

Seed dispersal and changing seed characteristics in a *Pinus halepensis* Mill. forest after fire

A. Saracino, R. Pacella, V. Leone & M. Borghetti

Dipartimento di Produzione Vegetale, Università della Basilicata, via N. Sauro 85, I-85100 Potenza, Italy

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Abstract

Seed density, seed colour and the number of seed damaged by birds were monitored for several months, after a late-spring fire, in two Aleppo pine (*Pinus halepensis* Miller) stands growing in South Italy. In one stand (S_1) the trees were completely burned ('charred'), in the other one (S_2) the trees were only 'scorched', with a crown in part still alive after fire. 37% and 61% of seeds were released during the first month, respectively in S_1 and S_2 . Damaged seeds accounted for 43% and 23% of seeds collected in the whole period, respectively in the charred and in the scorched stand. In both stands the percentage of empty seeds increased in late-dispersed seed lots. The colour of released seeds changed with time: dark grey-brown seeds were released at first, whereas late-dispersed seeds showed a yellowish colour. The principal component analysis performed on the categorical colour variables produced a good discrimination between seed lots collected at different dates. Seed dispersal and the characteristics of released seeds have been discussed in relation to the post-fire recruitment process and, in particular, to the possibility that the predation risk by granivorous birds may be reduced by a mimicry effect of seeds to the underlying soil.

Introduction

In the Mediterranean basin, where Aleppo pine (*Pinus halepensis* Miller) is naturally widespread (Nahal 1962), the population dynamics of plant species is often influenced by the occurrence of natural fires (Naveh 1975; Di Castri et al. 1981).

Some adaptive traits developed by *P. halepensis* to couple with fire-induced disturbances are known: large storage of seed in the crown, requiring great allocation of assimilates to reproductive processes (El Aouni 1980), and abundant seed release after fire, providing natural regeneration (Trabaud et al. 1985). Serotinous (late-to-open) cones increase canopy seed storage in Aleppo pine as in other woody plants evolved in fire-prone environments (Lamont et al. 1991). Seeds involved in the post-fire natural regeneration derive from the crown seed-bank, whereas seeds stored in the soil are killed by the fire-induced high temperatures. According to its reaction to fire disturbance, Aleppo pine is considered as an obligate 'seeder', i.e. it necessarily relies, for the population recruitment, on a sexual

reproductive strategy and on seed dispersal (Trabaud 1987).

After seed dispersal, suitable soil conditions are required for seed germination and seedling development, which both represent crucial stages in the post-fire recruitment process of pine population. A prompt germination and a rapid early root growth are particularly important on inhospitable charred surfaces and in drought prone environments, in which young Aleppo pine seedlings are often exposed to the risk of water stress (Scarascia Mugnozza 1980).

After fire the characteristics of the forest floor are variable: the amount of ash, the temperature and the humidity all change with time. Microenvironmental heterogeneity was found to affect markedly germination processes, the spatial distribution of seedlings and their growth rate after fire (Ne'eman et al. 1992). A prolonged seed dispersal may enhance the probability for released seeds to match good microenvironmental conditions for germination and seedling growth.

During previous surveys and preliminary work in recently burned stands of *Pinus halepensis* in Southern

Italy it was observed that, due to the gradual removal of the ash layer covering the sand horizon, in few months the forest floor turns from a dark-brown to a light-yellow colour (Saracino & Leone 1993). After massive seed dispersal, seeds at the forest floor are exposed to the risk of predation by granivorous birds, which may be reduced by the partial homocromy between the seed coat and the soil surface; this point has been poorly investigated in conifer populations, with very few information available in major reviews; see, for instance, the book edited by Fenner (1992).

In this work the hypothesis has been addressed that the amount and the colour of the seed released after fire change with time, and that seed predation by birds play a significant role in burned areas. Based on the data, an interpretation of the variation of seed colour as a cryptic strategy to reduce the predation risk has been suggested. The study was performed in two Aleppo pine natural stands, growing in Southern Italy, which were affected to a different extent by the occurrence of a late-spring fire.

