

Ecophysiology of fire-stimulated seed germination in *Cistus incanus* ssp. *creticus* (L.) Heywood and *C. salvifolius* L.

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Abstract. Seed germination characteristics were investigated in the most common *Cistus* species in Greece, namely *C. incanus* ssp. *creticus* and *C. salvifolius*. In addition to the soft seed subpopulation, both species produce a large fraction of hardcoated, water-impermeable seeds which can be softened and, thus, promoted to germinate by mechanical scarification and thermal pretreatment. Temperature and light control of seed germination are unimportant. In the ecological context of the Mediterranean ecosystems, the eventually advantageous, opportunistic strategy of germination is based on: (a) seed heterospermy (which allows the smaller, softcoated fraction to germinate promptly each year while the majority of the seeds, the hard ones, accumulate in the soil); (b) the seed population heterogeneity in relation to coat hardness (so that any heat conditions produced by fire induce the softening and germination of a certain seed fraction); (c) the notably low germination rate (which suppresses premature germination); (d) the wide, Mediterranean-type (relatively cool), temperature range of germination (while higher temperatures simply inhibit but do not induce any dormancy); and (e) the apparent lack of photosensitivity (enabling germination under every light regime). In non-fire years, the temporal distribution of field germination and seedling appearance might be partly determined by the seed dispersal strategy of the individual *Cistus* species. Nevertheless, the post-fire regeneration response is manifested in the form of a huge wave of germination (of practically all seeds softened by the fire heat), shortly after the onset of the rainy season.

Key-words: *Cistus incanus* ssp. *creticus* (L.) Heywood; *Cistus salvifolius* L.; Cistaceae; rockrose; pyrophyte; seed germination; seed coat; scarification; thermal pretreatment; phytochrome.

Introduction

According to the *Flora Europaea* (Wazburg, 1968) there exist 16 species of the genus *Cistus*, all of them shrubs of dry scrub or open woodland, inhabiting various regions around the Mediterranean Sea. Le Houerou (1973) mentioned 12 different *Cistus* spe-

cies as typical active pyrophytes, spreading by seeds and creating pure stands after fire. In addition, *Cistus* is considered as one of the main unpalatable fire followers of the 'degenerate fire climax' produced by fire and overgrazing (Shantz, 1947).

Cistus plants produce a large crop of seeds every year (Troumbis & Trabaud, 1986) and their regeneration in normal conditions or after fire is realised almost exclusively by seeds (e.g. Montgomery & Strid, 1976; Arianoutsou-Faraggitaki & Margaris, 1982). *Cistus salvifolius* L. and *C. incanus* L. (formerly *C. villosus* L.) ssp. *creticus* (L.) Heywood (sometimes considered as an individual species *C. creticus* L.) are both shrubs of a relatively short life span (up to 15 years, according to Arianoutsou-Faraggitaki & Margaris, 1982). Nevertheless, they are major components of Greek Mediterranean vegetation, especially in the phrygic ecosystems (Margaris, 1976) and it is most probably these two species which were described by Theophrastus (*Enquiry into Plants*, Book VI, II. 1).

The fact that *Cistus* seeds have a primary dormancy imposed by the seed coat which, in the natural environment, is eventually released massively by wildfires, often resulting in prolific dense stands, is well documented, both directly (Arianoutsou & Margaris, 1981; Vuillemin & Bulard, 1981; Troumbis & Trabaud, 1986) and indirectly (Martin & Juhren, 1954; Juhren, 1966; Le Houerou, 1973; Naveh, 1974; Montgomery & Strid, 1976; Papanastasis, 1977; Arianoutsou-Faraggitaki & Margaris, 1981; Arianoutsou-Faraggitaki & Margaris, 1982; Trabaud, 1984; Thanos *et al.*, 1985). The importance of *Cistus* for the recolonization of the burnt areas is indicated by the considerably high, post-fire seedling densities reported (e.g. 500 m⁻². Arianoutsou & Margaris, 1981; 50–1640 m⁻² and, in an exceptional case, 29,000 m⁻², Thanos *et al.*, 1985). The aim of this study was to investigate, in detail, the seed physiology and, more specifically, the germination mechanisms and their ecological implications in the two *Cistus* species most common in Greece.

Materials and methods

Seeds of the rockrose species *Cistus incanus* ssp. *creticus* (L.) Heywood and *C. salvifolius* L. were

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collected ripe from the plants during summertime. Two seed lots were collected from the former species (hills of University Campus near Mt Hymettus, Athens—July 1982; Fourni isles, East Aegean Sea—August 1984) and one from the latter (eastern hills of Samos island, East Aegean Sea—September 1984). The collection sites are all found at elevations between 50 and 200 m above sea level. The mean weights of 50 seeds (\pm SE) of the three seed lots were found to be 31.2 ± 0.2 mg, 32.0 ± 0.3 mg and 50.9 ± 0.3 mg, respectively ($n = 45$). Therefore, the estimated average seed weight of the two lots of *C. incanus* ssp. *creticus* was 0.62 mg and 0.64 mg respectively (very close to the values obtained by Argyris, 1977 and Troumbis & Trabaud, 1986, i.e. 0.6 and 0.59 mg, respectively) while that of *C. salvifolius* was 1.02 mg (higher than that, 0.87 mg, reported by Troumbis & Trabaud, 1986).

