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Original article

Germination behaviour of 3 species of the genus *Pinus* in relation to high temperatures suffered during forest fires

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Summary — The action of fire was simulated in the laboratory using thermic shocks. To this aim, samples of seeds of *Pinus pinaster*, *P radiata* and *P sylvestris* were subjected to high temperatures. Following the treatments, both the treated and untreated seeds were sown under standard laboratory conditions. The results of the germination test demonstrated that significant differences exist between the behaviour of the 3 species, but none of them were seen to be specially favoured by the high temperatures.

germination / fire / high temperatures / *Pinus*

Résumé — Réponse germinative de 3 espèces de *Pinus* en relation avec les températures élevées atteintes au moment des feux de forêts. *On a simulé l'action du feu en utilisant des chocs thermiques. Des échantillons de semences de* Pinus pinaster, P radiata *et* P sylvestris *ont été exposés à de hautes températures. Ensuite, les semences traitées et non traitées ont été semées en conditions standard au laboratoire. Les résultats des tests de germination ont montré des différences significatives entre les 3 espèces, mais aucune d'elles n'a été spécialement stimulée sous l'action des hautes températures.*

***germination / feu / hautes températures /* Pinus**

INTRODUCTION

Intensity is one of the most important characters of a disturbance regime, and particularly that of fire (Malanson, 1984; Sousa, 1984). Two factors characterize the strength of a fire, the period of time and the temperature reached. These 2 factors are very important, as on these will depend the number of seeds available for germination, the possibility of sprouting and the characteristics of the populations and communities after the fire.

Many seeds need to be exposed to high temperatures during a certain period of time in order to germinate, or at least their germination is stimulated in these conditions, as occurs with *Cistus salvifolius*, *C monspeliensis* and *C albidus* (Trabaud and Oustric, 1989a). For other seeds, principally in some species of legumes, fire plays an important part in the rupture of dormancy. In these cases, fire can act as a scarifying agent of the seed coat, as in the case of *P brutia* (Thanos *et al*, 1989). In addition, certain populations require periodic fires in order to maintain their position in the ecosystem and the role of fire has been recognized in the maintenance of species such as *P longifolia* (Greswell, 1926), *P palustris* (Chapman, 1946), *P ponderosa* (Cooper, 1961; Weaver, 1967), *P halepensis* (Trabaud, 1989), and more.

In this study, we intend to analyze the behaviour of 3 species, *Pinus pinaster*, *Pinus radiata* and *Pinus sylvestris*, during germination, in relation to fire and to try to integrate the results obtained into the frame of reproductive strategy.

MATERIALS AND METHODS

The biological material used in this study were seeds of *Pinus pinaster* Aiton, *Pinus radiata* D Don and *Pinus sylvestris* L. The seeds of *P pinaster* and *P radiata* came from harvest made in several sites in the provinces of A Coruña and Lugo (NW Spain), during the summer and autumn of 1990. The seeds of *P sylvestris* were obtained from the Forest Centre of Lourizan (Pontevedra, NW Spain).

For conservation, the seeds were stored in open plastic bags, which permitted ventilation, at the laboratory temperature in a dry place until the moment of use. The seeds were submitted to vernalization at 4°C during 1 month before the test.

In order to perceive the effects 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 no-selected seeds to high temperatures during 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 only during a short period of time (between 5 and 15 mn), and the temperatures reached at 2.5 cm under the soil surface vary between 44°C and 150°C.

Based on these facts, we selected the following combinations of temperature and exposition time, in order to simulate fire action on the seeds: 90°C for 1 mn, 90°C for 5 mn, 110°C for 1 mn, 110°C for 5 mn and 150°C for 1 mn. To obtain these temperatures, a hot air heater was used in which the required temperature for each treatment was selected.

Six samples of 30 seeds from each species were made for each treatment. These treatments were compared with another group of 6 samples which was not given thermic shock.

