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Effect of high temperatures and ash on germination of ten species from gorse shrubland

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Abstract

Seeds of ten species of Cistaceae, Ericaceae and Poaceae were examinated to compare their responses to high temperatures and ash, simulating the direct effect of fire on germination. A variable response to these factors between families and within species from the same family was detected.

In Cistaceae, heat treatment pre-sowing stimulated germination. In Ericaceae, germination was stimulated by thermic shock, but a wide range of response was detected (between all four species), from *Erica ciliaris*, very sensitive, to *Daboecia cantabrica* and *Calluna vulgaris* which showed no significant response. The range of reaction shown by the species of this family suggest that the size of the seeds is directly related to the difference in response, at least in species with a similar structure. In Poaceae, germination was not found to be dependent upon thermic shock.

The effect of ash varies in magnitude. Although it decreased the germination percentage in all species, in *Avenula marginata* (Poaceae) the effect was not statistically significant, whilst in Ericaceae, particularly in those showing the highest levels of germination in the control (*C. vulgaris* and *E. umbellata*), the effect is to inhibit germination completely. In respect to the effect of ash the families could be arranged in the order Ericaceae>Cistaceae>Poaceae.

Complex interactions between various dormancy types and seed size could explain these results. In species which depend on physical dormancy temperature has an important role. When other dormancy type is dominant in the control of germination, the medium characteristics could have a relevant role on seed response. In addition, the seed-size could determine the threshold of tolerance to temperature.

Nomenclature Tutin et al. (1985).

Introduction

Fire is one of the external agents that stimulates germination in many species of diverse types of vegetation all over the world, and this has, at times, been interpreted as a feature of adaptation to fire. However, it is often difficult to know which features are really adaptations to fire, as many of them appear to be of advantage to the plants in response to other disturbances or environmental forces. In this context, Trabaud (1987) discusses the term 'adaptation to fire' and 'pyrophytic'.

The part played in the breaking of dormancy by each of the agents related to germination (light, temperature, stratification, chilling, leaching of inhibitors, bioquimical 'trigger') changes according to the dormancy type of seed on which they are acting. In the case of a post-fire environment, the mechanism which starts germination is subject to controversy, and in relation to the breaking of dormancy of the seeds after fire two theories have been elaborated (Keeley et al. 1985):

a) One which relates germination to the loss of allelopathic compounds present in mature communities, or the elimination of toxins produced by microorganisms in the litter.

b) A second which attributes a direct effect to the fire itself.

Fire as an active agent in germination has been habitually related to two factors: the high temperatures generated in the burning and the presence of ash produced by the combustion of biomass. Studies which take into account the effect of temperature have been concerned with changes in intensity and exposure time, whilst studies with ash are based on its quantity or in the degree of biomass combustion (charred or total combustion).

Temperature has a special relevance in species having a hard seedcover (impermeable or semi-impermeable). For this reason Leguminosae and Cistaceae seeds usually show improbed germination with increasing temperature, within certain ranges. Some examples of this can be seen in the numerous studies carried out (Stone & Juhren 1951; Floyd 1966; Añorbe 1988; Tárrega et al. 1992; Valbuena 1990; Pereiras 1984; Troumbis & Trabaud 1986; Trabaud & Oustric 1989; Aronne & Mazzoleni 1989; Arianoutsou & Margaris 1981). In general, in these cases, the effect of fire was attributed to its capacity for altering the seed cover, which Stone & Juhren (1951) and Aronne & Mazzoleni (1989) proved to be modified due to the effect of the heat.

The part played by the ash (charred plant parts or ash) has also been studied in many species. Charred material favours germination in species from diverse families (Keeley 1987; Keeley & Keeley 1987; Jones & Schlesinger 1980; Keeley et al. 1985). However, this did not occur with ash from totally consumed wood. Thus, Sweeney (1956) detected a decrease in the germination of forbs, while Pereiras (1984) found that germination in *Ulex europaeus* was better when the ash came from lightly burned gorse rather than well burnt gorse, and Trabaud & Casal (1989) found a decrease in germination in *Rosmarinus officinalis*.