Scarification of seeds was achieved either with a razor blade or a piece of sandpaper. Preheating was carried out on dry seeds spread on glass dishes in an incubator and the temperature was maintained stable within a range of ± 3 °C. Germination tests were performed in Petri dishes (8 cm in diameter) lined with two filter papers and moistened with 2.5 cm³ H₂O or appropriate mannitol (Merck, Darmstadt, W. Germany) solution. The criterion of germination was visible radicle protrusion. Measurements were generally taken in weekly intervals (for intact seeds) or otherwise as specified (for scarified ones); after each count, the germinated seeds were discarded. Germination tests were considered finished when no additional seeds germinated; these tests lasted 10 weeks for intact and one week for scarified seeds. Each value is the mean from five samples of 50 seeds and \pm numbers (in the Table) and vertical bars (in Figs) represent standard error (SE). T_{50} is the time needed for manifestation of half of the final germination level and it was calculated from the two median values.

The experiments were performed in controlled temperature cabinets (model BK 5060 EL, Heraeus, Hanau, W. Germany) or chambers (model EF-7, Controlled Environments, Winnipeg, Canada), where in all cases temperature was kept constant within ± 0.5 °C. The intermittent far red, FR, (broad band) light source consisted of eight white incandes-

cent tubes (6276 \times 60 W, Philips Philinea, Holland) and three sheets of 'Plexiglas' filters (two blue, 527, and one red, 601, 3-mm thick each; Röhm GmbH, Darmstadt, W. Germany). Total fluence rate at the region 675–800 nm was 4.5 W m^{-2} . The growth chambers were equipped with a white light source of an emission spectrum quite similar to natural daylight ($Q_{660}/Q_{730} = 1.00$). The source consisted of four white fluorescent tubes (Cool White F48T12/CW/HO, 60 W, Sylvania, U.S.A.) and eight white incandescent bulbs (40 W, Osram, W. Germany) and the total fluence rate in the range 400–800 nm was 16.7 W m^{-2} . When this light was filtered through the three sheets of 'Plexiglas' filters described above, a broad band FR light was obtained (total fluence rate 1.7 W m^{-2} in the range 675–800 nm). Total fluence rates were estimated by integration of the spectral fluence rate curves constructed after the measurements taken with a spectroradiometer (model SR, ISCO, Lincoln, U.S.A.). All manipulations of imbibed seeds were carried out under a dim green safelight (green fluorescent tube F 15T8 · G · 6, 15 W Green-Photo, General Electric, U.S.A.; two sheets of plexiglas filter, 3-mm thick each, one red orange, 478, and one green, 700, Röhm GmbH, Darmstadt, W. Germany; emission at 525–575 nm, maximum at 550 nm, total fluence rate 10 mW m^{-2}).

Results

The germinability of untreated *Cistus* seeds was generally low (always less than 25%) throughout the temperature range 10–30 °C (Table 1). No significant changes of final germination levels seemed to occur among the various temperatures with the exception of a slight decrease at 30 °C in the two lots of *C. incanus* ssp. *creticus*. The germination rate was considerably slow as shown both by the T_{50} values (Table 1) and the germination time-courses (Fig. 1). When seeds were thermally pretreated for 15–60 min at either 80 or 100 °C a significant increase of germinability (tested at 15 °C) was observed in each treatment. Though only a slight promotion was brought about by 60 min at 100 °C and 15 min at 80 °C, the maximum effect was obtained by 15 or 30 min at 100 °C. The T_{50} values estimated from the curves 4–8 were about 2–3 weeks, slightly increased

Table 1. Final dark germination (%) of untreated *Cistus* seeds in various constant temperatures. The \pm values represent one standard error (SE) and the numbers in parentheses are T_{50} values (in weeks)

Temperature (°C)	<i>C. incanus</i> ssp. <i>creticus</i> (1982)	<i>C. incanus</i> ssp. <i>creticus</i> (1984)	<i>C. salvifolius</i>
10	13.3 ± 1.6 (2.5)	16.7 ± 2.2 (2.2)	11.7 ± 1.4 (2.8)
15	22.4 ± 3.8 (1.5)	24.8 ± 3.0 (1.4)	12.0 ± 2.6 (3.6)
20	17.6 ± 3.2 (1.1)	20.0 ± 1.7 (1.0)	16.8 ± 1.6 (2.7)
25	20.4 ± 1.0 (3.0)	18.0 ± 2.3 (2.6)	9.2 ± 2.2 (4.2)
30	7.3 ± 2.3 (3.0)	9.0 ± 2.6 (2.5)	7.0 ± 2.8 (2.5)