Material and methods

Study area

This study was carried out within a large (3200 ha) natural *P. halepensis* forest growing on alluvial sandy dunes facing the Ionian Sea, in the Province of Taranto, Southern Italy (40° 30' N, 17° 01' E). In this zone, the climate is Mediterranean, semi-arid type, with a drought period between May and October. Average annual temperature is 16.5 °C, annual rainfall is 501 mm. Understory vegetation is made up by evergreen sclerophyllous species, mainly *Phillyrea angustifolia* L., *Pistacia lentiscus* L., *Rosmarinus officinalis* L., *Cistus salvifolius* L. (Francini 1953).

On 13 May 1992, a fire burnt the forest over a surface of 35 ha. After 36 hours, two pine stands showing a different degree of damage were recognised. In one stand (S_1) the trees were completely burned ('charred'), in the another one (S_2) the trees appeared only 'scorched', with a crown in part still alive. Both these stands, which were also different in their structural characteristics and age (Table 1), were selected for this study.

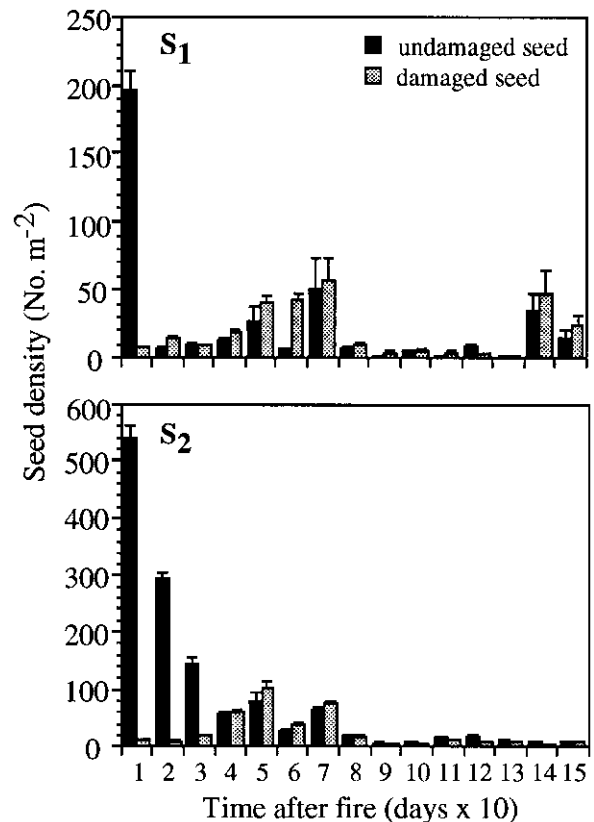


Figure 1. Seed density of undamaged and damaged (preyed) seeds at different dates after fire (day 1 is May 13, 1992) in the S_1 charred and the S_2 scorched stand; vertical bars denote standard errors of the mean ($n = 25$).

Sampling, seed characteristics and data analysis

Soon after fire, in each stand 25 rectangular sampling areas (surface area: 1 m²) were permanently defined on the ground, 0.3 m apart each other, along a transect which was positioned at random within the studied area. Starting on May 23, and throughout five successive months, every 10 days both undamaged as well as broken seeds were retrieved, using a sieve, from the ash layer of each sampling area.

For each seed lot, the number of undamaged seeds was determined. By careful inspection of seed fragments the number of seeds preyed by granivorous birds was estimated. Bird predation usually destroys the seed, leaving its basal portion (Bang & Dahlström 1990, Saracino personal observation). Seeds with damaged coats (in general found empty) were interpreted as the result of attempts of feeding by birds and classified as 'preyed' seeds as well.

Table 1. Characteristics of the studied stands

Stand	Condition	Age (years)	Tree density (n ha ⁻¹)	Basal area (m ² ha ⁻¹)	Average height (m)
S ₁	Charred	37	807	31.1	15.5
S ₂	Scorched	70	385	18.3	14.0