The response to temperature is related to the hard seedcoat, but the response to ash is less well known. Keeley (1987) proposes an oligosaccharine (hemicellulose) as a stimulus to germination, produced by the action of the high temperatures on the wood, pointing out at the same time that this molecule is produced only in the case of fire. Keeley & Keeley (1987) also suggested that the response to ash could be related to some type of polymorphism in the seeds of a species, and in their opinion (Keeley 1991), the action of the ash is a more exact measurement of the effect of fire on germination than the study of response to temperature.

During a fire, a wide range of exposure times and temperatures are produced. This leads to the question of whether or not the seeds of the shrub species subjected to fire have identical requirements for heat and a similar response to the presence of ash in order to germinate. Trabaud & Oustric (1989) propose that differential requirements for heat could have an adaptive value, as such a mechanism could permit the regeneration of these species in a wide range of micro-environments in accordance with the temperatures reached by the fire.

Post-fire regeneration of communities dominated by some species from families analysed in this paper has been studied in many other works (see Pitot & Masson 1951; Whittaker & Gimmingham 1962; Kayll 1966; Stinson & Wright 1969; Vogl 1974; Ivens 1978; Zabkiewicz 1979; Casal 1982; Hobbs & Gimingham 1984; Arianoutsou & Faraggitaki 1984; Troumbis & Trabaud 1986, 1987; Alonso *et al.* 1992). However, the response to high temperature and ash separately are not clearly analysed.

The aim of this study was to quantify the variations found in germination of seed of ten species coexisting in matorral when submitted to the action of thermic shocks and of ash and to elucidate the factors causing these variations.

Methods

Ten species encountered in *Ulex* scrublands were selected. Most of these occurred in the one plot situated on Monte Castro Valente, Padrón (42 °44′N, 8 °38′0), except *E. ciliaris* which is most abundant in more humid areas (Basanta et al. 1988), and was collected on Monte Devesa Negreira (42 °48′N, 8 °14′E). Both plots have similar characteristics: age after fire (3 years) is the same, the dominant species is *U. europaeus*, and the species which form the community are largely the same. The predominance of *U. europaeus* in many of these gorselands is due, clearly, to anthropic effects including the frequency of fires and the former sowing of seeds of this species (Dalda 1972).

The species selected are three Cistaceae (*Halimium alyssoides*, *Tuberaria guttata*, *Cistus psilosepalus*) four Ericaceae (*D. cantabrica*, *E. umbellata*, *E. ciliaris*, *C. vulgaris*) and three Poaceae (*Agrostis curtisii*, *A. delicatula* and *A. marginata*). Seeds were collected from June 1988 until December 1988, coinciding with the dispersion period of these species (Table 1). The seed obtained from each species, derived from three samples gathered during the dispersion period from a large number of individuals and from various branches and inflorescences of each, was stored in 60 bags of 30 seeds/bag.

Seed from some of the species requires a period of treatment at low temperature (stratification) in order to overcome embryo dormancy. This phenomenon was not studied. Rather all seed were stratified for 45 days at 4 °C and then sown on filter paper discs in glass Petri dishes (diam. 9 cm). Thirty seeds per dish were used in ten lots per treatment.

Two temperatures were selected: 80 °C (T1) and 110 °C (T2). The seeds were heated for five minutes in a forced convection oven prior to sowing (these treatments were selected to cover conditions potentially encountered by seed in the soil during fire (DeBano et al. 1977; Trabaud 1977; Díaz-Fierros et al. 1990). Ten lots of seeds that were not subjected to thermic shock served as controls (T0).

The influence of ash was studied by watering 10 lots of seed, which had not been subjected to thermic shock, and seeds subjected to 110 °C, with a mixture of water and ash. These dishes were designated A1. Controls were watered with de-ionized water (A0). The ash suspension was obtained from the combustion of the different groups of species from the scrubland mixed in a proportion of 7 parts of *Ulex*, 1 part of the other species and then diluted with de-ionized water at the rate of 50 g of ash to 5 litres of water. The mixture 7 *Ulex*:1 other species was chosen to reflect the greater proportion of *Ulex* biomass with respect to the others species. The mixture 50 g: 5 l corresponded to an application of 0.5 g of ash/treatment, similar to the application employed by Keeley & Keeley (1987), but quantitie of ash and extend of combustion used by other authors are different (Keeley 1984; Keeley et al. 1985; Keeley 1987; Trabaud & Casal 1989).