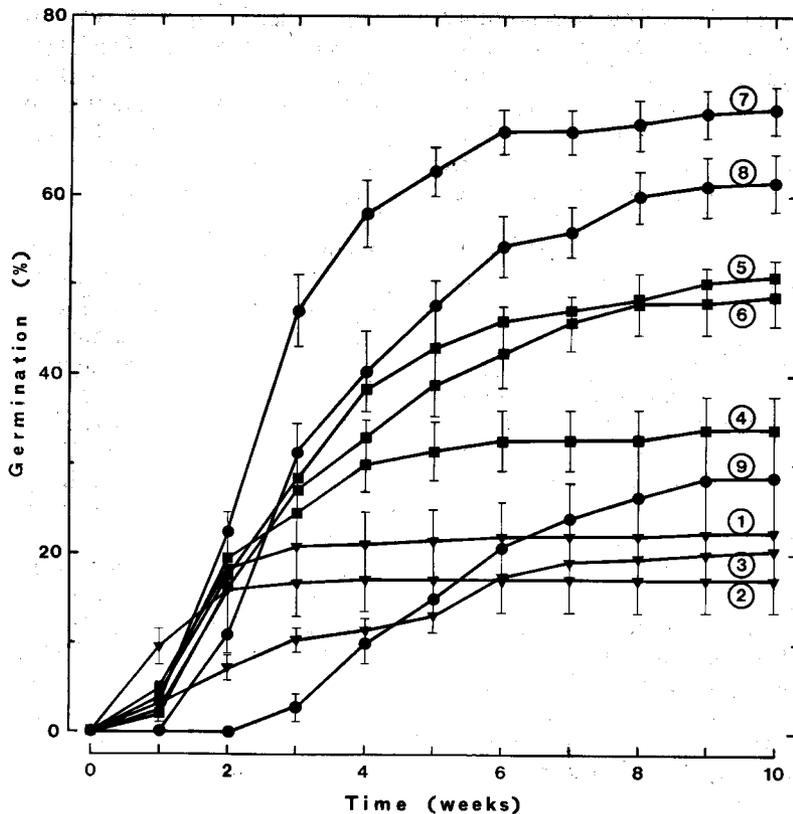


Figure 1. Germination time-courses of preheated *C. incanus* ssp. *creticus* (1982) seeds at 15 °C in darkness. Seeds were preheated at 80 °C (■) or 100 °C (●) for 15, 30 and 60 min (curves 4-6 and 7-9, respectively). Germination of untreated seeds (▼) was tested at 15, 20 and 25 °C (curves 1-3 respectively). Vertical lines: 2 · SE.

in comparison to the corresponding value (1.5 weeks) of untreated seeds (Table 1). Moreover, a considerably higher value of T_{50} (between 5 and 6 weeks) was estimated for the curve 9 (60 min at 100 °C).

The promotive effect of thermal pretreatment on seed germination of *C. salvifolius* is shown in Fig. 2. Final germination levels for each treatment did not differ significantly among the three temperatures tested. A maximum germination of nearly 60% was obtained with 15 min at 100 °C while with 30 min at 80 °C the final germination was slightly lower. The corresponding results for the 1984 lot of *C. incanus* ssp. *creticus* are presented in Fig. 3. The thermal promotion was either slightly (after 15 min at 100 °C) or more strongly (after 30 min at 80 °C) reduced in comparison to the other two *Cistus* lots (Figs 1 & 2). A second thermal treatment of 15 min at 100 °C promoted germinability to a nearly equal final level (around 68%), irrespective of the temperature and the kind of the first treatment.

The mechanical sacrifice of the seed coat (Fig. 4) resulted in a dramatic increase of germinability. Around 90% of unheated seeds germinated and, even more impressive, the decrease of T_{50} to about only 2 d while final germination was obtained in no more than one week in every treatment (Fig. 4). The

combined action of thermal pretreatment and scarification is illustrated by the experiments presented in Fig. 4. The final germination level of intact seeds showed an abrupt increase (from 25–60%) after a short exposure (15–30 min) to heat and a subsequent smooth decline (to around 40%) by longer exposures (45–90 min). On the other hand, the germinability of scarified seeds dropped linearly as a function of the exposure time from 90 to 50%. The regression equations for lines A and B, respectively, are: $Y_1 = 85.618 - 0.655X$ ($r^2 = 0.933$) and $Y_2 = 89.846 - 0.465X$ ($r^2 = 0.918$), where Y_1 and Y_2 are germination (%) measured after 3.5 and 7 days, respectively, and X is pretreatment duration (min) at 100 °C. The data of Fig. 4 made possible an estimation of the relative size of each of the three 'seed types' in the entire population of *C. incanus* ssp. *creticus* (1982 lot). From the pie charts of Fig. 4, it is clear that these relative sizes of the three subpopulations were clearly affected by heating. Thus, the hard seed portion decreased progressively from 65 to 10% while the dead seed fraction increased from 10 to 50%.

