

CISTACEAE: A PLANT FAMILY WITH HARD SEEDS

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ABSTRACT

An examination of 203 seed lots from 42 Old World species (or 54 taxa), with representatives from all five genera (*Cistus*, *Fumana*, *Halimium*, *Helianthemum*, and *Tuberaria*) and an additional seed lot of the New World *Lechea maritima* shows that the phenomenon of hardseededness is a prominent characteristic of the entire Cistaceae family. Promotion of seed germination in the laboratory can be obtained by mechanical scarification and thermal pretreatment, while light seems to be totally ineffective. A seed ecology syndrome for Cistaceae is postulated, featuring small seed size, hardcoatedness (primary dormancy), short-distance dispersal, long-term persistence in soil seed banks, fire- or heat-induced seed "softening", an opportunistic strategy of germination (germination at a wide range of temperature and light conditions), and a slow germination rate of "softened" seeds. This syndrome is suggested to endow Cistaceae, a principally Mediterranean family, with a considerable ecological advantage in the summer-dry and fire-prone Mediterranean climatic conditions.

INTRODUCTION

Cistaceae is a medium-sized family of shrubs, subshrubs, and occasionally herbs which are characteristic of dry, sunny habitats (Proctor, 1978). It is comprised of 7 genera (*Cistus*, *Fumana*, *Halimium*, *Tuberaria*, *Helianthemum*, *Hudsonia*, and *Lechea*) with a total of about 175 species (Mabberley, 1987). The distribution of the family is chiefly north temperate, especially in the Mediterranean region (ca. 100 species) and more specifically in its western part. In particular, all the species of the first 4 genera mentioned above (numbering 17, 13, 9, and 11, respectively) are distributed, almost exclusively, in the Mediterranean rim (Dansereau, 1939; Greuter et al., 1984). In addition, almost half of the 110 species of *Helianthemum* are also found mainly in the Mediterranean, although several (out of a total of 31 European species) are distributed over most of Europe (Tutin et al., 1986). About 25–30 *Helianthemum* species (formerly grouped under the generic name *Crocantenum*; Meusel, 1978) are found in North and South America. Finally, the genera *Hudsonia* and *Lechea* are represented by a total of about 20 New World species.

Hardseededness, a specific type of primary seed dormancy, is widespread in flowering plants. A total of 12 angiosperm families with species producing water-impermeable ("hard") seed coats is cited in numerous relevant reviews (Barton, 1965; Côme, 1970;

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Ballard, 1973; Rolston, 1978; Werker, 1980/81; Koller and Hadas, 1981; Bewley and Black, 1982; Tran and Cavanagh, 1984; Egley, 1989). Surprisingly, as pointed out previously (Thanos and Georghiou, 1988), Cistaceae is not mentioned at all in these reviews. Moreover, no specific reference is made of the release of the coat-imposed dormancy for any members of Cistaceae in the compendia of seed germination rules (Atwater, 1980; Association of Official Seed Analysts [AOSA], 1981; Ellis et al., 1985; International Seed Testing Association [ISTA], 1985). A recent reference to Cistaceae as having hard seed coats was made with regard to the Sheffield flora (Thompson and Booth, 1993).

Scattered and indirect information on the presence of hard seed coats in species of Cistaceae has been recently complemented by a considerable number of mainly ecophysiological works which have revealed hardseededness in wildfire-following *Cistus* species and related plants. A compilation of the available data is presented in Table 1. Although

Table 1

List of plant species belonging to the Cistaceae family, previously reported for hardseededness

<i>Cistus albidus</i> L.	Vuillemin and Bulard (1981), Trabaud and Oustric (1989), Corral et al. (1990), Roy and Sonié (1992)
<i>C. creticus</i> L.	Argyris (1977), Troumbis and Trabaud (1986), Thanos and Georghiou (1988), Aronne and Mazzoleni (1989)
<i>C. ladanifer</i> L.	Corral et al. (1990), Valbuena et al. (1992)
<i>C. laurifolius</i> L.	Corral et al. (1990), Valbuena et al. (1992)
<i>C. monspeliensis</i> L.	Vuillemin and Bulard (1981), Aronne and Mazzoleni (1989), Trabaud and Oustric (1989), Roy and Sonié (1992)
<i>C. salviifolius</i> L.	Troumbis and Trabaud (1986), Thanos and Georghiou (1988), Trabaud and Oustric (1989), Corral et al. (1990)
<i>Fumana thymifolia</i> (L.) Webb	Doussi and Thanos (1993)
<i>Helianthemum nummularium</i> (L.) Miller	Grime et al. (1988)
<i>H. oelandicum</i> (L.) DC.	Widen (1980)
<i>H. scoparium</i>	Keeley et al. (1985)
<i>H. ventosum</i> Boiss.	Guterman and Agami (1987)
<i>H. vesicarium</i> Boiss.	Guterman and Agami (1987)
<i>Tuberaria guttata</i> (L.) Fourr.	Juby and Pheasant (1934)

Table 2

List of plants (species and subspecies of the Cistaceae family) surveyed for hard seed coats in the present study

