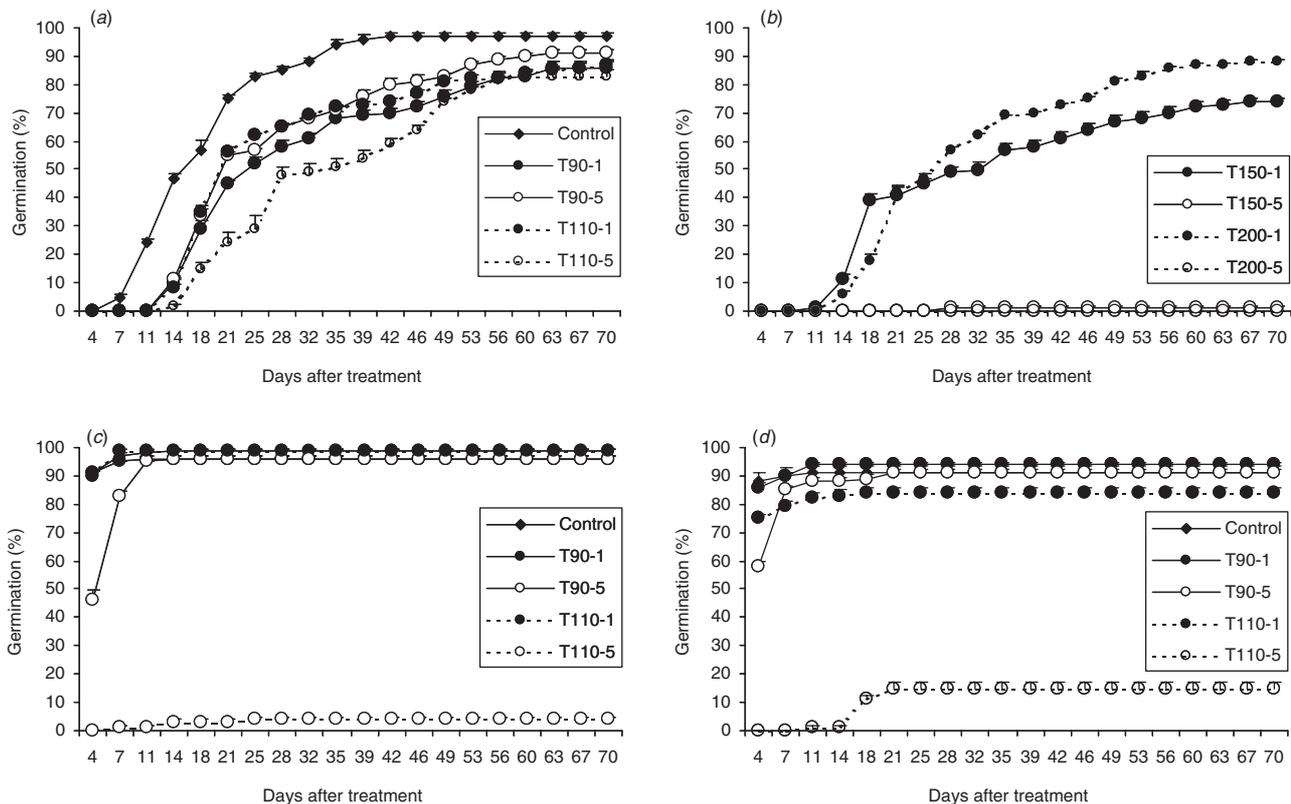

Fig. 2. Distribution of germination times and standard deviation (s.d.) for (*a*, *b*) *Pinus pinaster*, (*c*) *Pinus sylvestris* and (*d*) *Pinus nigra* in control samples and in each thermal shock treatment: 90, 110°C (*P. pinaster*, *P. sylvestris* and *P. nigra*), and (*b*) 150, 200°C (only *P. pinaster*) with exposure times of 1 and 5 min.
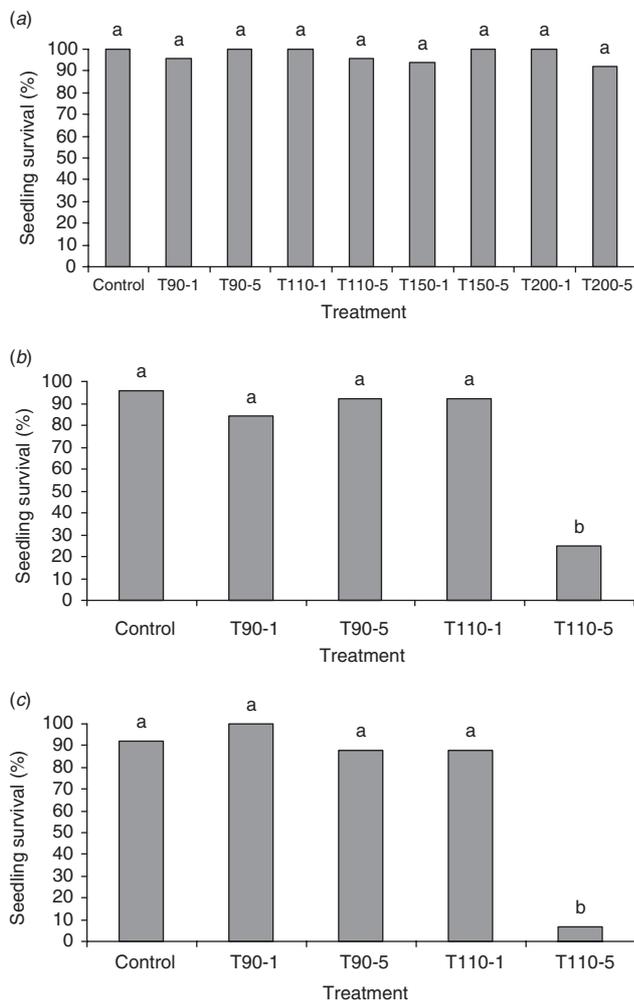
Fig. 3. Percentage seedling survival for *Pinus pinaster* (*a*), *Pinus sylvestris* (*b*) and *Pinus nigra* (*c*) in the control and after different thermal shock treatments at 90, 110, 150 and 200°C (exposure times 1 and 5 min). Different letters indicate significant differences between treatments at 95% ($P < 0.05$) in each species.