The germinability of the two seed lots of *C. incanus* ssp. *creticus* after scarification was maximal (around 80–90%) for the range 10–25 °C, though germination rate was highest at 15 and 20 °C (Fig. 5). At 30 °C, germination of the majority of the seeds

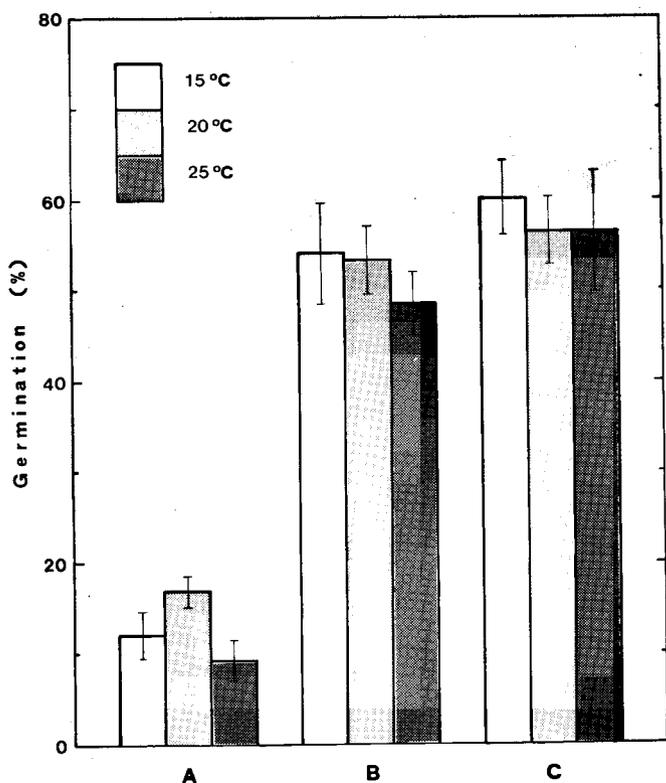


Figure 2. Final germination levels of *C. salvifolius* seeds at 15, 20 and 25 °C in darkness. Seeds were tested untreated (A) or preheated for either 30 min at 80 °C (B) or 15 min at 100 °C (C). Vertical lines: 2 · SE.

was inhibited, while germination was normally manifested after a subsequent transfer to 15 °C.

Finally, the response of *Cistus* seed germination towards light was investigated. Since scarified seeds could germinate fully under intermittent far-red light (Fig. 6), imbibition was further performed in mannitol solutions (producing an additional stress to germination) in order to detect any light (and phytochrome) mediated control. Fig. 6 shows the germinability of scarified seeds as a function of the osmotic concentration; only a slight decrease of germination in the highest molarity values was observed when seeds were imbibed under intermittent far-red irradiation compared with darkness. In the last set of experiments, thermally pretreated seeds showed germination characteristics (rate and final level) impressively similar in all three light regimes applied on each type of seed treatment (Fig. 7).

Discussion

The major characteristic of *Cistus* seeds is seed coat hardness. Thus, only a small fraction (always less than 25%) of a given *Cistus* seed population (the 'soft' seeds) can germinate while the rest simply cannot imbibe water. *Cistus* seed germination can be significantly promoted by mechanical scarification or thermal pretreatment. These results are consistent

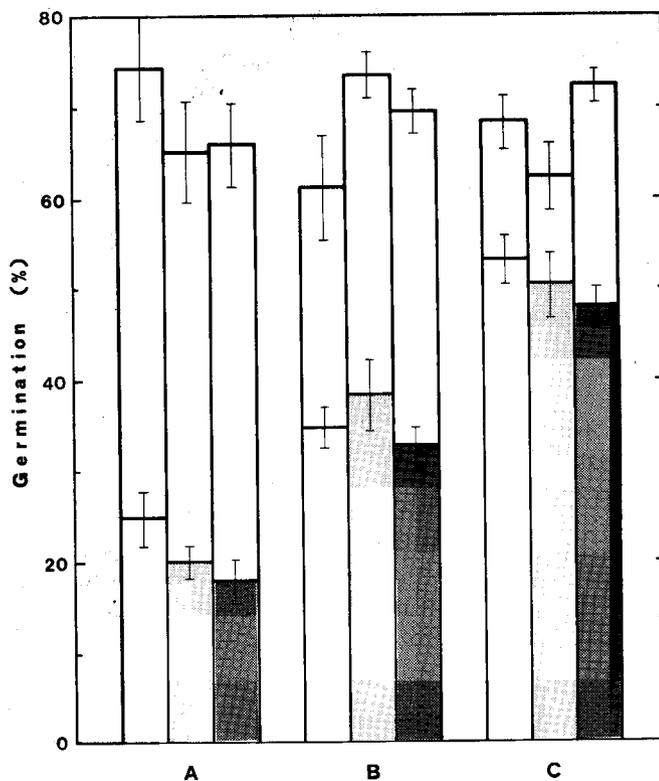


Figure 3. Final germination levels of *C. incanus ssp. creticus* (1984) seeds at 15, 20 and 25 °C in darkness (white, lightly shaded and heavily shaded bars, respectively). Seeds were tested untreated (A) or preheated for either 30 min at 80 °C (B) or 15 min at 100 °C (C). When germination was completed (10 weeks after sowing) the ungerminated seeds from every treatment were left to dehydrate, then were heated for 15 min at 100 °C and were finally reimbibed and returned to their previous temperature. The superimposed bars indicate the eventual, additional germination levels. Vertical lines: 2 · SE.