Lot No.	Taxon	Seed weight (mg)
1	<i>Cistus acutifolius</i> Sweet	0.86
2-3	<i>C. albanicus</i> Heywood	1.11
4-17	<i>C. albidus</i> L.	1.05
18-19	<i>C. clusii</i> Dunal	0.32
20-36	<i>C. creticus</i> L. ssp. <i>creticus</i>	0.86
37-38	<i>C. creticus</i> L. ssp. <i>corsicus</i> (Loisel.) Greuter & Burdet	0.99
39-40	<i>C. creticus</i> L. ssp. <i>eriocephalus</i> (Viv.) Greuter & Burdet	0.69
41-42	<i>C. crispus</i> L.	0.47
43-44	<i>C. ladanifer</i> L.	0.27
45-53	<i>C. laurifolius</i> L.	1.00
54-65	<i>C. monspelienses</i> L.	0.94
66	<i>C. monspeliensis</i> x <i>parviflorus</i>	0.90
67-68	<i>C. osbeckiaefolius</i> Webb ex Christ	0.36
69-70	<i>C. palhinhae</i> Ingram	0.29
71-72	<i>C. parviflorus</i> Lam.	0.68
73	<i>C. populifolius</i> L.	1.41
74-79	<i>C. psilosepalus</i> Sweet	0.97
80-98	<i>C. salviifolius</i> L.	0.97
99	<i>C. symphytifolius</i> Lam.	0.44
100-101	<i>Fumana ericoides</i> (Cav.) Gand.	2.29
102	<i>F. laevipes</i> (L.) Spach	1.07
103-107	<i>F. procumbens</i> (Dunal) Gren. & Godron	1.99
108-110	<i>F. thymifolia</i> (L.) Webb	0.97
111	<i>Halimium atriplicifolium</i> (Lam.) Spach	1.04
112-114	<i>H. halimifolium</i> (L.) Willk. ssp. <i>halimifolium</i>	0.51
115-117	<i>H. ocymoides</i> (Lam.) Willk.	0.69
118	<i>H. umbellatum</i> (L.) Spach	1.08
119	<i>H. viscosum</i> (Willk.) Pinto da Silva	1.05
120-135	<i>Helianthemum apenninum</i> (L.) Miller	1.22
136	<i>H. cinereum</i> (Cav.) Pers.	0.32
137-143	<i>H. croceum</i> (Desf.) Pers.	1.34
144	<i>H. hirtum</i> (L.) Miller	1.55
145	<i>H. juliae</i>	0.80
146-150	<i>H. ledifolium</i> (L.) Mirxer	0.33
151	<i>H. leptophyllum</i> Dunal	1.56
152	<i>H. macranthum</i>	1.59
153	<i>H. marifolium</i> (L.) Miller	1.57
154-164	<i>H. nummularium</i> (L.) Miller	1.27
165	<i>H. nummularium</i> (L.) Miller ssp. <i>berteroanum</i> (Bertol.) Breistr.	1.13
166	<i>H. nummularium</i> (L.) Miller ssp. <i>glabrum</i> (Koch) Wilczek	0.93

Table 2 (cont.)

No.	Taxon	Seed weight (mg)
167–168	<i>H. nummularium</i> (L.) Miller ssp. <i>grandiflorum</i> (Scop.) Schinz & Thell.	1.38
169–170	<i>H. nummularium</i> (L.) Miller ssp. <i>nummularium</i>	1.29
171–176	<i>H. nummularium</i> (L.) Miller ssp. <i>obscurum</i> (Celak) J. Holub	1.16
177	<i>H. nummularium</i> (L.) Miller ssp. <i>pyrenaicum</i> (Janchen) Hegi	1.66
178	<i>H. nummularium</i> (L.) Miller ssp. <i>tomentosum</i> (Scop.) Schinz & Thell.	1.67
179	<i>H. oelandicum</i> (L.) DC.	0.55
180–184	<i>H. oelandicum</i> (L.) DC. ssp. <i>canum</i> (L.) Bonnier	1.06
185	<i>H. piliferum</i> Boiss.	1.74
186–188	<i>H. pilosum</i> (L.) Pers.	0.91
189–192	<i>H. salicifolium</i> (L.) Miller	0.39
193	<i>H. squamatum</i> (L.) Pers.	0.83
194	<i>H. stipulatum</i> (Forsskal) C. Chr.	0.42
195–197	<i>Tuberaria guttata</i> (L.) Fourr.	0.14
198–203	<i>T. lignosa</i> (Sweet) Samp.	0.14

the number of species included in Table 1 is relatively small (13), it was considered a solid basis to encourage a broader survey. Therefore, the aim of the present work was to investigate to what extent the phenomenon of hardcoatedness characterizes the entire family of Cistaceae.

MATERIALS AND METHODS

Seed material was furnished by 25 botanical gardens (see the Acknowledgments section). A total of 203 seed lots (Table 2) was investigated, representing 42 species (and 54 taxa) of Old World Cistaceae; in addition, a lot of *Lechea maritima* Leggett was also tested. In most cases, the seeds were harvested in 1988 or 1989 from plants cultivated in the respective gardens; detailed data for each seed lot have been recorded (but not presented). Nomenclature follows the Med-Checklist (Greuter et al., 1984) although a few taxonomic problems were impossible to solve.