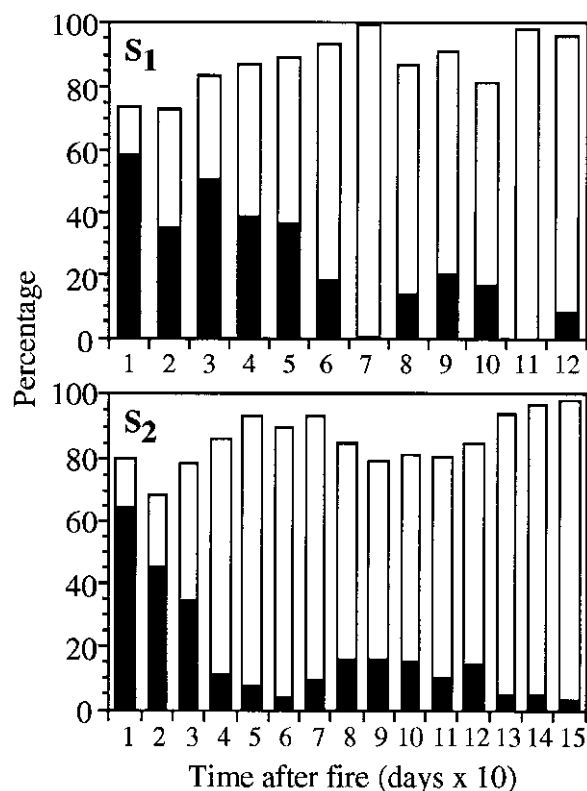


Figure 2. Percent of germination (solid boxes) and percent of empty seeds (open boxes) in seed lots collected at different dates after fire (day 1 is May 23, 1992) in the S₁ charred and the S₂ scorched stand.

For each seed lot, the percent of germination, the percent of empty seeds and the seed colour were determined.

Four 50-(undamaged) seed-replicates for each seed lot were germinated on continuously moistened filter paper at the constant temperature of 20 °C (photoperiod: 16 hours of dark and 8 hours of cool-white fluorescent light). Germination counts were made every two days for 30 days. Seeds were considered germinated when their roots were 2 mm in length. At the end of the germination test, nongermminated seeds were examined

to exclude empty seeds and the cumulative percent of germination was calculated on a full-seed basis.

To assess the colour, 60 undamaged seeds were randomly sampled from each seed lot and a code made up by three colour variables (*Hue*, *Value* and *Chroma*) was attributed, according to the Munsell Soil Color Charts, to both the 'convex' and 'flat' side of each seed. The *Hue* notation of a color indicates its relation to red, yellow, green, blue and purple; the *Value* notation indicates its lightness; the *Chroma* notation indicates its strength. Therefore, each seed was classified with respect to six colour categorical variables. Colour attribution was made by the same person under the same light conditions.

The variation of seed colour with time has been summarized by principal component analysis performed on colour categorical variables and multivariate means of sampling periods have been displayed in the plane of the first two principal components; the PRINQUAL procedure (principal component analysis for qualitative data) of SAS statistical package (SAS Institute 1988) was used.

Results

Soon after fire, up to 190 ± 14.4 and 540 ± 19.7 (mean \pm standard error, $n=25$) seeds m⁻² were retrieved in the charred S₁ and in the scorched S₂ stand, respectively (Figure 1). Differences between the stands in the characteristics of trees, which were considerably older and more widely spaced in S₂ than in S₁ (Table 1), can account for the larger seed densities observed in S₂. Seeds retrieved in the first month after fire accounted for 37% and 61% of seeds collected over the whole studied period, respectively in S₁ and S₂. A decreasing trend in seed density was observed with time in S₂; on the contrary in S₁ a sharp reduction was found after 10 days, with two minor peaks 70 and 140 days after fire (Figure 1).

The number of damaged seeds accounted for 43% and 23% of seeds collected during the studied period,