with those already reported for various *Cistus* species by Argyris (1977), Arianoutsou & Margaris (1981), Vuillemin & Bulard (1981) and Troumbis & Traubaud (1986). For the species investigated in this work, highest promotion was obtained, in descending order, by either 15 and 30 min at 100 °C or 30 min at 80 °C. All the available data clearly show that a thermal shock of 5–30 min at 80–100 °C results in a nearly optimal germination of *Cistus* seeds. It is noteworthy that the temperature conditions commonly encountered during fires in the soil surface horizons (Floyd, 1966; Traubaud, 1979) are within the range mentioned above.

The promotive effect caused by fire or thermal shock seems to be clearly different from that brought about by mechanical scarification. This latter treatment results in an impressive enhancement of germination which is completed in less than one week. On the other hand, a thermal pretreatment allows the penetration of water but the eventual germination is markedly slow, even slower than that of the untreated seeds (Figs 1 & 4). Similar results have been obtained by Argyris (1977) and Troumbis & Tra-

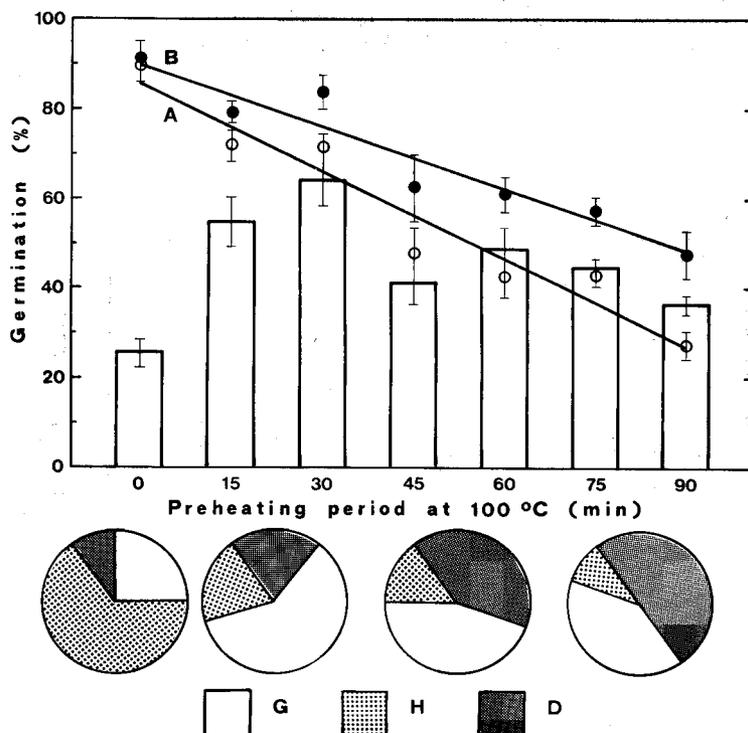


Figure 4. The germinability of scarified *C. incanus* ssp. *creticus* (1982) seeds at 20 °C as a function of the duration of the preheating period at 100 °C. Germination was scored half or one week after onset of imbibition (lines A and B respectively). Final germination levels of intact seeds are represented by the bars. The sectors of the circles correspond to the germinating (G), hard coated (H) and dead (D) portions of the seed populations (untreated or preheated for 15–30, 45–60 and 75–90 min at 100 °C, respectively). Scarification was done with a piece of sandpaper, following the thermal treatment. Vertical lines: 2 · SE.

baud (1986). The explanation of this large difference is unknown, though presumably associated with the nature of the water-impermeable obstacle.

The phenomenon of hardseededness is widespread and in the three most recent, relevant reviews (Ballard, 1973; Rolston, 1978; Werker, 1980/1981) a total of 12 angiosperm families with species producing water-impermeable, hard seeds is cited. Surprisingly enough, the Cistaceae is not included in the lists mentioned above. Not only most (if not all) of the species of *Cistus* are active pyrophytes (Le Houerou, 1973) but, in addition, the germination tests in the species of the same family *Helianthemum guttatum* Miller (Juby & Pheasant, 1934) and *H. vesicarium* Boiss. and *H. ventosum* Boiss. (Gutterman & Agami, 1987) showed a dormancy imposed by water-impermeable seed coats.

In natural conditions, the 'softening' of the hard seed coat has been repeatedly suggested to result from either microbial degradation or weathering. However, there is nearly no experimental support for these hypotheses. In addition, the importance of fire as a release factor of the coat-imposed seed dormancy is surprisingly marginal and only seldom realized by seed physiologists. On the other hand, the ecological role of fire in the stimulation of seed germination (indirectly concluded by the impressively increased, post-fire seedling densities of certain

species) is, of course, well documented for several fire-prone ecosystems (e.g. Floyd, 1966; Naveh, 1975; Rundel, 1981).