The seed weight for each taxon (shown in Table 2) is the mean value of the average weights of all the seed lots included in the particular taxon. Seed average weight was determined by weighing 100 seeds for each lot. Seed weights should be considered only as indicative because, in several instances, large variation was recorded among the various lots of a particular taxon.

Scarification of seeds was achieved by abrasion between two pieces of sandpaper. Air-dry seeds spread on glass dishes were preheated (1, 5, or 15 min) within an incubator set at $100 \pm 3^\circ\text{C}$.

Germination tests were performed in Petri dishes (8.5 cm in diameter) lined with two filter paper disks and moistened with 4 ml of deionized water. Germination experiments were accomplished at 15 and 20°C . Despite the broad range of temperatures which permit germination, these are the optimal ones not only for the previously studied *Cistus* species

(e.g., Thanos and Georgiou, 1988) but also for Mediterranean plants in general (e.g., Thanos et al., 1991). The criterion of germination was visible radicle protrusion. Measurements were taken at weekly intervals and germinated seeds were discarded. For each seed lot a sample of 100 seeds was used per treatment.

Germination experiments in the dark were carried out at 15 °C, in temperature-controlled plant growth cabinets (model BK 5060 EL, Heraeus, Hanau, Germany). The experiments under continuous Far-Red light were performed at 20 °C. The broad band Far-Red light source consisted of a bank of ten white incandescent tubes (Sylvania, 60 W, USA), three sheets of Plexiglas filters (two blue, 527, and one red, 601, 3 mm thick each, Röhm GmbH, Darmstadt, Germany), and a water bath, 10 cm deep.

RESULTS

Germinability levels (at 15 °C, in the dark) for untreated and abraded seeds of 203 seed lots are presented in Figs. 1 and 2. Almost invariably, mechanical scarification of the seed coat resulted in a dramatic increase of final germination as well as in a considerable enhancement of the germination rate. Scarification was shown to promote germination in

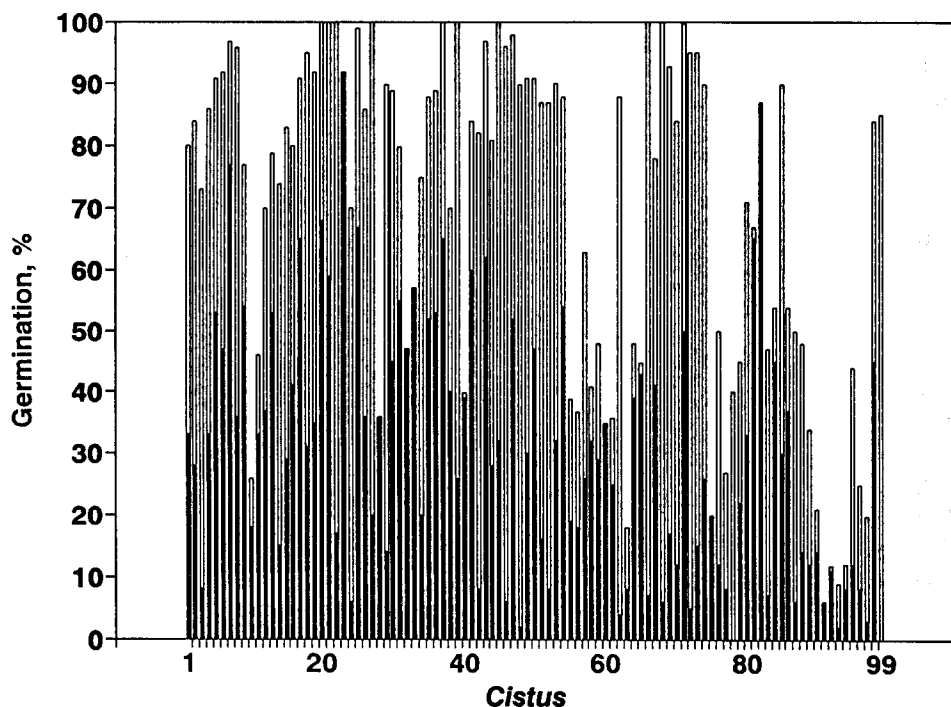


Fig. 1. The effect of seed coat scarification on the germinability (15 °C, darkness) of 99 lots of *Cistus* spp. Closed bars: untreated seeds, open bars: abraded seeds. Lot numbers correspond to those of Table 2.