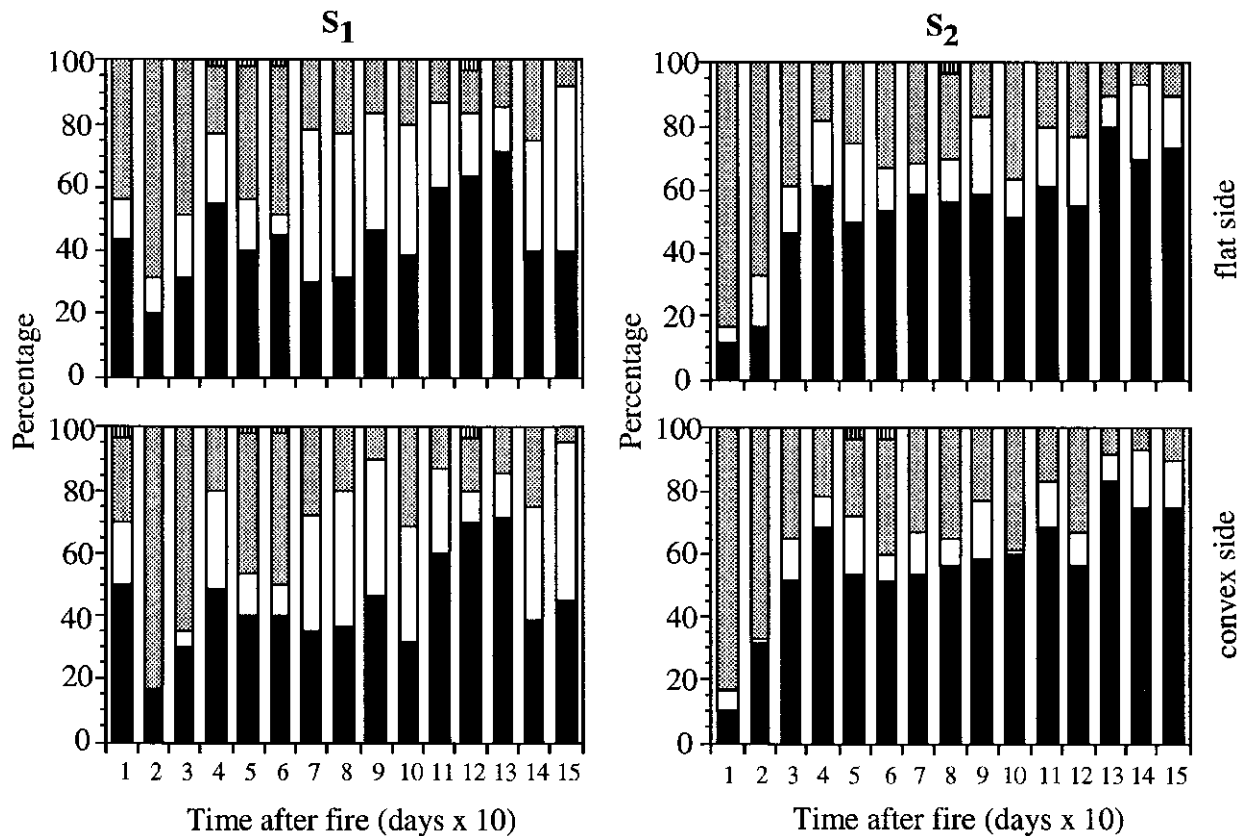


Figure 3. Temporal variation (day 1 is May 23, 1992) of the seed colour in the S_1 charred stand and the S_2 scorched stand. Seed colour is represented as the *Hue* colour variable of the Munsell Soil Color Charts, showing four colour categories: 10YR (solid boxes); 7.5YR (open boxes); 5YR (shaded boxes); 2.5YR (dashed boxes); the variation from the 10YR to the 2YR category represents, in qualitative terms, a transition from yellowish to brown colours. Upper graph, seed flat side; lower graph, seed convex side.

respectively in S_1 and S_2 . In the scorched S_2 stand undamaged seeds exceeded damaged seeds for longer than in the charred S_1 stand. In S_1 the number of damaged seeds peaked 70 days after fire, then it decreased until 140 days after fire, when a second peak was apparent; in S_2 the number of damaged seeds peaked between 50 and 70 days after fire, then it decreased (Figure 1).

The percent of germination and the percent of empty seeds respectively decreased and increased with time, in both stands. The percent of germination decreased from a value of 60–65% in early released seed lots to a value of 5–10% in late dispersed seed lots, with a more rapid reduction in S_2 . The percent of empty seeds, which was less than 20% soon after fire, exceeded 80% in late dispersed seed lots (Figure 2).

The colour of released seeds changed with time. In qualitative terms, dark grey-brown seeds were released at first, whereas late-dispersed seeds tended to a light

yellowish colour. The temporal variation of seed colour has been demonstrated quantitatively. Indeed, different frequencies of the Munsell's *Hue* categories were observed with time, with a gradual decrease of the brown category and an increase of the yellowish category (up to 70–75% in late collected seed-lots), especially in S_2 (Figure 3). Summarizing the colour variables by the principal component analysis, an interpretable ordination of sampling periods was obtained (Figure 4). In particular, the individual scores of sampling periods on the first principal component showed a significant linear correlation with Julian dates, suggesting a gradual change of seed colour with time (Figure 5).