Cistus seed populations have been regarded as possessing a considerable heterogeneity in their germination behaviour (Vuillemin & Bulard, 1981). This conclusion is further reinforced by the data of the present work. Though in all cases there was a small percentage of seeds (10–25%) ready to germinate without any treatment (seeds with 'soft', 'thin' or 'ruptured' seed coats), the hard but viable fraction of the population presents a whole range of hardseededness 'values', as shown in Fig. 4. The major conclusion from Fig. 4 is that water-impermeable seeds do not respond in the same way towards a certain thermal pretreatment; a 'weak' thermal shock can promote the germination of a certain (smaller or larger) portion, a 'medium' one results in maximum effect (though not all viable seeds can finally germinate) and a 'strong' shock may lead to some promotion of germination. The seeds germinating with this latter treatment are clearly different from those germinating either untreated or after a weak thermal shock. This conclusion is based on the much slower germination rate of the former seeds (Fig. 1). A further *Cistus* seed population forms a 'hardness continuum', which means that a certain heat treatment may soften a seed population portion while

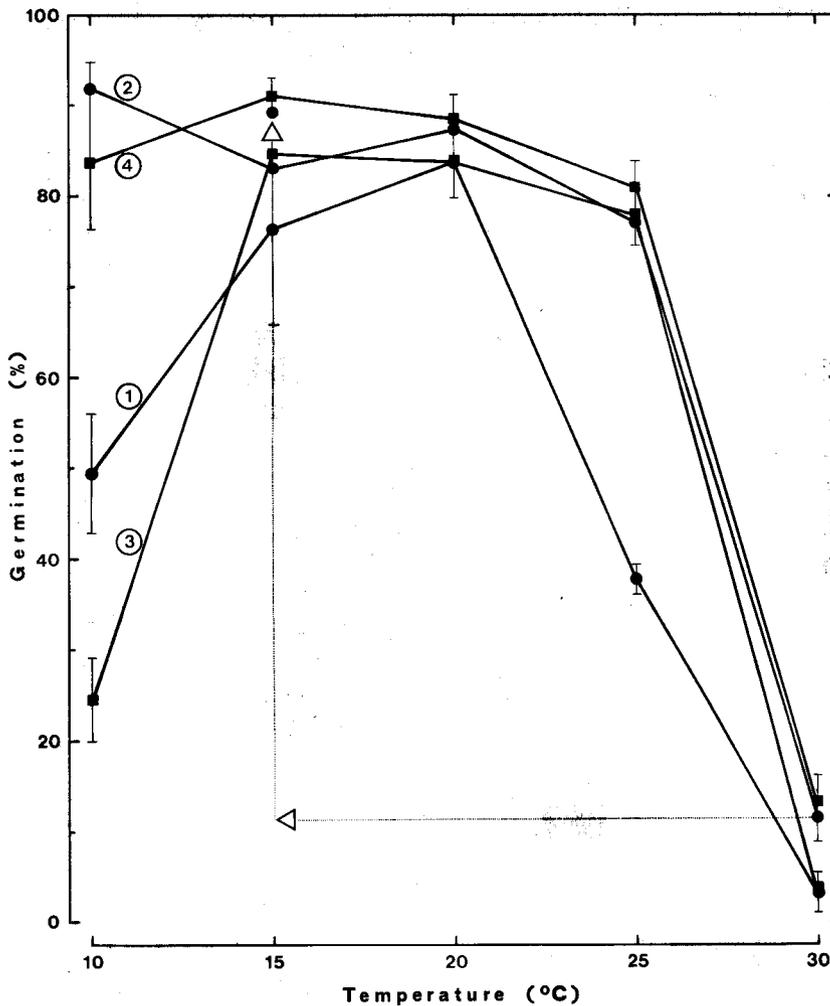


Figure 5. The germinability of scarified *C. incanus* ssp. *creticus* seeds (1982, curves 1 and 2; 1984, curves 3 and 4) as a function of temperature. Germination was scored half (curves 1 and 3) or one week (curves 2 and 4) after onset of imbibition. Scarification was done with sandpaper. Vertical lines: $2 \cdot SE$.

killing, at the same time, a fraction of the most vulnerable seeds at the softest end of the scale. Moreover, it seems that softer, or less hard, seeds have a faster germination rate in comparison to harder ones.

In natural conditions, during the non-fire years, there is an annual production of a seed crop, the soft portion of which is appointed to germinate promptly, contributing in this way to the maintenance and expansion of the existing *Cistus* plant populations. In the phrygic ecosystems studied by Arianoutsou & Margaris (1981) and Troumbis & Trabaud (1986), the appearance of *Cistus* seedlings measured was about 25 and 15 seedlings $\cdot m^{-2}$, respectively. The large part of the seed population is hardcoated and, therefore, accumulates in the soil seed bank. Due to the heterogeneity of these impervious seeds, when a fire takes place there is always a relatively high number of *Cistus* seeds released from dormancy, irrespective of the intensity and the duration of the fire heat. Thus, even when all the soft

seeds and some of the less hard ones are destroyed by fire there still is a considerable quantity of hard ones promoted to germinate. Therefore, both a 10- or 20-fold increase of *Cistus* seedling density, measured during the post-fire rainy season (Juhren, 1966; Arianoutsou & Margaris, 1981; respectively), is not at all unexpected.