The dishes were placed in a controlled environment cabinet at a temperature of 20 °C±1 °C and a photoperiod of 15 hours light/9 hours dark using 19 fluorescent tubes of 58 w each. A temperature of 20 °C was used following other studies of germination in which temperatures varied between 20 °C and 23 °C (Whittaker & Gimingham 1962; Floyd 1966; Keeley 1987; Trabaud & Oustric 1989).

Germination rate (t_{90}), that is the time required for 90% of final germination percentage to be attained, germination interval and percentage germination were determined in each of the ash and temperature treatments. The study lasted 62 days and counts were made every day during the first 32 days and every two days during the last month. The seed was considered to have germinated when the radicle emerged, following Evenari (1957) and Come (1970).

Statistical analysis was carried out with ANOVA after angular transformation of germination percentage (Sokal & Rohlf 1979). One way ANOVA's were calculated for each of the variables studied, temperature and ash. In the cases where the temperature was significant the REGWQ (Ryan-Eynot-Gabriel-Wells; Anon. 1985) test was used in the *a posteriori* comparison of the means. A sum of the squares Type III was calculated in order to quantify the interaction between the two factors in each species separately (except in *C. vulgaris* and *E. umbellata*, where this was not possible as no germination was detected in the treatments with ash suspension). A combined analysis of the species pertaining to the same family was used to study the effect of ash and temperature in each family.

Results

Effect of temperature

The results (Tables 2, 3 and 4) indicate that the higher temperatures has a favourable effect on germination in five of the tested species. The three Cistaceae are clearly stimulated by the temperature of 110 °C. *C. psilosepalus* is also significantly stimulated at 80 °C, although the highest average percentages are obtained at 110 °C, which treatment also produces the longest germination interval (Table 3) and the shortest t_{90} of the species (Table 4). In *E. ciliaris* the lowest value for t_{90} also corresponds to the most favourable temperature for germination (Table 2 and 4); but in this species the optimum germination temperature is 80 °C. *E. umbellata* has a response pattern similar to *E. ciliaris*, but statistically both temperatures favour germination. The other two Ericaceae *D. cantabrica* and *C. vulgaris* are indifferent statistically to thermic shock, although they show a slight increase in germination with the temperature. In the three Poaceae no significant effects of temperature were shown.

Effect of ash

The part played by the ash is more uniform, statistically, than temperature. In all the species (except

Table 1. Fruiting characteristics of the species studied. The data shown in the first, second and last columns are the results of this study, whereas the other columns were obtained from the bibliography.

Species	Seed/fruit	Seed mass(g)	Life form	Family	Regeneration	Dispersal period
Tuberaria guttata	55(40–71)	5.9×10^{-5}	Pterophyte	Cistaceae	Seed	May-June
Halimium alyssoides	36(34–40)	6.5×10^{4}	Chamaephyte	Cistaceae	Seed and sprout	July-August
Cistus psilosepalus	38(30–43)	1.0×10^{-3}	Chamaephyte	Cistaceae	Seed	July-August
Daboecia cantabrica	57(34–80)	1.3×10^{-4}	Chamaephyte	Ericaceae	Seed and sprout	August-September
Erica umbellata	30(25–40)	2.0×10^{-5}	Chamaephyte	Ericaceae	Seed and sprout	August-October
Erica ciliaris	56(23–109)	1.9×10^{-5}	Chamaephyte	Ericaceae	Seed and sprout	August-October
Calluna vulgaris	26(20–32)	4.0×10^{-5}	Chamaephyte	Ericaceae	Seed and sprout	October-December
Agrostis curtisii	–	5.5×10^{-5}	Hemicrytophifite	Poaceae	Seed and sprout	July-August
Agrostis delicatula	–	8.9×10^{-5}	Hemicryptophite	Poaceae	Seed and spruot	July-August
Avenula marginata	–	2.0×10^{-3}	Hemicryptophite	Poaceae	Seed and sprout	June-July

Table 2. Germination percentage of selected herbs and shrubs of gorse shrubland in response to 80 °C (T1) and 110 °C (T2) for five minutes, in controls (T0), or with application of powdered ash (A1) suspension to the germination medium (n = 10 dishes of 30 seeds each). With significant differences, treatments with the same superscript letter are not significantly different at P>0,05, for the same factor.