Sowing was carried out under greenhouse conditions, in Petri dishes on filter paper, incubated during 64 days and watered with deioniced water. Counting of germinated seeds was carried out every day during the whole period of incubation. A seed was considered to have germinated when the root projected 1 mm outside the tegument (Côme, 1970).

Using the data obtained, an initial analysis of variance (ANOVA) was carried out to detect the differences existing between the 3 species, after which a second ANOVA was carried out to determine the differences which existed within the same species when subjected to different treatments. In all cases, the number of germinations per sample were used as a basis without effecting any transformations. In some cases, an *a posteriori* test was applied (Gabriel test or SS-STP test) to analyze which treatments were significantly different.

The average time for germination has also been estimated using the expression:

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

where N_1 is the number of seeds which have germinated in time T_1, N_2 is the number of seeds which germinated between time T_1 and T_2, and so on (Côme, 1970). An ANOVA was carried out to test the existence or not of significative differences in the average time for germination and to verify if it was related to the treatment applied or to the species studied.

RESULTS

Although the species belong to the same genus, more significant differences were noted between *P sylvestris* and the other 2 species than between *P radiata* and *P pinaster*. These differences are expressed in the time of germination as well as in the germination percentage.

Time in which germination is completed

We observed that *P pinaster* completed its germination 42 d after sowing and *P radiata* after 43 d, while *P sylvestris* took only 31 d (fig 1). But, perhaps the most significant difference in germination between *P sylvestris* and the other 2 species was that *P sylvestris* (fig 1A) took only 3 d after sowing to begin germination and showed a strong peak between d 5 and 9. In figures 1B and 1C, *P pinaster* and *P radiata* showed smaller and much less defined germination peaks. *P pinaster* started germination on the 5th d but, in general, this is very low. Germination is even more delayed in *P radiata*, beginning after 7 d; it shows no defined peak and continues with very low values during the whole process.

The average germination time (table I) is significantly shorter for *P sylvestris* (8.89 d) than for *P pinaster* (17.29 d) and *P radiata* (18.77 d). Within each species, the same trends, with reference to average germination time and to the beginning and ending of germination, are maintained, although with some variations, in all treatments. Therefore, the thermic treatments tested did not change the temporal germination response.

Percentage of germination

The percentage of germination is higher for *P sylvestris*, with an average of 68.83% for untreated seeds, followed by *P pinaster* with 28.50% and *P radiata* with 16.18% (table I).

An ANOVA was applied to the data of the number of seeds germinated in each replicate in order to verify whether or not the differences existing between the various treatments and species were significant. As a result of this analysis, it was observed that highly significant differences exist between the germination levels of the species and, without taking into account the species, between the treatments themselves ($P < 0.001$). The interaction species x treatment is also highly significant ($P < 0.001$).

However, on studying the germinative behaviour of each species separately and considering the treatment applied for each, the ANOVA showed significant differences only for *P sylvestris* ($P < 0.01$). Thus the differences in the number of germinations, in both *P pinaster* and *P radiata*, does not depend on whether or not they have been subjected to heat, nor on the temperature, nor on the exposure time (at least in the combinations of temperature and exposure investigated), but are simply due to chance.

When comparing the values of the different treatments, the control showed the highest rate of germination for *P pinaster* (table I and fig 1B). The rest showed lower levels of germination which were similar in all, and never differing significantly.

P radiata followed, with lower germination levels, the same trends as *P pinaster*. The highest germination levels were found in the control and 90°C for 1 mn treatment, and germination decreased as the temperature and exposure time increased (table I), especially in those of 110°C for 5 mn and 150°C for 1 mn (fig 1C), and the differences were not significant.

