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Original article

Germination of *Pinus pinaster, P. radiata* and *Eucalyptus globulus* in relation to the amount of ash produced in forest fires

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Abstract – Many studies have found that ash beds favour seedling growth, but the effect of ash on the germinative behaviour of tree species has received little attention. We therefore designed an experiment in which *Pinus pinaster, P. radiata* and *Eucalyptus globulus* seeds underwent four different ash treatments and one control. The treatments chosen were three solutions of ash in water (0.5, 1 and 5 g L^{-1}) which were used to periodically water the seeds of each species, and a treatment in which a certain amount of ash was applied directly to seeds which were moistened with distilled water only. Six replicates of 30 seeds per replicate from each species were used for each treatment. Seeds were incubated on a double layer of filter paper in Petri dishes under laboratory conditions. Germination counts were taken every 2 days until the end of the germination period. The results indicated that ash (in the quantities and under the conditions studied) had no postive effect on the germination of these species. The ash solutions did not significantly alter the germination rate with respect to the control. Only the germination percentages obtained in the ash treatment markedly reduced the germinative capacity of *P. pinaster* and *P. radiata* and had a completely inhibitory effect in the case of *E. globulus*. The mean germination times increased, although only slightly, for each of the three species, with increasing concentrations of ash. Temporal distribution patterns were scarcely modified by the treatments. (© Inra /Elsevier, Paris.)

germination / ash / fire / *Pinus* / *Eucalyptus*

Résumé – Germination de *Pinus pinaster, P. radiata* et *Eucalyptus globulus* en relation avec l'importance des cendres produites pendant les feux de forêt. De nombreuses études affirment que la couche de cendres est favorable à la croissance des plantules ; cependant, l'effet des cendres sur le comportement germinatif des espèces arborescentes a été très peu étudié. Nous avons réalisé une expérience qui a consisté à soumettre des graines de *Pinus pinaster, P. radiata* et *Eucalyptus globulus* à quatre traitements différents de cendres et à un témoin. Les traitements sélectionnés consistent en trois dissolutions de cendres dans l'eau (0,5, 1 et 5 g L^{-1}) avec lesquelles on a arrosé périodiquement les graines de chaque espèce, et un traitement dans lequel on a appliqué directement aux graines

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une certaine quantité de cendres que l'on a arrosées uniquement avec de l'eau distillée. Pour chaque traitement, on a réalisé six répétitions de chaque espèce, avec 30 graines chacune qui ont été mises en incubation dans des plaques de Petri, sur une double couche de papier-filtre, dans des conditions de laboratoire. Le dénombrement des germinations obtenues s'est fait tous les jours jusqu' à la fin de la période de germination. Les résultats nous indiquent que les cendres (dans les quantités et les conditions étudiées) n'ont exercé aucun effect positif sur la germination de ces espèces. Les cendres dissoutes dans de l'eau n'ont pas modifié de façon significative le taux de germination par rapport au témoin. Seuls les taux de germination obtenus dans le traitement Cendres diminuent de façon significative la capacité germinative de *P. pinaster* et *P. radiata*, et dans le cas de *E. globulus* ils l'inhibent totalement. Dans les trois espèces, les temps moyens de germination ont augmenté légèrement avec l'augmentation de concentration des cendres. Enfin le mode de distribution dans le temps n'a pratiquement pas été modifié par les traitements. (© Inra /Elsevier, Paris.)

germination / cendres / feu / *Pinus* / *Eucalyptus*

1. INTRODUCTION

Both the genus *Pinus* and the genus *Eucalyptus* are characterized by an aerial seedbank [8, 15, 21, 34] in which seeds can remain viable for several years although their soil seedbank only lasts for a very short time [3, 18, 20, 22, 27]. Fire triggers the massive opening of pine and eucalyptus fruits, and a large amount of seeds are released.

Most of the species of the genus *Pinus* do not resprout, nor do any of the species we studied: post-fire survival depends exclusively on seeds. Contrary to this, many of the species of the genus *Eucalyptus* have a great resprouting capacity [5].

Both *Pinus* and *Eucalyptus* live in fire-prone environments and behave like opportunistic species which are capable of invading open sites without the presence of aggressive competitors [4, 25, 28, 35].