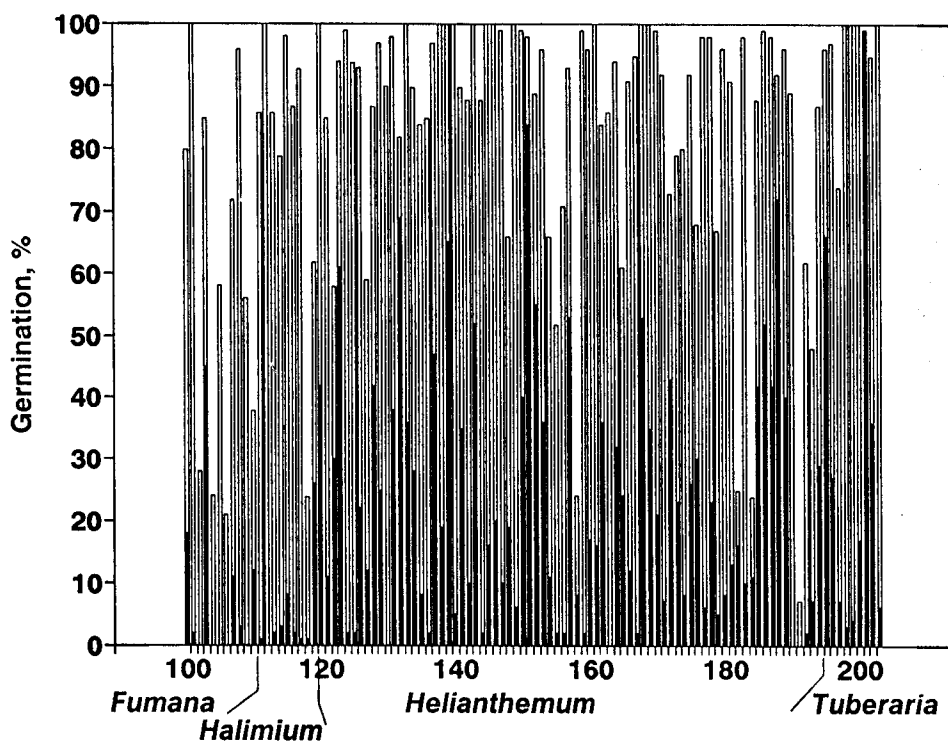


Fig. 2. The effect of seed coat scarification on the germinability (15 °C, darkness) of 104 lots of several species of *Fumana*, *Halimium*, *Helianthemum*, and *Tuberaria*. Closed bars: untreated seeds, open bars: abraded seeds. Lot numbers correspond to those of Table 2.

189 lots. Only in 14 of them (23, 28, 32, 33, 40, 60, 65, 75, 81, 82, 91, 92, 94, 201) final germination was not enhanced. Seed lots in which scarification was ineffective were: 4 of 17 in *Cistus creticus* ssp. *creticus*, 1 of 2 in *C. creticus* ssp. *eriocephalus*, 2 of 12 in *C. monspeliensis*, 1 of 6 in *C. psilosepalus*, 5 of 19 in *C. salviifolius*, and 1 of 6 in *Tuberaria lignosa*. Thus 13 of these lots belong to *Cistus* species and in 9 of them final germination was lower than 50%. In all 203 lots the germination rate of abraded seeds was much higher than that of untreated seeds (results not presented). Furthermore, in most cases, full germination of scarified seeds was obtained in less than two weeks while untreated seeds continued to germinate gradually for up to five weeks.

The effect of thermal pretreatment on seed germination of several members of the Cistaceae family was also investigated. Preheating seeds of 34 lots (from 33 species) for 15 min at 100 °C resulted in either increased, decreased, or no germination at all, in 8, 2, and 21 lots, respectively, while in 3 lots germination remained almost the same (results not presented). Since this treatment might have been lethal to seeds, the duration of preheating was reduced to 5 or, when necessary, to 1 min. Thus, 14 seed lots of different

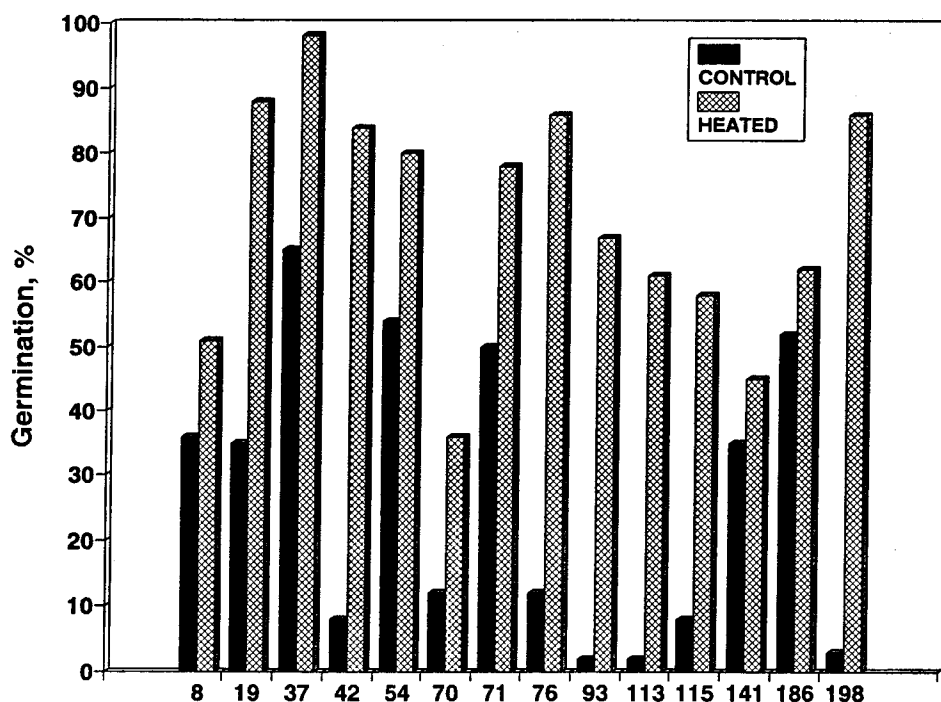


Fig. 3. The effect of heating on final seed germination (15 °C, darkness) of several Cistaceae species. Heat treatment: 100 °C for 5 min (1 min for lots 141 and 186). Lot numbers correspond to those of Table 2.

species (belonging to 4 genera) were tested and a considerable promotion of germination was observed (Fig. 3). In most cases, the germination rates (data not presented) closely resembled those of the untreated seeds and, in a few cases, were even slower.