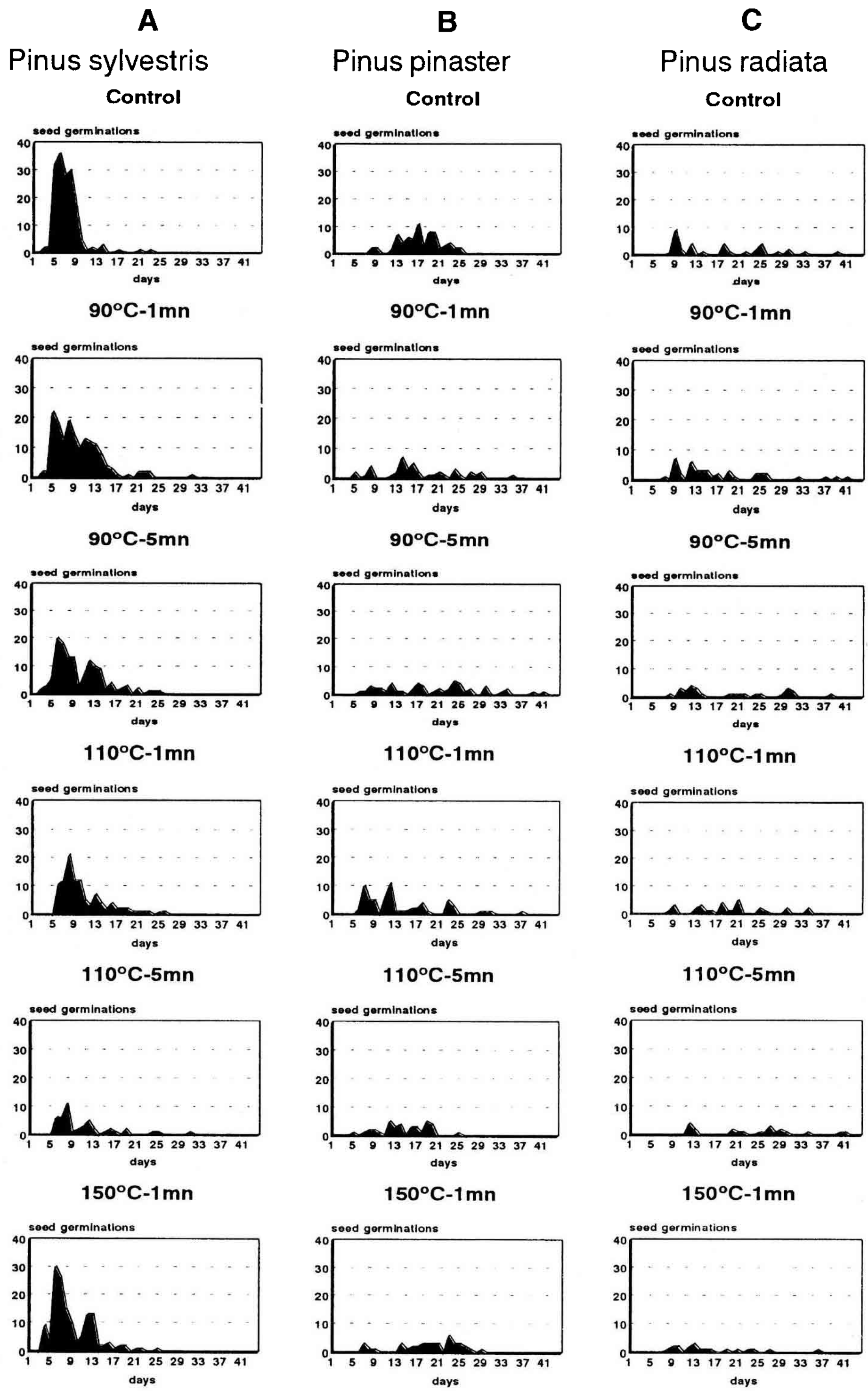

Fig 1. Distribution of germination times of the *Pinus sylvestris*, *Pinus pinaster* and *Pinus radiata* under greenhouse conditions.

Table I. Germination rates of 3 *Pinus* species for several thermics treatments.