germination, but also on the direct effects of fire on germination and seedling survival. The results presented here show differences in germination between *P. pinaster*, *P. sylvestris* and *P. nigra* after thermal shocks. *Pinus pinaster* seeds can tolerate higher temperatures than those of *P. sylvestris* and *P. nigra*. These differences may be related to seed size, as *P. pinaster* has larger seeds (mass: 67.88 ± 9.97 mg) (R. Álvarez, L. Valbuena and L. Calvo, unpublished data) than *P. sylvestris* (mass: 10.4 ± 2.3 mg) (García-Fayos *et al*. 2001) and *P. nigra* (mass: 19.7 ± 2.8 mg) (García-Fayos *et al*. 2001), and for this reason, *P. pinaster* seed has a higher probability of survival due to greater embryo isolation (Escudero *et al*. 2000). Other authors have also found a positive relation between seed size and percentage germination (Kandya and Ogino 1986; Reyes and Casal 2001). Higher percentage germination in *P. pinaster* could also be explained by a tough seed coat that may allow it to tolerate higher temperatures.

The resistance of *Pinus pinaster* to high temperatures could be one reason why it usually shows very good field regeneration after fire (Rodrigo *et al*. 2004). Serotinity and early flowering in *P. pinaster* reflect its evader strategy in relation to frequent fires (Tapias *et al*. 2004; Álvarez *et al*. 2005). The study area (Tabuyo, located in Sierra del Teleno, NW Spain) has experienced frequent fires (two fires per year, started by lightning) (Tapias *et al*. 1998) and several previous workers have demonstrated the presence of both characteristics (Prada 1992; Tapias *et al*. 2001, 2004; Torres Carretero 2002; Álvarez *et al*. 2005). By contrast, *P. nigra* seeds are not adapted to fire at all, as has already been shown by several studies (Skordilis and Thanos 1997; Escudero *et al*. 1999). Similarly, Núñez and Calvo (2000) demonstrated that high temperatures negatively affect *P. sylvestris* seeds. Both species, *P. sylvestris* and *P. nigra*, have non-serotinous cones with low resistance to fire effects (Habrouk *et al*. 1999), grow in cold areas and disseminate seeds in late winter to spring (Tapias and Gil 2000; Panayiotopoulos and Thanos 2002; Rodrigo *et al*. 2004). The last characteristic results in minimal regeneration in the field after summer wildfires (Trabaud and Campant 1991; Ibáñez and Retana 1997; Habrouk *et al*. 1999), because seeds stored in cones or in the soil seed bank or seedlings that have already germinated will be negatively affected during the fire.

Table 2.   Mean length (cm) of aerial part (AP) and subterranean part (SP) and aerial/subterranean ratio (AP/SP) of the *P. pinaster*, *P. sylvestris* and *P. nigra* seedlings

Treatment	*P. pinaster*			*P. sylvestris*			*P. nigra*		
	AP	SP	AP/SP	AP	SP	AP/SP	AP	SP	AP/SP
Control	9.1[a]	9.5[a]	0.96[a]	8.1[c]	8.0[c]	1.01[c]	9.1[e]	14.7[e]	0.62[e]
90°C – 1 min	9.3[a]	9.5[a]	0.98[a]	8.1[c]	6.8[d]	1.19[c]	7.6[f]	8.3[f]	0.92[f]
90°C – 5 min	9.0[a]	9.9[a]	0.91[a]	8.6[c]	6.0[d]	1.43[d]	8.5[e]	9.2[f]	0.92[f]
110°C – 1 min	9.2[a]	9.4[a]	0.98[a]	8.2[c]	5.4[d]	1.52[d]	8.0[f]	12.1[f]	0.66[e]
110°C – 5 min	9.0[a]	10.4[a]	0.87[a]	6.9[d]	5.4[d]	1.28[c]	8.4[e]	18.2[g]	0.46[e]
150°C – 1 min	9.0[a]	9.1[a]	0.99[a]	–	–	–	–	–	–
150°C – 5 min	8.8[a]	7.9[b]	1.11[a]	–	–	–	–	–	–
200°C – 1 min	9.4[a]	9.6[a]	0.98[a]	–	–	–	–	–	–
200°C – 5 min	–	–	–	–	–	–	–	–	–

Significant differences between treatments in each species: [a,b] *P. Pinaster*; [c,d] *P. Sylvestris*; [e–g] *P. nigra*.