The two species of *Cistus* studied in this work germinate in a wide temperature range, 10–25 °C, though the rate of germination is faster at 15–20 °C. According to Thompson (1970), the Mediterranean species show a rapid germination at low temperatures and have relatively low temperature maxima. This is regarded as a straightforward adaptation to the rather low temperatures prevailing during the rainy season (October–May) in the Mediterranean-type ecosystems. Temperatures higher than 20 °C (Thompson, 1970), 23 °C (Vuillemin & Bulard, 1981) and 25 °C (Table 1, Fig. 5) are inhibitory for *Cistus* seed germination. However, this inhibition does not lead to the induction of a secondary dormancy (ther-

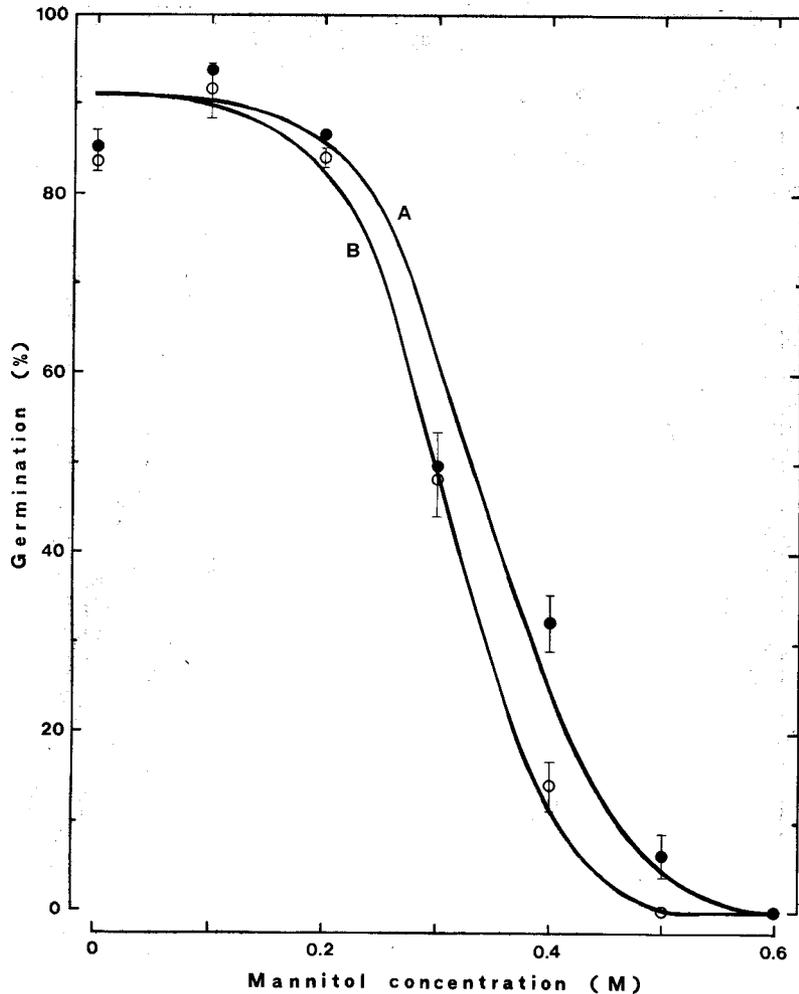


Figure 6. Germination potential curves of scarified *C. incanus* ssp. *creticus* (1982) seeds at 20 °C in darkness (●, curve A) or under intermittent (1 min every 30 min) Far-Red illumination (○, curve B). Scarification was done with sandpaper. Vertical lines: 2 · SE.

modormancy), as shown in Fig. 5. Therefore, in the ecological context, the concurrence of high temperature and water availability (which though highly improbable might sometimes occur during summer and early autumn) prevents the untimely manifestation of germination without affecting in any way the germinability later in the season when temperatures have become cooler.

Light seems to play no role in the control of seed germination for the *Cistus* species tested. Even under the highly adverse, intermittent far-red illumination no suppression of germination was observed. When different levels of osmotic stress were further added no light inhibition was indisputably revealed (Fig. 6), as it was shown in the case of the, well known as 'light indifferent', seeds of *Zea mays* (Thanos & Mitrakos, 1979). An explanation of this apparent lack of photosensitivity might be provided 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). In more 'natural' light (and temperature) regimes, the germination of thermally-pretreated *Cistus* seeds is again manifested at quite high levels (Fig. 7) either with white light during daytime (regime regarded as simulating germination conditions on the soil surface in an open habitat) or under far-red light (seeds imbibing under dense plant canopy) or even in complete darkness (seeds buried in the soil). Both final germination levels and germination rates are strikingly similar in all three light regimes used. These results constitute additional and decisive evidence for the complete ineffectiveness of light on *Cistus* seed germination though, at first sight, this conclusion seems contradictory to the heliophilous nature ascribed to *Cistus* plants (Juhren & Montgomery, 1977; Vuillemin & Bulard, 1981).