Species	Treatments				
	T0+A0	T1+A0	T2+A0	T0+A1	T2+A1
Tuberaria guttata	37.4a	31.8a	48.5b	17.9a	7.4b
Halimium alyssoides	7.4a	13.0a	48.5b	1.4	2.9
Cistus psilosepalus	41.2a	62.9b	71.7c	8.5	14.8
Agrostis delicatula	97.3	95.9	95.9	81.7	78.0
Avenula marginata	17.4	21.9	22.3	13.4	17.7
Agrostis curtisii	16.7	8.9	16.5	10.5	6.5
Calluna vulgaris	78.2	83.4	87.6	0.0	0.3
Erica umbellata	43.1a	67.1b	60.3b	0.0	1.0
Erica ciliaris	32.4a	51.2b	40.7a	1.1	1.1
Daboecia cantabrica	11.2	15.6	18.9	4.3	4.9

A. marginata) the presence of ash significantly reduces germination (Table 2). However, differences in the magnitude of the effect were detected. This negative effect on germination is higher in species of Ericaceae and lower in the Poaceae. Whereas in *A. delicatula* the mean percentage germination in the two treatments in the presence of ash reaches 80% germination, in *A. curtisii* it reaches 8.5% with ash and 14.8% without ash, and in *A. marginata* a level of 16% with ash, which is not significantly different from germination without ash. In Cistaceae a certain relationship is maintained between the percentage germination of the species with and without ash, but the negative effect is greater than in Poaceae (Table 2). Between *T. guttata* and *C. psilosepalus* there is also a divergent tendency in response to the temperature of 110 °C and a statistically significant interaction between the two factors (ash and temperature, calculated using a SS Type III) was detected in the three species of Cistaceae.

The species of Ericaceae are more negatively affected by ash. The species which reached the highest germination values in the controls (*C. vulgaris* and *E. umbellata*) are completely inhibited by ash. However, *D. cantabrica*, which has very low germination averages in the control (11%), registered about 4.5% of germination in the treatments using ash, which is the

Table 3. Germination intervals of each species (in days) for each of the experimental conditions.

Species	Treatments				
	T0+A0	T1+A0	T2+A0	T0+A1	T2+A1
Tuberaria guttata	2-48	3-56	1-59	4-16	7-12
Halimium alyssoides	5-53	5-56	6-56	6-15	6-20
Cistus psilosepalus	5-44	5-46	5-58	5-22	6-28
Agrostis delicatula	4-15	4-14	4-11	6-40	6-48
Avenula marginata	7-30	7-30	7-26	8-39	8-44
Agrostis curtisii	7-16	7-15	7-26	12-34	10-24
Calluna vulgaris	16-58	16-58	15-58	–	34-34
Erica umbellata	15-46	15-55	15-58	–	30-44
Erica ciliaris	16-58	16-50	16-58	20-46	46-50
Daboecia cantabrica	18-58	17-58	17-48	28-48	26-43

Table 4. Number of days in which the value of 90% germination t_{90} was reached in each treatment and species.

Species	Treatments				
	T0+A0	T1+A0	T2+A0	T0+A1	T2+A1
Tuberaria guttata	16	27	17	10	10
Halimium alyssoides	53	34	32	16	20
Cistus psilosepalus	17	21	19	21	16
Agrosris delicatula	6	6	6	17	17
Avenula marginata	20	16	14	37	20
Agrostis curtisii	14	15	15	24	24
Calluna vulgaris	40	33	32	–	34
Erica umbellata	29	30	29	–	34
Erica ciliaris	32	29	38	46	50
Daboecia cantabrica	53	44	45	46	41

highest value of response to ash detected in this family. In *C. vulgaris*, in treatments without ash, the average germination value is 83%, only surpassed by the grass *A. delicatula*. The latter species is also characterised by the lowest t_{10} value of the 10 species studied.