In the event of fire, both the seeds held in the aerial seedbank and those on the soil seedbank which were released before the disturbance occurred are exposed to very special conditions which include a more or less abundant ash bed, depending on the intensity of the fire and the type and amount of fuel. Ash may influence the germinative process and later seedling development.

Many authors (Burns, 1952; Loneragan and Loneragan, 1964; both cited in [6]; [1, 2, 6, 7, 9, 12, 30, 33, 37]) have observed in different environments that post-fire seedling abundance and growth is greater in burned areas, and attribute this phenomenon partly to the ash produced during fires since it may favour the release of a greater amount of plant-available nutrients.

These studies are based on field observations which do not afford an accurate analysis of the effect and concentrations of ash, nor do they allow this effect to be isolated from other possible consequences of fire such as the reduction in frugivorous pressure, the elimination of allelopathic effects, the reduction in competition for water, light and nutrients, and so on.

The effect of ash on seed germination must therefore be examined under more isolated conditions to eliminate as far as possible the interference of other factors.

Some authors have already dealt with this question in other species [16, 17, 25, 32, 36], but the germinative behaviour of many species in the presence of ash is still unknown.

The aim of this experiment was to analyse the effect of ash on the seed germination of *Pinus pinaster* Aiton, *Pinus radiata* D. Don and *Eucalyptus globulus* Labill. and to determine whether ash affects the mean germination time, percentage and temporal distribution of germination.

2. MATERIALS AND METHODS

Four treatments were designed to study the effect of ash on the germination of *P. pinaster*, *P. radiata* and *E. globulus*: three solutions of ash in water, a fourth treatment in which ash was placed on Petri dishes and a control treatment, without ash, which was used as a reference.

Ash was obtained from the total combustion (approximately 20 min) of dry material (mainly thin branches and leaves) from each of the species studied. Seeds from each species were treated with ash obtained from the biomass of individuals of their own species.

Ash solutions were obtained by diluting the corresponding amount of ash in distilled water and periodically watering the seeds with this solution. The ash concentrations tested were: 0.5, 1 and 5 g L^{-1}. These concentrations were based on real data corresponding to the amount of ash m^{-2} found on the soil in Monte Pedroso after an experimental burn and the rainfall m^{-2} in that region during the first rains after the burn [29].

The ash treatment involved placing 0.454 g ash on Petri dishes (this quantity coincides with that found on the soil of the burned area prior to the rains) and simulating the conditions frequently found on natural soil when considerable amounts of ash accumulate in small hollows where a large number of seeds are also usually found. The ash treatment and the control were moistened with distilled water only.

Seeds were collected during the summer of 1993 and sown on 28 February 1994 under laboratory conditions. Germination counts were carried out every 2 days starting the day after sowing and continuing until 15/4/94, that is, for a total of 46 days, after which time germination had ended.

Once the germination period was over the germination percentage was calculated, as was the mean germination time in days using the expression:

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

where N_1 represents the number of seeds germinated in time T_1, N_2 is the number of seeds which germinated between time T_1 and time T_2, and so on [11].

Statistical processing was carried out separately for each of the species using a one-way ANOVA followed by a Tukey HSD test with 95 % confidence limits. The arcsine transformation (germination rate) and the log10 transformation (mean germination time + 1) were used to increase the normality of the germination data. The Tukey test was only applied when significant differences were detected between the treatments.

3. RESULTS

3.1. Germination rate

The mean germination rate found for *P. pinaster* was 41.77 % ± 0.91, that of *P. radiata* 55.55 % ± 1.44 and that of *E. globulus* 58.33 % ± 1.78. Furthermore, notable differences were found between the results of some treatments and those of others (*figure 1*). Analyses of variance determined that the differences between the treatments in the three species studied were highly significant ($P < 0.001$).

In *P. pinaster* marked differences were found between the treatments with a significance of $P < 0.001$. The Tukey test determined that these differences in the germination rate were due to the treatment in which the ash was placed directly on Petri dishes. This ash treatment revealed the lowest percentage with only 17.77 % ± 1.37 while all the other treatments gave almost 50 %: 43.88 % ± 1.46 in the case of the 5 g L^{-1} treatment, 50.00 % ± 1.62 in that of the 1 g L^{-1} and 48.33 % ± 1.43 for the 0.5 g L^{-1} treatment. The control results coincided with these, and gave a value of 48.88 % ± 1.46.