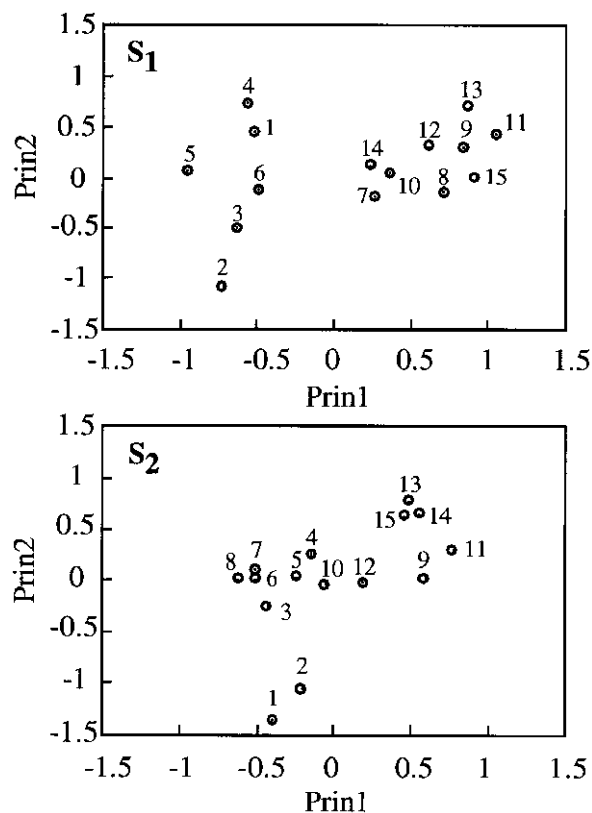


Figure 4. Results of the principal component analysis performed on the six categorical colour variables according to the Munsell Soil Color Charts: the multivariate means of sampling periods are displayed in the plane of the first two principal components (Prin1 and Prin2, respectively). Numbers indicate successive sampling periods (i.e. 1 = 13–23 May, 2 = 24 May–2 June, etc.); the first two principal components explained 68% and 30% of total variance in the S₁ charred stand and 66% and 32% of total variance in the S₂ scorched stand.

Discussion

The high seed densities observed soon after fire in both stands agree well with previous knowledge on the ecological reaction of *P. halepensis* populations to fire disturbance (Moravec 1990).

Dispersal of good quality seed is required for assuring the recruitment. Indeed, germination rates higher than 50% were observed in the first three decades after fire in both stands. A large proportion of viable seeds was recorded in the highly damaged charred stand. It is well known that woody scales act as effective insulator, preventing the occurrence of lethal temperatures inside closed pine cones; vaporisation of moisture from woody tissues also protects seeds from overheating (Beaufait 1960). In a recent experiment we found

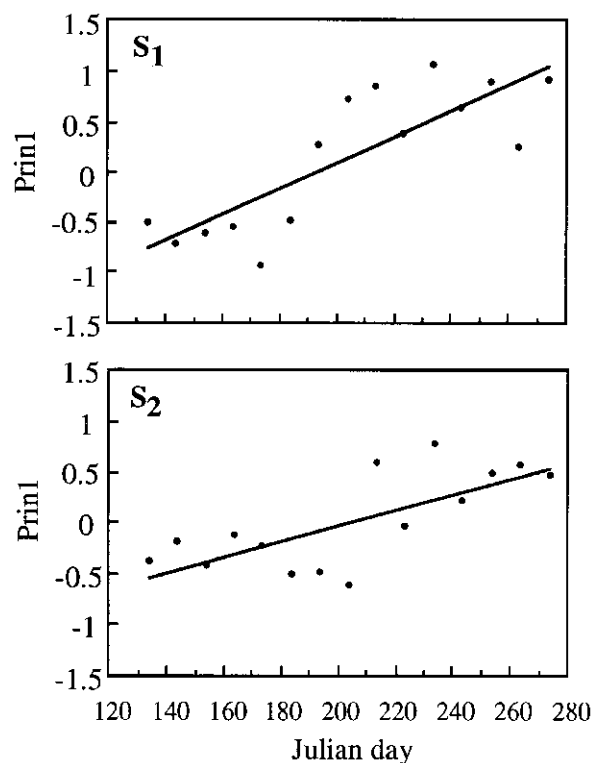


Figure 5. Results of the principal component analysis performed on the six categorical colour variables according to the Munsell Soil Colour Charts: linear regression between the scores of sampling periods on the first principal component (y) and the Julian dates corresponding to the different sampling periods (x); S₁ charred stand: $y = -1.508 + 0.013 x$ ($r = 0.823$, $P < 0.01$, $n = 15$); S₂ scorched stand: $y = -1.573 + 0.008 x$ ($r = 0.730$, $P < 0.01$, $n = 15$).