Behaviour of families and species

In the unifactorial analysis of the species grouped by families, the percentage germination of the Poaceae is higher and statistically different from the other two groups ($F_{2,494} = 12.29$; $p<0.0001$; Poaceae $= 40.0^b$, Ericaceae $= 30.5^a$, Cistaceae $= 26.5^a$). The favourable response of the Cistaceae to the temperature increase is confirmed in the combined analysis of the three species (($F_{2,81} = 28.5$, $p<0.0001$; T0+A0 $= 28.6^a$; T1+A0 $= 35.9^b$; T2+A0 $= 50.3^c$). However, in Ericaceae germination at 110 °C was not significantly different from that at 80 °C ($F_{2,105} = 16.6$; $p<0.0001$; T0+A0 $= 41^a$, T1+A0 $= 55^b$, T2+A0 $= 53^b$), while the Poaceae species, which did not respond to thermic shock ($F_{2,81} = 0.91$, NS), are less adversely affected by the addition of ash ($F_{1,54} = 13.6$, $p<0.0001$: A0+T0 $= 43.8^a$, A1+T0 $= 35.2^b$). Both the Cistaceae and the Ericaceae suffer the unfavourable effect of ash manifested to a greater degree in the Ericaceae (Cistaceae: $F_{1,54} = 75.9$, $p<0.0001$; A0+T0 $= 28.6^a$,

$A1 + T0 = 9.2^b$; Ericaceae: $F_{1,72} = 688.1$, $p<0.0005$; $A0 + T0 = 41^a$, $A1 + T0 = 1.4^b$).

Between the species within in the same family, germination differences are always significant (Cistaceae: $F_{2,135} = 96.4$; $p<0.0001$; *H. alyssoides* $= 11.0^a$, *T. guttata* $= 28.6^b$, *C. psilosepalus* $= 39.8^c$; Ericaceae: $F_{3,177} = 70.47$, $p<0.0001$, *C. vulgaris* $= 49.9^a$, *E. umbellata* $= 34.3^b$, *E. ciliaris* $= 24.8^c$, *D. cantabrica* $= 10.7^d$; Poaceae: $F_{2,135} = 699.8$; $p<0.0001$, *A. delicatula* $= 89.8^a$, *A. marginata* $= 18.5^b$, *A. curtisii* $= 11.8^c$).

The germination rate in Ericaceae and Cistaceae varies inversely with the germination percentage. The greatest t_{90} values correspond to the species with the lowest germination percentages, *H. alyssoides* and *D. cantabrica* respectively (Table 4). This pattern is not detected in Poaceae, which moreover present the shortest germination intervals (Table 3), and lowest t_{90} values of three families (Table 4).

Discussion

The stimulation of germination by thermic shock in the three Cistaceae corroborates the results obtained in other studies (Arianoutsou & Margaris 1981; Troumbis & Trabaud 1987; Trabaud & Oustric 1989; Valbuena et al. 1992), which examined the response to temperature of the species of this family. This parallelism detected in the response of the Cistaceae is probably related to the similar structure of the seeds in the three species, as suggested by Atwater (1980), though their reproductive strategy is different: *T. guttata* is an annual, *H. alyssoides* both sprouts and produces seeds (although it is difficult for it to resprout after fire) and *C. psilosepalus* is an obligate seeder and perennial. The temperatures applied exercise a favourable effect because part of the dormancy is associated with the semi-impermeable seed cover, and because the temperatures were sufficiently low. In many species the temperature begins to be lethal above 150 °C (Keeley 1977; Keeley 1991; Trabaud & Oustric 1989; Valbuena et al. 1992; e.g. *C. salvifolius* does not germinate after a temperature treatment of 150 °C during 5 min or at higher exposure times, Trabaud & Oustric 1989).

The degree of development of the several components of seeds (testa, embryo, endosperm) is linked to some structural differences between them which some authors (Martin 1945; Nikolaeva 1969; Bewley & Black 1978; Atwater 1980) claim may be used as criteria in the selection of physiological groups for characterising dormancy. According to the classification of Atwater (1980), this family belongs to the group which has ligneous covered seeds with semi-permeable layers. These protect the seeds and even if not impermeable to water are semi-permeable or permeable to chemical substances such as endogeny inhibitors and gasses, especially oxygen. Evenari (1961) and Nikolaeva (1969) maintain that in Cistaceae the presence of an inhibitor in the layers of the seed cover could use the available oxygen and consume that required by the embryo. Therefore, damage to the seedcover could facilitate germination by activating some compound which promotes germination. This process of activation, which could be carried out by some element present in the ash, has not been found in any of the species examined here.

The indifferent response of the Poaceae to temperature coincides with other studies on species of this family, Keeley & Keeley (1987), with Poaceae exposed to 120 °C during 5 min. The temperature does not appear to play a decisive part in the rupture of dormancy in these seeds and germination is not affected by this factor, except when it reaches lethal levels or is combined with other factors.