In order to test the effect of Far-Red light (simulating the inhibitory light regime under a dense foliar canopy) on the seed germination in certain Cistaceae species, a preliminary experiment was carried out. Abraded seeds of ten different species were imbibed under temperature and light conditions simulating the climatic ones prevailing in southern Greece during November (Thanos et al., 1991). In all cases, final germination levels were almost identical under continuous darkness or Far-Red light (applied during the "day" period). In a subsequent experiment, seeds of 9 species (belonging to 5 genera) were imbibed under a most adverse, continuous Far-Red light of higher intensity, at a constant temperature of 20 °C. In order to avoid any interference with the abrasion effect, lots with high dark germinability were selected. Thus untreated (non-abraded) seeds of 7 different species, as well as two species (*Halimium halimifolium*, lot 113, and *Tuberaria lignosa*, lot 198) in which scarification was necessary for dark germination, were used. In all cases final germination and germination rates attained similar values in the dark and under Far-Red light (Fig. 4).

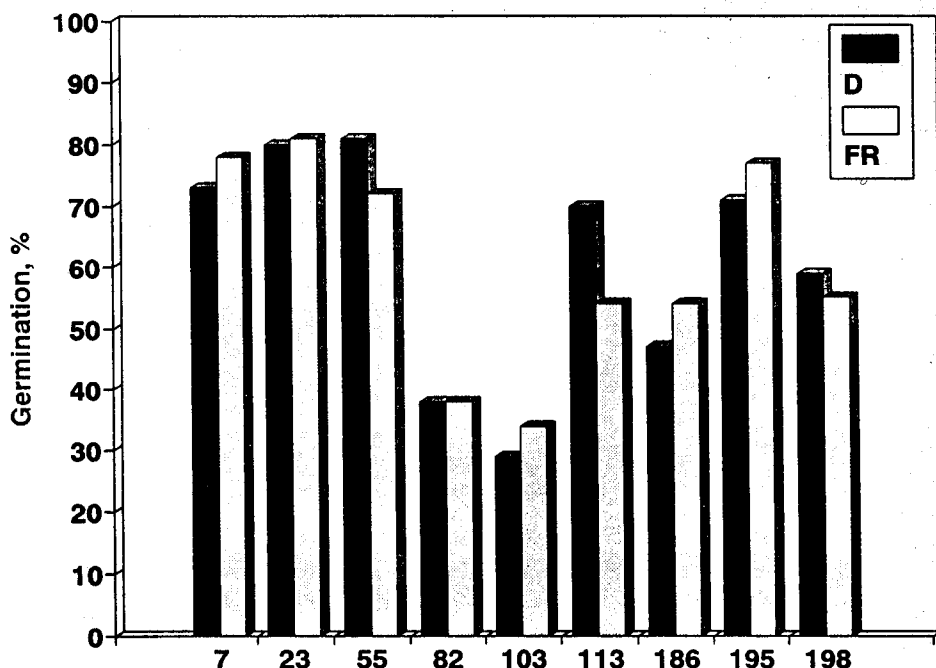


Fig. 4. The effect of continuous Far-Red irradiation on final seed germination (20 °C) of several Cistaceae species. Lot numbers correspond to those of Table 2.

In the single New World taxon investigated, *Lechea maritima*, untreated seeds germinated very poorly (6%) at 15 °C in the dark, while abraded seeds reached a quite high final germination (73%) within a week. However, heating of dry seeds for various durations (1, 5, and 15 min) was ineffective in enhancing germination.

DISCUSSION

In the present study, it is clearly shown that the phenomenon of hardseededness is a prominent characteristic of the entire Cistaceae family. All 42 species investigated (out of a total of about 130 Old World species), with representatives from all five genera, were shown to possess hard-coated seeds. As a general rule, the majority of the seeds in a given seed population have a hard and impermeable seed coat, while only a relatively small fraction of seeds can imbibe water and, eventually, germinate. Promotion of seed germination of the Cistaceae species can be obtained in the laboratory by mechanical scarification and thermal pretreatment. Nevertheless, the inductive effect of these two treatments is evidently different. Mechanical scarification results in a dramatic increase of germinability and germination is completed in less than two weeks. On the other hand, although thermal pretreatment promotes germination to high levels as well, observed

germination rates were much lower than in scarified seeds and almost similar to those of untreated seeds. The same behavior has been noted previously by Argyris (1977), Troumbis and Trabaud (1986), and Thanos and Georghiou (1988). Although this difference has not been explained yet, it is likely to be associated with dissimilar effects of mechanical scarification and thermal pretreatment on the seed coat structures. Furthermore, this differential action might subsequently affect the rate of water penetration and/or the mechanical resistance to radicle expansion.