	Mean	*Treatments*					
		Control	*90°C-1 mn*	*90°C-5 mn*	*110°C-1 mn*	*110°C-5 mn*	*150°C-1 mn*
Germination percentage (%)	68.83	86.10	91.10	71.66	54.43	23.90	86.10
P sylvestris		a	a	b	ab	b	a
Germination average time (days)	8.89	7.31	9.61	9.94	8.04	9.03	9.42
		y	y	y	y	y	y
Germination percentage (%)	28.50	38.88	25.00	27.23	33.33	23.35	23.33
P pinaster		b	b	b	b	b	b
Germination average time (days)	17.29	17.33	19.89	18.69	14.97	13.66	19.21
		z	z	z	z	z	z
Germination percentage (%)	16.18	20.00	22.76	14.43	15.56	13.90	10.56
P radiata		b	b	b	b	b	b
Germination average time (days)	18.77	19.60	17.51	18.75	19.84	20.25	16.65
		z	z	z	z	z	z

Results with the same letter were not significantly different ($P > 0.01$).

P sylvestris has a significant lower level of germination as the temperature and exposure time increases.

In addition, the differences between treatments are so great that on carrying out the joint analysis of the 3 species, taking the treatments as variables, highly significant differences ($P < 0.01$) are continuously demonstrated. In the case of this species, a test *a posteriori* was carried out (SS-STP test) and showed highly significant differences ($P < 0.01$) between the treatment at 110°C for 5 mn and the treatments at 90°C for 1 mn, 90°C for 5 mn, 150°C for 1 mn and the control. On the other hand, the treatment at 110°C for 1 mn did not differ significantly from any of the others, not even that of 110°C for 5 mn. That is to say, it gives an intermediate germination value.

The fact that the seeds subjected to 110°C for 5 min show a lower germination level than in the other treatments might be because the embryo is not capable of resisting high temperatures during a prolonged period of time. Therefore, the germinative capacity of *P sylvestris*, subjected to a high intensity fire for a prolonged period, is greatly reduced.

If the germination values of the different treatments are observed (table I and fig 1A), it can be seen that *P sylvestris* never exceed the control. This suggests that the germination of this species is not stimulated by heat, although it does resist quite well, within limits, the high temperatures.

DISCUSSION

In order to interpret the germination behaviour of these 3 species and their relationship with fire, it is very important to have a good knowledge of their reproductive strategy.

Traditionally, it is considered that this genus has pyrophyte characteristics, although most of its species cannot sprout after fire (Naveh 1974; Trabaud, 1970, 1980) as occurs with *P pinaster*, *P radiata* and *P sylvestris*, which can only reproduce from seed.

The dissemination of the mature seed of *P pinaster* and *P radiata* coincides with the end of spring and lasts during the whole of summer (Vega, 1977). However, the availability of the seed for germination is not the same in all the species, either in time or in space. Although *P radiata* has lower fertility than *P pinaster* and *P sylvestris* (table I), it can keep the seed in its pinecone for several seasons (Vega, 1977), as also occurs with *P halepensis* (Barbero *et al*, 1987), *P banksia* (Chandler *et al*, 1983) and *P brutia* (Lotan, 1975), opening only after a fire and in this way assuring its regeneration.

Other authors, studying different species, found in certain cases similar behaviour to those of this study and in other cases totally opposite behavior. Trabaud and Oustric (1988b), using *P halepensis* seeds, observed that high temperatures lowered germination with respect to the control, and the same occurred with *Pinus contorta* (Knapp and Anderson, 1980), *Rosmarinus officinalis* (Trabaud and Casal, 1989), *Cytisus multiflorus* (Añorbe, 1988), *Acacia cyclops*, *Virgilia oroboides*, *Podalyria calyptrata* (Jefferey *et al*, 1987) and *Quillaja saponaria*, *Peumus boldus*, *Colletia spinosa*, *Shinus polygamus* (Muñoz and Fuentes, 1989). However, another large group of species exists, especially in Mediterranean areas, whose germination is favoured by high temperatures, such as *Cistus albidus*, *C monspeliensis* (Trabaud and Oustric, 1989a; Roy and Laurette, 1992), *C ladanifer* (Valbuena *et al*, 1992), *Genista florida*, *Cytisus scoparius* (Tárrega, 1992), *Ulex europaeus* (Pereiras, 1984), *Genista anglica* (Mallik and Gimingham, 1985), *Acacia saligna* (Jeffery *et al*, 1987), *Ceanothus integerrimus* (Kauffman and Martin, 1991), and *Colliguaya odifera*, *Muelenlackia hastulata*, *Trevoa trinervis* (Muñoz *et al*, 1989).