that after 30 minutes at 100 °C serotinous cones of *P. halepensis* were containing highly viable seeds (Sara-cino, unpublished data). Fraver (1992) found that, after 3 minutes at 500 °C, the temperature inside cones of *Pinus rigida* did not exceed 100 °C and Bradstock (1994) observed that the high temperatures occurring during bush-fires did not affect survival of seeds within serotinous fruits of *Hakea* species. It was observed, on the other hand, that the high temperatures experienced by seeds in the cones during a fire do not stimulate the germination (Martínez-Sánchez et al. 1995).

Seed dispersal was maximum soon after fire, but seeds continued to be released throughout the studied period. A prolonged seed dispersal may determine better chances for germination and seedling establishment, by allowing seeds to experience different ecological conditions. The temporal variability, after fire, of the forest floor environment has been documented. For instance, considerable amount of ash under the can-

opy were observed to be scattered by wind or surface runoff, creating a mosaic of physically and chemically contrasting microsites of litter debris and sand where patches of ashes, with high osmotic potential, alternate to bare sands (Thanos & Skordilis 1987; Ne'eman et al. 1992). Seeds were found to accumulate more in litter than in bare sand patches and greater viability and germination was also found in non-bare patches (Lamont et al. 1993).

Early released seeds were mainly sound, while an increasing percentage of empty seeds were found in late-dispersed seed lots. Similar characteristics for the early dispersed seeds were found in *P. halepensis* by Acherar et al. (1984). It may be argued that sound and thus heavier seeds are more promptly released from opening cones, prevailing in the first stages of seed dispersal. Also, sound seeds may be selectively located in the apical cone portion, which is more prone to opening. Sannikov (1994) found, in *Pinus sylvestris*, that the distal part of macrosporophyllous is pollinated more effectively, thus carrying better quality seeds.

The proportion of seeds preyed upon, which increased as the season progressed, may be due to birds. The presence of preyed seeds in early-picked up seed lots may indicate that granivorous birds were able to promptly colonize the burned area. Several bird species have a strong attraction to recent burns (Bock & Bock 1990; Prodon & Pons 1993); the increased habitat and forage diversity and the cover provided by dead standing trees may also favour bird colonisation in recently burned areas (Ffolliot 1990). In June and July we have recorded the presence of granivorous bird species – mainly *Serinus serinus*, *Passer domesticus* and *Fringilla coelebs* – at the study site. The lower proportion of damaged seeds in the S₂ scorched stand may be due to the repulsive effect on birds by the large amount of scorched biomass.

No rodents were observed in the area during the experiment, and no feeding signs by rodents were recorded on seeds; indeed, rodents are able to colonise burned areas in Mediterranean regions only few months after fire (Prodon et al. 1987). The role of ants as seed predators cannot be ruled out in our study, but ants (different species belonging to genus *Messor*) were observed to be active in the area only for few days after fire.

The colour of released seeds was demonstrated to change with time. On the contrary, no colour differences seem to exist between seeds extracted from cones of different age or between seeds extracted from different positions of the cone (Saracino, unpublished data).

A fine dark dust covers the seeds inside closed cones; the removal of this dust layer, leaving the underlying seed coat more and more exposed, may be the main factor causing the seed colour to change. Atmospheric factors are allowed to act on seeds retained in partially opened cones and it is stimulating to think that in *P. halepensis* the 'easily removable' dust layer may represent an adaptive trait, allowing late-released seeds to better couple, in terms of homocromy, with the changing characteristics of surface soil. From previous knowledge on the variation of the forest floor colour after fire (Saracino & Leone 1993) we can assume that the dashed grey-brown colour of early-dispersed seeds may allow them to be mimetic with the ash layer covering the soil soon after fire; the yellowish colour of late-dispersed seeds may, on the other hand, improve their mimicry to the underlying sandy soil, from which the ash layer is progressively removed. Birds use colour vision as the main cue for detecting food, and in several cases selection has favoured seed crypsis, reducing the foraging possibilities (Stiles 1992).

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