The water impermeability of the seed coat is obviously due to the structure of the testa, and most probably to the presence of a layer of palisade cells (Corral et al., 1989). "Softening" of the seeds can be promoted in several ways but, under natural conditions, the heat generated by fire is obviously the major trigger factor. Numerous ecological works on post-fire regeneration in Mediterranean ecosystems have allocated to *Cistus* spp. an eminent role among the fire-following plants (e.g., Arianoutsou and Margaris, 1981; Thanos et al., 1989). In an early report it was observed that fire promoted seedling emergence of 8 *Cistus* species during an experimental field burning in California (Martin and Juhren, 1954). In a subsequent work on the ecology of *Cistus* in the Mediterranean vegetation (Juhren, 1966), it was concluded that seed germination of *Cistus* species is generally stimulated by fire. Nevertheless, seedlings could also be found (but in considerably lower densities) in adjacent unburned sites. According to Le Houërou (1974), many species of the Cistaceae belong to the group of active pyrophytes whose propagation by seed is stimulated by fire. In particular, 11 *Cistus* species and *Halimium halimifolium* are cited as being encountered often in pure stands with high ground cover in frequently burned areas.

Whether other agents besides fire, e.g., heating of soil by sun, alternate soaking and drying, and seed weathering in general are also effective in eliminating hardseededness needs further investigation. The route by which water penetrates into the seed after it is naturally softened also needs to be examined. Alternative ways are either "cracks" through the palisade layer or an opening of the hilar fissure. Whatever the actual route it seems to be a rather narrow entrance since germination is considerably slower after heating than after abrasion (a fact observed and discussed previously; Thanos and Georghiou, 1988).

On the basis of the ineffectiveness of Far-Red light, a highly potent inhibitory regime, it is deduced that light, in general, is ineffectual on seed germination of the Cistaceae species. Seed germinability and germination rates of the tested species were similar in the dark and under continuous Far-Red light which is highly adverse for many other species. The complete ineffectiveness of light on Cistaceae seed germination could be explained (Thanos and Georghiou, 1988) by either a very low Pfr threshold level for phytochrome action (satisfied even under Far-Red light) or an inconspicuous level of phytochrome action (minimized by evolution). This result is in full agreement with previous findings on *Cistus creticus* (Thanos and Georghiou, 1988) and *Fumana thymifolia* (Doussi and Thanos, 1993). On the other hand, in a recent work (Roy and Sonié, 1992) on *Cistus albidus* and *C. monspeliensis*, it was concluded that germination of both species was enhanced by a change in light quality (although the differences in the experimental data were rather small). In the present study, no effect of an exceptionally adverse Far-Red light

regime was observed on the germination of two seed lots of the above mentioned species (lots 7 and 55, Fig. 4).

The relatively small seed size (mass of the order of 1 mg, in most of the taxa of the present survey; Table 2) can be associated with easier penetration and accumulation of seeds in the soil (Fenner, 1985). There seems to be no specialized mode of dispersal and seeds are assumed to disperse in the vicinity of the mother plant. Seed longevity may be considerable as a result of the increased protection offered by the impermeable coats. As a matter of fact most reports of extraordinary life spans refer to hardcoated seeds (Bewley and Black, 1982). Moreover, in the Sheffield flora, hardseededness (confined to the families Cistaceae, Geraniaceae, and Leguminosae) was strongly associated with a persistent soil seed bank (Thompson and Booth, 1993). By assembling the various seed ecology features of Cistaceae, it seems that this family is characterized by a syndrome consisting of small seed size, hardcoatedness, short-distance dispersal, long-term persistence in soil seed banks, fire- or heat-induced seed "softening", opportunistic strategy of germination (illustrated by the wide range of temperature and light conditions that permit germination), and slow germination rate of "softened" seeds. Such a seed ecology syndrome is a clearly favorable adaptation in the context of the dry and open habitats around the Mediterranean rim (and particularly in the burned or otherwise disturbed ecosystems).

A relevant syndrome, recognized by Keeley (1991) for the Mediterranean-type chaparral vegetation of California, is the fire-recruiter (or refractory seed) syndrome, characterized by a timing of seedling establishment confined to the first rainy season after fire. In addition, this syndrome includes other characteristics such as seed coat impermeability, local dispersion, persistence in a soil seed bank, and comparatively small size (possibly reflecting the favorableness of the post-fire environment for seedling establishment). The application of Keeley's approach to the Mediterranean vegetation would obviously classify many members of the Cistaceae family in the fire-recruiter syndrome.

Furthermore, according to Keeley (1991), seeds of some fire-recruiters may require cold stratification and/or light in addition to the fire stimulus for their germination. However, this is not applicable to the Cistaceae since optimal germination is promptly obtained under any light regime as well as at several temperature combinations (Thanos and Georgiou, 1988; Doussi and Thanos, 1993) provided the seed coat has already become permeable. In addition, the accumulation of seeds in a persistent soil seed bank would eventually place the seeds well below the soil surface, in virtual darkness, where the fire event could only be perceived in terms of heat generated by the fire itself (and not in terms of a light quality change).