There is still an important lack of information on the germination processes and strategies of these species after fire, and it is also difficult to extract conclusive results from laboratory experiments that are directly applicable to burnt areas, as under field conditions there are many other interacting factors. As pointed out by Moreno and Oechel (1991), the number of seedlings that emerge after fire reflect only a fraction of the seeds available for germination.

The high rate of germination of *P sylvestris* leads us to belive that these seeds act as *r* type strategists. Its sensitivity to high temperatures also characterizes it as a rarely pyrophite species, which would appear logical if we consider that we are dealing with a species that lives in cold areas (by latitude or altitude) (Tutin *et al*, 1969-1981) where the probability of natural fire is very low.

The size of the seeds is different in each of these species, and the seed size probably represents a compromise between the requirements for dissemination and establishment (Fenner, 1983). The small sizes of seed facilitate dissemination over long distances, while the storage of considerable reserves in the large seeds favours the subsequent establishment of the seedlings (West and Lott, 1992). The average weight of the seeds studied (including seed cover) were 50.273 ± 0.163 mg for *P pinaster*, 27.551 ± 0.866 mg for *P radiata* and 19.033 ± 0.442 mg for *P sylvestris*. The differences in the weight of the seeds are relatively great, and the thickness of their cover is also clearly different, with *P sylvestris* having the thinnest cover, followed by *P pinaster* and by *P radiata*. All these differences could be sufficiently important to explain their different behaviour during the germination process and their different degree of sensitivity to high temperatures.

Two important observations can be made about the effect of high temperatures on germination: i) The thermic shocks tested do not stimulate either the speed or germination rate of any of the 3 species, and ii) only *P sylvestris* is sensitive to the heat treatments applied.

The first observation suggests that the pyrophyte character of these species is not due to the high temperatures directly favouring the germination of their seeds, but due to other circumstances such as the opening of the pinecones or the preparation of an appropriate seedbed (Trabaud, 1987).

From the second observation, we conclude that the *P sylvestris* seeds are more sensitive to external factors and, in the case of a moderately severe fire, loose their germinative capacity more rapidly than *P pinaster* or *P radiata*. Probably for this and other reasons, *P sylvestris* bases its reproductive strategy on smaller seeds, easily dispersed by the wind, that can colonize wide areas. The influence of the model and design of the seed's wing in this process should be studied.

The seeds of *P pinaster* and *P radiata* possess a lower percentage of germination, but the high temperatures produced in a fire do not reduce this fact. Besides, it is known that above all *P radiata* needs fire to open its cones and spread its seeds. These facts bring the 2 species within the range of K type strategists and define them as clearly pyrophyte.

Even within the non-sprouting species, the reproductive strategies may vary widely. Different species may have different regeneration patterns in a burnt area, leading to some establishing themselves better in more open zones and others doing so more efficiently in zones where the vegetation cover is denser (Keeley and Zeedler, 1978; Moreno and Oechel, 1992). On a small scale, the differences in the characteristics of a site may play an important role in determining the survival of the seedlings (Moreno and Oechel, 1992).

To discover the adaptive advantages in the event of a fire of the reproductive strategies of each of the species studied, it is necessary to take into account factors other than germination, and a very important factor is the production of seed. Some species invest a great amount of energy in producing a lot of small seeds, while others produce less seeds but of larger size. There must exist a balance between the energy output used in the production of each seed and the probabilities of success in the germination and posterior development of the seedling.

It is hoped that the larger seeds, as well as being more resistant to fire (Keeley, 1977), give rise to more vigorous seedlings and with a death rate lower than smaller sized seeds (Harper, 1977; Fenner, 1978; Gross, 1984). These features of the plants must be thoroughly studied in the light of the evolutive role of fire.

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