Another stage in the post-fire regeneration analysis involves seedling recruitment. In general, the results of the laboratory germination experiment showed a high percentage of seed germination, but the number of seedlings in the field are lower (Torres Carretero 2002) than may be expected from studies of seed reserves in the soil seed bank in these areas (Núñez and Calvo 2000; Torres Carretero 2002). This means that either not all of the seeds from the soil seed bank germinate or not all of the seedlings survive (Ferrandis *et al*. 1996; Valbuena and Calvo 1998; Torres Carretero 2002). Germination problems could be related either to the loss of viability due to abiotic factors or consumption by seed predators. This has been demonstrated in several studies carried out on *Pinus nigra* populations, whose seeds are consumed by mice and ants (Ordóñez García 2004), in common with other *Pinus* populations (Reyes and Casal 2002*a*; Côte *et al.* 2003; Reed *et al*. 2004). By contrast, in relation to seedling survival, in the present laboratory study, we demonstrated that seedling survival is high for *P. pinaster* and is not influenced by the temperature to which seeds have been exposed. Large seed size in *P. pinaster* allows successful embryo recovery and more vigorous seedling growth with a lower mortality index (Escudero *et al*. 2000; Reyes and Casal 2001). Larger seed size protects seeds from internal structural changes and does not have a negative effect on growth and survival. Similarly, some authors (Westoby *et al*. 1992; Hanley and Fenner 1998) point out that seedlings from larger seeds may in general be able to emerge more successfully from deep soil than smaller seeds. However, seedling survival in *P. sylvestris* and *P. nigra* is negatively affected by thermal increases and both species have smaller seeds. Consequently, the results obtained in the laboratory could explain the scarcity of recovery by *P. sylvestris* and *P. nigra* in the field (R. Alvarez, L. Valbuena and L. Calvo, unpublished data), as both species are non-serotinous and their post-fire regeneration depends on seeds in the soil seed bank. In both species, these small seeds do not endure the high temperatures attained in the upper centimetres of the soil (Trabaud 1980) and, in addition, lack the ability to germinate from greater depths in the soil (Westoby *et al*. 1992; Hanley and Fenner 1998).

In relation to aerial growth of seedlings, *Pinus pinaster* seedlings show greater growth than *P. sylvestris* and *P. nigra* following thermal shock, probably owing to larger seed size. Authors such as Escudero *et al*. (2000) and Reyes and Casal (2001) have shown a relationship between seed size and seedling growth due to the greater nutrient reserves present in bigger seeds (Stock 1990). Authors such as Hanley and Fenner (1998) have shown that the effects of thermal shock on seedling growth are related to the duration of exposure to high temperatures, such that long durations significantly reduced seedling growth. The present laboratory study demonstrates similar results in *P. sylvestris* and *P. nigra*.

Finally, aerial stem/root length ratios in adult plants in Mediterranean ecosystems are lower than in temperate habitats. A larger root area relative to aerial growth may represent an adaptation to the dry summer season (Lloret *et al*. 1999). Authors such as Gracia and Sabate (1996) have demonstrated that, in general, when water and nutrients are very limited in one zone, the proportion of root biomass is higher than in areas where water and nutrients are not limiting factors. This could explain the lower aerial/ root ratio in *P. nigra* and *P. pinaster*, which have a more Mediterranean distribution pattern than *P. sylvestris*. A larger root system allows Mediterranean species to penetrate the soil more deeply, so making water available throughout the summer (Lloret *et al*. 1999) and producing better adaptation to the Mediterranean climate.

Conclusion

Pinus pinaster survives higher thermal shocks and shows longer mean germination time than *P. nigra* and *P. sylvestris*. These properties represent successful adaptations to surviving fires. All three *Pinus* species show an increase in mean germination time following thermal shocks. High temperatures do not affect *P. pinaster* seedling survival after seed germination. By contrast, temperatures of 110°C and exposures times of 5 min have negative impacts on *P. sylvestris* and *P. nigra* seedling survival. Seedling growth rates in *P. pinaster* are significantly greater than in *P. sylvestris* and *P. nigra*. Thermal shocks reduce subterranean shoot development relative to aerial growth in *P. pinaster* (150°C – 5 min) and *P. sylvestris* (in all thermal shocks relative to the control).

Pinus pinaster seeds and seedlings survive high temperatures during fires, conferring better adaptation to fire than *P. sylvestris* and *P. nigra*. Similarly, higher mean germination times in *P. pinaster* seeds, together with more vigorous seedling growth, could represent an efficient regeneration strategy after recurrent perturbations due to forest fires.

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