It is concluded that in nature, seeds softened in different ways (e.g., by fire heat) are stimulated to germinate irrespective of temperature or light conditions. Therefore, the previous conclusion of an opportunistic germination strategy (Thanos and Georgiou, 1988) can be extended to the entire Cistaceae family: the absence of any particular dormancy mechanisms, beyond the seed coat water impermeability and the slow germination rate of "softened" seeds, is an obvious ecological advantage in the summer-dry and fire-prone Mediterranean climatic conditions.

ACKNOWLEDGMENTS

We thank the following botanical gardens which readily contributed seed material for this study: Botanischer Garten Aachen (Germany), Hortus Botanicus Barcinonensis, Barcelona (Spain), Botanischer Garten der Universität Basel (Switzerland), University of California Botanical Garden, Berkeley, California (USA), Hortus Botanicus Berolino-Dahlemensis, Berlin (Germany), Botanischer Garten, Ruhr-Universität Bochum (Germany), Botanischer Garten der Universität Bonn (Germany), Istituto ed Orto Botanico Hanbury, Genova (Italy), Plantentuin der Rijksuniversiteit, Gent (Belgium), Royal Botanic Gardens, Kew (UK), Jardin Botanique de l'Université de Liège (Belgium), Botanic Garden, University of London (UK), Orto Botanico Comunale, Lucca (Italy), Real Jardin Botánico, Madrid (Spain), Jardin Botanique National de Belgique, Meise (Belgium), Botanischer Garten München-Nymphenburg (Germany), Jardin Botanique de l'Université, Neuchâtel (Switzerland), Università di Padova, Orto Botanico (Italy), Orto Botanico dell'Università, Palermo (Italy), Orto Botanico Pisano, Pisa (Italy), Botanischer Garten der Universität Salzburg (Austria), Università di Siena, Orto Botanico (Italy), University Botanic Garden, St. Andrews (UK), The Botanic Gardens, Tel Aviv University (Israel), Civico Orto Botanico, Trieste (Italy).

REFERENCES

- Argyris, J.P. 1977. Seed ecology of some phryganeic species. Ph.D. thesis, University of Athens (in Greek).
- Arianoutsou, M. and Margaris, N.S. 1981. Early stages of regeneration after fire in a phryganeic ecosystem (East Mediterranean). I. Regeneration by seed germination. *Biol. Ecol. Mediter.* 8: 119–128.
- Aronne, G. and Mazzoleni, S. 1989. The effects of heat exposure on seeds of *Cistus incanus* L. and *Cistus monspeliensis* L. *G. Bot. Ital.* 123: 283–289.
- Association of Official Seed Analysts. 1981. Rules for testing seeds. *J. Seed Technol.* 6: 1–125.
- Atwater, B.R. 1980. Germination, dormancy and morphology of the seeds of herbaceous ornamental plants. *Seed Sci. Technol.* 8: 523–573.
- Ballard, L.A.T. 1973. Physical barriers to germination. *Seed Sci. Technol.* 1: 285–303.
- Barton, L.V. 1965. Dormancy in seeds imposed by the seed coat. In: Ruhland, W. ed., *Encyclopaedia of plant physiology*, Vol. 15/2. Springer-Verlag, Berlin, pp. 727–745.
- Bewley, J.D. and Black, M. 1982. Physiology and biochemistry of seeds in relation to germination. Vol. 2. Viability, dormancy, and environmental control. Springer-Verlag, Berlin.
- Côme, D. 1970. Les obstacles à la germination. Masson, Paris.
- Corral, R., Perez-Garcia, F., and Pita, J.M. 1989. Seed morphology and histology in four species of *Cistus* L. (Cistaceae). *Phytomorphology* 39: 75–80.
- Corral, R., Pita, J.M., and Perez-Garcia, F. 1990. Some aspects of seed germination in four species of *Cistus* L. *Seed Sci. Technol.* 18: 321–325.
- Dansereau, P.M. 1939. Monographie du genre *Cistus* L. *Boissiera* 4: 1–90.
- Doussi, M.A. and Thanos, C.A. 1993. The ecophysiology of fire-induced germination in hard-seeded plants. In: Côme, D. and Corbineau, F., eds. *Fourth International Workshop on Seeds. Basic and applied aspects of seed biology*, Angers (France) 20–24 July 1992, ASFIS, Paris. Vol. 2. pp. 455–460.