For *P. radiata*, the ANOVA carried out on the germination data indicated that it responded very differently to the treatments ($P < 0.001$) and the Tukey test showed that these differences were due to two treatments: the ash treatment (as in the case of *P. pinaster*) and the 5 g L^{-1} treatment. Both were significantly different from the other treatments and even from one another. The ash treatment, with a value of 12.77 % ± 1.37 was once again the treatment with the lowest germination percentage. It was followed, in increasing order of importance,

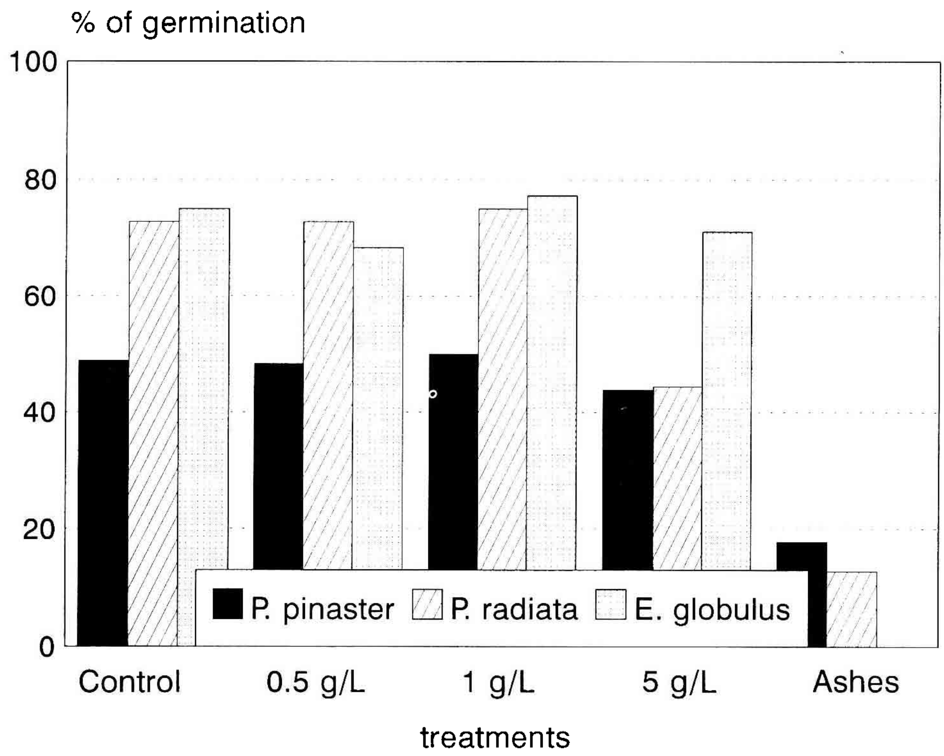

Figure 1. Germination percentage for each of the treatments and species.

by the 5 g L^{-1} treatment (44.44 % ± 1.46), the value of which was high enough to make the difference between them significant. The between-treatment response for the other treatments was very homogeneous (75.00 % ± 1.19 for the 1 g L^{-1}, 72.77 % ± 0.77 for the 0.5 g L^{-1} treatment and 72.77 % ± 1.00 for the control), a result that was very different from those for the two first-mentioned treatments.

Eucalyptus globulus also showed great differences between treatments. The germination rate for the ash treatment was null; if this treatment is excluded, the mean rate for the other treatments indicates a much greater value: 72.91 % ± 0.84. The analysis of variance detected significant differences ($P < 0.0001$) in the germination percentages between treatments. The Tukey test determined that these differences were only significant when the ash treatment was compared with any of the other four. From the observations noted in *figure 1*, it can be deduced that the treatments involving a small concentration of ash (0.5, 1 and 5 g L^{-1}) did not affect the germination percentage since their values (68.33 % ± 1.54, 77.22 % ± 1.07 and 71.11 % ± 2.74, respectively) were very similar to that of the control treatment (75.00 % ± 1.67). Only when the seeds were sown directly on the ash was its inhibitory effect on germination evident.