In the Ericaceae, two patterns of response to temperature are evident. In the case of *C. vulgaris* and *E. umbellata* the response to increase of temperature though favourable is not statistically significant, while *E. ciliaris* and *E. umbellata* are significantly affected by the temperature. *E. umbellata* is significantly stimulated by temperatures of 80 °C and 110 °C. It was also noticied that at 110 °C germination is slightly lower than at 80 °C and this tendency towards lower germination at 110 °C was statistically confirmed in *E. ciliaris*, the species which had the smallest seeds (Table 1). The range of responses to thermic shocks is possibly related to seed size. Keeley (1977) suggested the importance of the surface/volume ratio of the seed in its capacity to tolerate high temperatures. Valbuena (1990) and Valbuena et al. (1992) found that the temperatures required to block germination in *C. laurifolius* are higher and require more exposure time than in *C. ladanifer*, a species having smaller seeds. Judd (1994) also suggests that the size of seed-capsules appears to affect their insulating capacity in four small Myrtaceous species. *E. ciliaris* (with the smallest seeds) is the only species where germination is clearly reduced at a temperature of 110 °C. We therefore support the proposal made by Keeley (1977) and consider that the surface/volume ratio is critical in the observed response to temperature. Moreover, it is possible that this relation is true only in seeds which have a similar structure. This structural relation could be a family characteristic. Therefore, for example, *D. cantabrica* has a weight between that of *T. guttata* and *H. alyssoides* (Table 1), both of which are stimulated by temperature. Barro & Poth (1988) also suggested that seeds with a low activation energy (E_a) might be less damaged by heat and, therefore, more adapted to fire than those which are stimulated more quickly by heat, but related the response to temperature with adaptive traits (no sprouting shrubs of *Ceanothus* are lower E_a that the sprouting).

C. vulgaris and *E. umbellata*, have polychromatic seeds, a trait which could be related to a polymorphic response as suggested by Keeley (1991). This could help to explain the lack of significant response to temperature in seeds of both species. The variability of the data distribution for *E. umbellata*, for example, probably reflects the heterogeneity of responses within the populations of seeds studied.

The part played by the ash in germination has not been shown so unambiguously, neither has it been related to a particular seed type, as with temperature. In other studies where germination was stimulated by the presence of charred wood, the species show low levels of germination in the absence of these materials in the incubation medium – e.g. species of genus *Phacelia*, Keeley et al. (1985) – in species such as *Adenostoma fasciculatum* (Rosaceae), in *Arctostaphilos glandulosa* (Ericaceae), *Garria flavescens* (Garryaceae), *Salvia mellifera* (Lamiaceae), *Romneya trichocalix* (Papaveraceae) and others (Keeley, 1987). Most of these species share a characteristic: in a similar way to the species of the genus *Phacelia* they have a low percentage of germination in the absence of charred wood. In some, no germination takes place without charred wood, in any of the treatments.

González-Rabanal et al. (1994) found a favourable effect of ash on apical seed in three grasses and unfavourable in basal seeds, and suggested that this response could be due to the different degrees of development of the seeds. In this study the ash is almost always unfavourable in the germination medium. It is also noticeable that, particularly in the Ericaceae, the effect is more pronounced in species with higher germination percentages in the controls (see Table 2). These results, and those found by previously mentioned authors, permit us to suggest that the action of the ash on germination could be related to some non-physical type and that the species which display this dormancy type are more sensitive to the properties of the medium, for example the pH, which in the ash-suspension was alkaline. A high pH in the medium may depress germination in some Ericaceae (Gimingham 1965; Bannister 1965).

It might be expected that reponse to high temperature and the presence of ash would be uniform in each family. However a range in the germination percentage in the species of a particular family is evident. Variation between species has also been found in other studies, for Ramnaceae germination values in the controls varied between 0% and 48%, in four Anacardiaceae the ranges were between 10% and 68%, in three Rosaceae between 4 and 99% (Keeley 1987); Keeley & Keeley (1987) showed similar variation in Asteraceae, Scrophulariaceae and Amarillidaceae. As did Trabaud & Oustric (1989), with three Cistaceae and Reyes (1992) with three pine species. This variation may be common to all families, and suggests the presence of various types of dormancy acting simultaneously in each whose action varies among then. As Martin stated in (1945) on seeds, their basic internal organization varies only slightly among related species and genera, and the differences that exist may properly be regarded as significant phylogenetically.

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