Therefore, once a fire takes place, a certain fraction of the hardcoated *Cistus* seed bank in the soil is softened and becomes ready to germinate irrespective of temperature and light conditions, provided water is available. An additional characteristic of possible

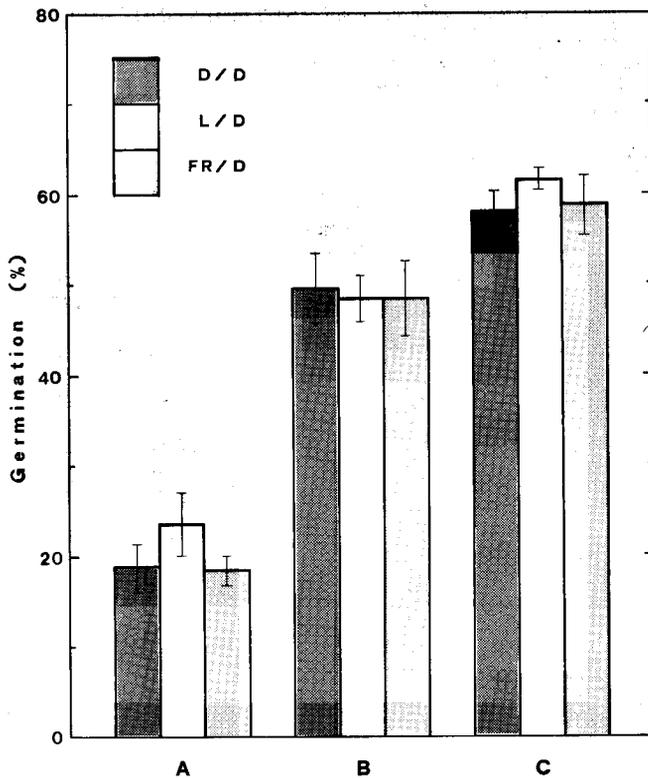


Figure 7. Final germination levels of *C. incanus ssp. creticus* (1982) seeds imbibing under a daily temperature program of 10 h at 15 °C and 14 h at 10 °C. D/D: continuous darkness; L/D: white 'natural' light during the warm period; FR/D: Far Red light during the warm period. Seeds were tested untreated (A) or preheated for either 30 min at 80 °C (B) or 15 min at 100 °C (C). Vertical lines: 2 · SE.

ecological importance should be noted: the markedly slow germination rate which seems to prevent a premature and risky burst of seedling emergence during the rapid alternations of dry and wet conditions (frequently encountered early in the autumn) at the same time allows a somewhat delayed but safe and prolific germination well into the rainy season. The lack of temperature- and light-controlled germination mechanisms leads to the conclusion that under natural conditions the onset of the rainy season should trigger a massive germination, the temporal pattern of which would follow a unimodal but skewed distribution. This conclusion is consistent with the field germination data for *C. incanus ssp. creticus*, collected by Argyris (1977) in two unburnt phryganic communities. Germination burst out during November and then declined progressively until February when no additional seedling emergence was scored. A unimodal temporal pattern of germination is also, though indirectly, suggested by a monthly survey of the *Cistus* ssp. seedling density during the first 2 years after fire in a phryganic ecosystem (Arianoutsou & Margaris, 1981). An apparently inconsistent, bimodal distribution of *Cistus* seed germination, investigated in two unburnt phryganic

ecosystems, has been obtained by Troumbis & Traubaud (1986). Seedling emergence of *C. incanus ssp. creticus* and *C. salvifolius* occurred in two distinct waves with a major peak in November and December (more than 80% of total germination) and a minor one in March (about 15%). No explanation was furnished for this bimodal pattern but after a closer examination of the other data it seems probable that the second peak might be attributed exclusively to seeds of *C. salvifolius*, the dissemination of which is more diffuse and considerably delayed in comparison to *C. incanus ssp. creticus*. So under non-fire conditions, the former *Cistus* species is additionally dispersed in time and could be regarded as less opportunistic than the latter one, a conclusion already reached in different ways (Troumbis & Traubaud, 1986).

Finally, it is clear that both species investigated in this work (and probably other *Cistus* species as well) show an overall opportunistic strategy of seed germination. The absence of any particular dormancy mechanisms, beyond the seed coat impermeability and the slow germination rate, is an obvious ecological advantage in the fire-prone Mediterranean climatic conditions. Furthermore, it is this opportunistic strategy of seed germination which has given these species of *Cistus* an eminent, post-fire regeneration role in the Mediterranean ecosystems.

Acknowledgments

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