In the three species studied, it was found that the higher the concentration of ash to which the the seeds were exposed, the more

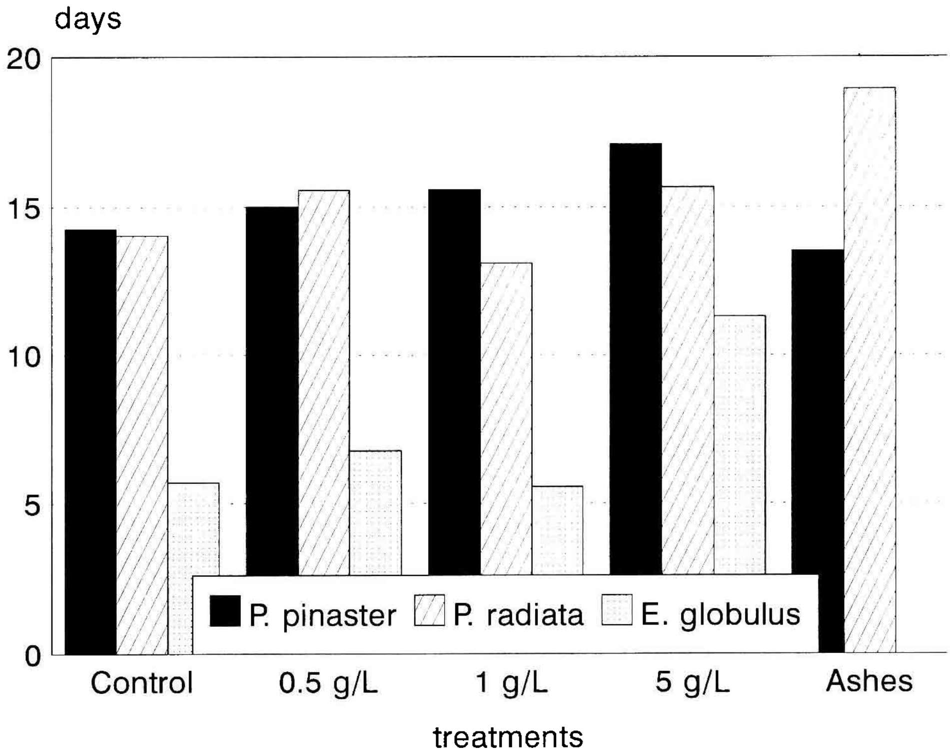

Figure 2. Mean germination time for each of the treatments and species.

germination was reduced. The ash treatment had the most inhibitory effect, or at least it made germination more difficult. The 5 g L^{-1} treatment also considerably reduced germination, although not to the same extent.

3.2. Mean germination time

Mean germination time (*figure 2*) was 15.10 ± 0.66 days for *P. pinaster*, 15.47 ± 0.73 days for *P. radiata* and 7.58 ± 0.73 days for *E. globulus*. The lowest mean germination time in *P. pinaster* corresponded to the ash treatment (13.52 ± 3.09 days), followed by the control treatment (14.26 ± 1.02 days), and the 0.5 g L^{-1} and 1 g L^{-1} treatments gave practically the same values (15.02 ± 1.02 and 15.60 ± 0.76 days, respectively). The treatment which most delayed germination was the 5 g L^{-1} (17.10 ± 0.84 days). In the case of *P. radiata*, the highest germination values corresponded to the 1 g L^{-1} treatment (13.11 ± 0.75 days) followed by the control (14.04 ± 1.10 days). The 0.5 g L^{-1} (15.58 ± 2.02 days) and the 5 g L^{-1} (15.68 ± 1.19 days) treatments gave similar values, while in this case the ash treatment showed the greatest delay (18.95 ± 2.42 days) in germination. Although the mean germination time for *E. globulus* was 7.58 ± 0.78 days, as a global value there were important differences between one treatment and another. The control treatment showed the longest delay and gave a mean germination time of 11.31 ± 0.36 days. The 0.5, 1 and 5 g L^{-1} treatments achieved similar mean germination time values (5.70 ± 0.51, 6.78 ± 0.56 and 6.56 ± 2.75 days, respectively) and the ash treatment with a germination rate of 0 % gave a null mean germination time.