- Egley, G.H. 1989. Water-impermeable seed coverings as barriers to germination. In: Taylorson, R.B., ed. Recent advances in the development and germination of seeds. Plenum Press, New York, pp. 207–223.
- Ellis, R.H., Hong, T.D., and Roberts, E.H. 1985. Handbook of seed technology for genebanks. Vol. 2. Compendium of specific germination information and test recommendations. International Board for Plant Genetic Resources, Rome.
- Fenner, M. 1985. Seed ecology. Chapman and Hall, London.
- Greuter, W., Burdet, H.M., and Long, G., eds. 1984. Cistaceae. In: Med-checklist. Vol. 1. Conservatoire et Jardin botaniques, Ville de Genève. Med-Checklist Trust of OPTIMA, Genève, pp. 315–330.
- Grime, J.P., Hodgson, J.G., and Hunt, R. 1988. Comparative plant ecology: a functional approach to common British species. Unwin Hyman, London.
- Gutterman, Y. and Agami, M. 1987. A comparative germination study of seeds of *Helianthemum vesicarium* Boiss. and *H. ventosum* Boiss., perennial desert shrub species inhabiting two different neighboring habitats in the Negev desert highlands, Israel. J. Arid Environ. 12: 215–221.
- International Seed Testing Association. 1985. International rules for seed testing. Annexes 1985. Seed Sci. Technol. 13: 356–513.
- Juby, D.V. and Pheasant, J.H. 1934. On intermittent germination as illustrated by *Helianthemum guttatum* Miller. J. Ecol. 21: 445–451.
- Juhren, M.C. 1966. Ecological observations on *Cistus* in the Mediterranean vegetation. For. Sci. 12: 415–426.
- Keeley, J.E. 1991. Seed germination and life history syndromes in the California chaparral. Bot. Rev. 57: 81–116.
- Keeley, J.E., Morton, B.A., Pedrosa, A., and Trotter, P. 1985. Role of allelopathy, heat and charred wood in the germination of chaparral herbs and suffrutescents. J. Ecol. 73: 445–458.
- Koller, D. and Hadas, A. 1981. Water relations in the germination of seeds. In: Lange, O.L., Nobel, P.S., Osmond, C.B., and Ziegler, H., eds. Encyclopedia of plant physiology. New Series, Vol. 12A. Physiological plant ecology I. Springer-Verlag, Berlin, pp. 401–431.
- Le Houërrou, H.N. 1974. Fire and vegetation in the Mediterranean basin. In: Proceedings of the 13th annual tall timbers fire ecology conference, 1973. Tall Timbers Res. Stn., Tallahassee, FL, pp. 237–277.
- Mabberley, D.J. 1987. The plant-book. Cambridge University Press, Cambridge.
- Martin, L.B. and Juhren, M.C. 1954. *Cistus* and its response to fire. Lasca Leaves 4: 65–67.
- Meusel, H. 1978. Vergleichende Chorologie der Zentraleuropäischen Flora. VEB Gustav Fischer Verlag, Jena.
- Proctor, M.C.F. 1978. Cistaceae. In: Heywood, V.H., ed. Flowering plants of the world. Oxford University Press, Oxford, pp. 108–109.
- Rolston, M.P. 1978. Water impermeable seed dormancy. Bot. Rev. 44: 365–396.
- Roy, J. and Sonié, L. 1992. Germination and population dynamics of *Cistus* species in relation to fire. J. Appl. Ecol. 29: 647–655.
- Thanos, C.A. and Georghiou, K. 1988. Ecophysiology of fire-stimulated seed germination in *Cistus incanus* ssp. *creticus* (L.) Heywood and *C. salvifolius* L. Plant, Cell Environ. 11: 841–849.
- Thanos, C.A., Marcou, S., Christodoulakis, D., and Yannitsaros, A. 1989. Early post-fire regeneration in *Pinus brutia* forest ecosystems of Samos Island (Greece). Acta Oecol./Oecol. Plant. 10: 79–94.
- Thanos, C.A., Georghiou, K., Douma, D.J., and Marangaki, C.J. 1991. Photoinhibition of seed germination in Mediterranean maritime plants. Ann. Bot. 68: 469–475.
- Thompson, K. and Booth, R.E. 1993. Dormancy breaking. In: Hendry, G.A.F. and Grime, J.P., eds.

- Methods in comparative plant ecology. A laboratory manual. Chapman & Hall, London. pp. 187–190.
- Trabaud, L. and Oustric, J. 1989. Heat requirements for seed germination of three *Cistus* species in the garrigue of southern France. *Flora* 183: 321–325.
- Tran, V.N. and Cavanagh, A.K. 1984. Structural aspects of dormancy. In: Murray, D.R., ed. *Seed physiology*. Vol. 2. Germination and reserve mobilization. Academic Press, Sydney, pp. 1–44.
- Troumbis, A. and Trabaud, L. 1986. Comparison of reproductive biological attributes of two *Cistus* species. *Acta Oecol./Oecol. Plant.* 7: 235–250.
- Tutin, T.G., Heywood, V.H., Burges, N.A., Moore, D.M., Valentine, D.H., Walters, S.M., Webb, D.A., eds. 1968. *Cistaceae*. In: *Flora Europaea*. Vol. 2. Cambridge University Press, Cambridge, pp. 282–292.
- Valbuena, L., Tarrega, R., and Luis, E. 1992. Influence of heat on seed germination of *Cistus laurifolius* and *Cistus ladanifer*. *Int. J. Wildland Fire* 2: 15–20.
- Vuillemin, J. and Bulard, C. 1981. Ecophysiologie de la germination de *Cistus albidus* L. et *Cistus monspeliensis* L. *Natur. Monspel., Ser. Bot.* 46: 1–11.
- Werker, E. 1980/81. Seed dormancy as explained by the anatomy of embryo envelopes. *Isr. J. Bot.* 29: 22–44.
- Widen, B. 1980. Flowering strategies in the *Helianthemum oelandicum* (Cistaceae) complex on Oland, Sweden. *Bot. Not.* 133: 99–115.