No significant statistical differences were found between the mean germination times of *P. pinaster* and *P. radiata* seeds in any of the treatments. In the case of *E. globulus*, marked differences were detected between treatments at a significance level of $P < 0.05$. The Tukey test showed that the treatments responsible for these differences were the control, with the shortest, and the 5 g L^{-1} treatment with the longest germination time.

On the whole, a trend towards increased mean germination time was detected in the three species with an increasing concentration of ash, but statistically this had little or no significance.

3.3. Temporal distribution of germination

As shown in *figure 3*, *P. pinaster* and *P. radiata* have very similar germination distribution patterns. The first germinations occur 6 days after sowing, and in almost all the treatments the most notable germination peak starts around day 8 and remains until about day 16 of the experiment. These peaks are stronger in the case of *P. radiata* than in that of *P. pinaster*; moreover, the former had a more prolonged germination time, since this lasted until day 46 as opposed to day 42 in the case of *P. pinaster*. Germination commenced in *E. globulus* in all the treatments 4 days after sowing (*figure 3*), except for the ash treatment in which no germination occurred. Although the last germination was recorded on day 40, all the treatments in which germination occurred showed a marked peak between days 4–6, during which time the greatest number of germinations were concentrated. After day 12 some peaks were recorded, but these were of little importance. *Figure 3* shows how the treatments with the greatest ash concentrations decrease the size of the germination peaks; but on the whole, these do not dramatically alter the temporal distribution of germination in any of the three species.

4. DISCUSSION

Most of the studies which mention the positive effect of ash on the regeneration of different species refer to the survival, vitality or development of the emerged seedlings, but not to the number of germinations which occur. Hence, Burrows et al. [6] found that *Eucalyptus wandoo* regenerated much better on ash beds than on mineral soil, as also did *Pinus coulteri* [38], *P. banksiana* [10] and *P. palustris* [26]. Burns (1952; in [6]) attributes this exceptional regeneration to the increase in pH and the nutrients available to seedlings. Other authors [13, 19] have also pointed out that ash beds favour the edaphic conditions under which eucalyptus seedlings develop and, moreover, reduce competition from other seedlings.

The data obtained in this experiment indicate that low concentrations of ash neither stimulate nor inhibit germination in *P. pinaster*, *P. radiata* or *E. globulus*; however, high concentrations do reduce or nullify germination. The germination values obtained for the three species in the 1 g L^{-1} treatment are slightly higher than those of the control, but these differences are not significant. As opposed to this, the ash treatment inhibited germination in all species, in particular *E. globulus*. The mean germination time tends to increase the greater the concentrations of ash.

Our results coincide with those found by González-Rabanal and Casal [17], Neéman et al. [25], Thomas and Wein [32] and Trabaud and Casal [36]. Neéman et al. [25] found that a thick layer of ash had a negative effect on seed germination, but this effect

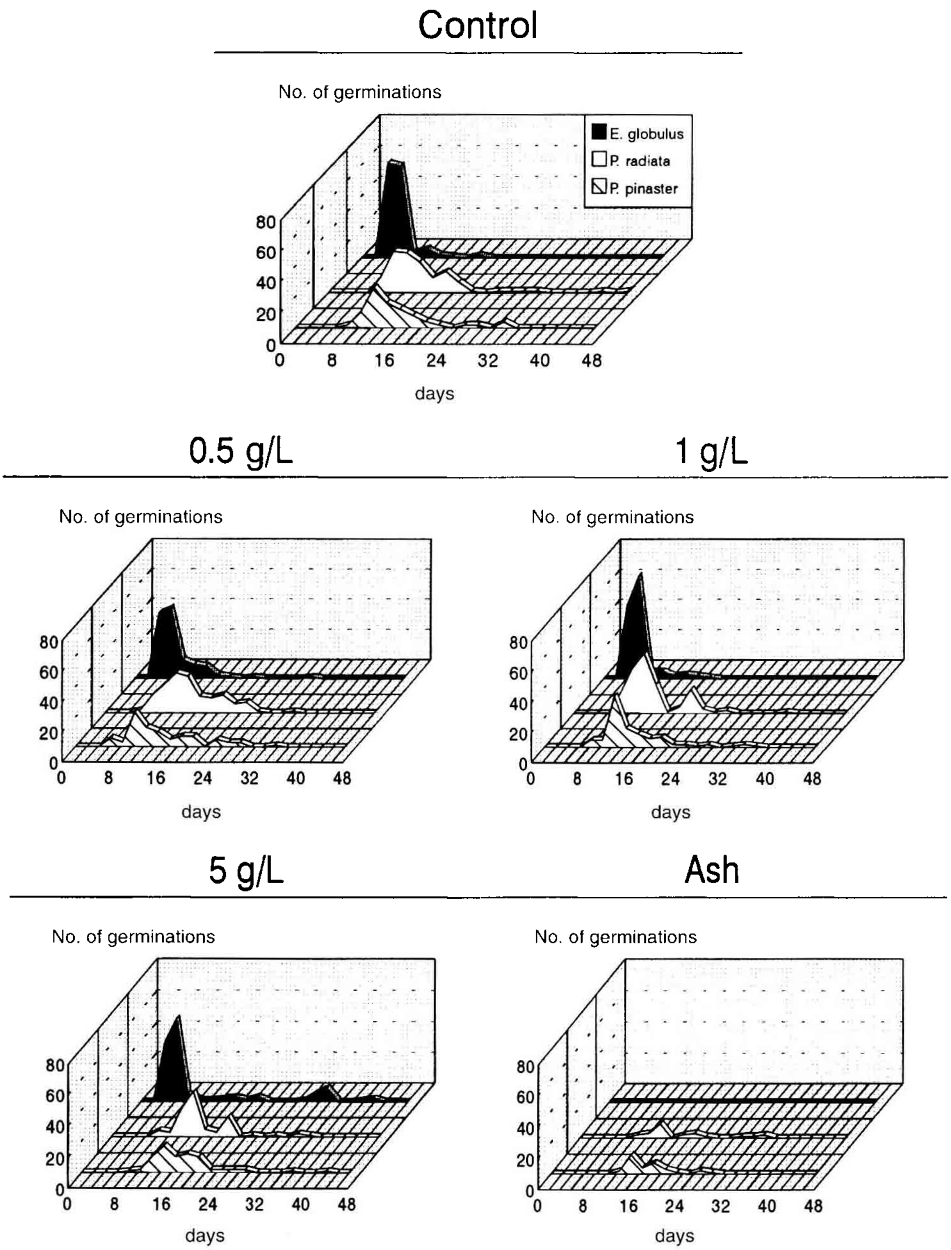

Figure 3. Distribution of the seed germination of *P. pinaster*, *P. radiata* and *E. globulus* for each of the ash treatments studied.

was more notable in *Cistus salviifolius* and *C. creticus* than in *P. halepensis*. González-Rabanal and Casal [17] studied ten woody and herbaceous Atlantic species of four different families and also found differences in the response of each of the three. Moreno and Oechel [23], studying the effect of ash on the emergence of several woody and herbaceous species of mixed chaparral, also detected differences among them. In both studies, ash had a negative effect either on germination or on emergence, or did not alter them at all. We found that although germination was reduced with high concentrations of ash in all three species, this effect was more notable in *E. globulus*, somewhat less in *P. radiata* and less still in *P. pinaster*.

A great range of hypotheses exists as regards the mechanism by which ash reduces germination. According to Neéman et al. [25], the inhibition of germination caused by a large amount of ash may be due to the fact that water is prevented from reaching the embryo given the high osmotic pressure in the medium, or that the embryo is poisoned by the toxic effects of certain ions. Edgar [14] and Zohar et al. [39] found that germination in *Eucalyptus occidentalis*, *E. calmadulensis* and *E. regnans* is sensitive to the value of osmotic pressure, with germination being reduced with the increasing osmotic pressure of the substrate; this same effect was detected by Thanos and Skordilis [31] in *P. halepensis* and *P. brutia*. Other authors [16] have suggested that certain nutrients released by ash (for example the ion Ca^{+}) probably participate in seed germination processes. Thomas and Wein [33] postulate that the inhibition produced by ash is due to the alkaline pH of the solution.

These mechanisms are all probably interrelated, but further studies should be carried out to analyse how different native species from different mediums react to explain the internal mechanisms by which ash acts on seed germination, since its role in post-fire environments could be extremely important in the seed regeneration of plant populations affected by fire.

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