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THE ECOPHYSIOLOGY OF FIRE-INDUCED GERMINATION IN HARD-SEEDED PLANTS

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SUMMARY

The ecophysiology of seed germination was investigated in representative fire-following plants belonging to the families Leguminosae (*Anthyllis vulneraria* and *A. hermanniae*), Convolvulaceae (*Convolvulus elegantissimus*) and Cistaceae (*Fumana thymifolia*). It is concluded that the effect of mechanical scarification on germination behaviour is by far the most important factor in comparison to various constant temperatures, diurnally fluctuating temperatures (simulating the natural conditions during the rainy season) and far-red ("canopy-like") irradiation.

INTRODUCTION

The severe summer drought combined with high temperatures leads to a high frequency of fires in Mediterranean-type ecosystems. The relation of this climatic type with fire has been long ago noted; moreover, the numerous adaptations of plants dominating mediterranean-type ecosystems indicate that fire has been a long-term, important stress factor as well as a selective force in Mediterranean ecosystems. Consequently, the latter can be considered as "fire-induced" or "fire-adapted" (e.g. Trabaud, 1987).

The post-fire positive feedback of the ecosystem is brought about chiefly by a vigorous and prolific regeneration through both seed germination and resprouting (e.g. Thanos et al., 1989). In all types of Mediterranean ecosystems fire stimulates germination in many species (e.g. Arianoutsou and Margaris, 1981). The seed bank in the canopy or in the soil can perceive fire occurrence by different means. Therefore, heat generated by fire induces seed dispersal or satisfies the scarification requirement of seeds of certain species).

The ecological role of fire in the induction of seed germination of hard-seeded plant species is well documented for the Mediterranean-type ecosystems, though mainly indirectly through floristic investigations. Among the fire-induced plants eminent are several *Cistus* spp. as well as numerous legumes. The aim of the present study was to investigate the germination mechanisms and their ecological implications in representative fire-following plants belonging to the families Leguminosae (*Anthyllis vulneraria* and *A. hermanniae*), Convolvulaceae (*Convolvulus elegantissimus*) and Cistaceae (*Fumana thymifolia*).

MATERIALS AND METHODS

Plant material

Seeds of *F. thymifolia* were collected in June 1990 at Mt Parnes, Attica. Fruits of *C. elegantissimus* and *A. vulneraria* were collected in July 1991 from a burnt pine-forest at Mt Parnes, Attica (elevation 400-450 m above sea level) during the first post-fire year. Fruits of *A. hermanniae* were collected in July 1989 in Diomides Botanical Garden, Haidari, Attica. The seeds of *F. thymifolia* and *C. elegantissimus* as well as the one-seeded fruits of *A. vulneraria* and *A. hermanniae* were stored in light- and water-proof plastic tins, at room temperature (20±5 °C). The average weight (n=50) of the one-seeded fruits of the two *Anthyllis* species was found to be 4.7±0.1 mg (*A. vulneraria*) and 2.3±0.1 mg (*A. hermanniae*); the average seed weight of *F. thymifolia* and *C. elegantissimus* was 2.8±0.6 mg and 11.6±0.4 mg, respectively. Throughout the present work seeds of *A. vulneraria* and *A. hermanniae* were used after removal of the surrounding fruit tissues. No variation in germination characteristics was observed during the experimentation period.

Germination experiments

Scarification of seeds was achieved either with a razor blade or a piece of sandpaper. Germination tests were performed in Petri dishes (7 cm diameter) and each value is the mean of five samples of seeds (25 for *F. thymifolia* and *A. hermanniae*, 20 for *A. vulneraria* and 10 for *C. elegantissimus*).

The experiments were performed in plant growth cabinets as described previously (Thanos and Georghiou, 1988). The germination experiment presented in table I was carried out on a temperature- and light-programmable growth bench, model GB48 (Conviron, Canada) (Thanos et al., 1991). Far-red light was obtained by using three sheets of Plexiglas filters (two blue, 527, and one red, 601, 3-mm thick each; Rohm GmbH, Darmstadt, Germany).

RESULTS

The major characteristic of all four species is their water-impermeable hard seeds. The pie charts in figure 1 show the soft and hard fractions of the seed population for each of the four species, as determined by imbibition swelling. The actual germination data (not shown) of untreated seeds fully confirmed those results since germinability was extremely low

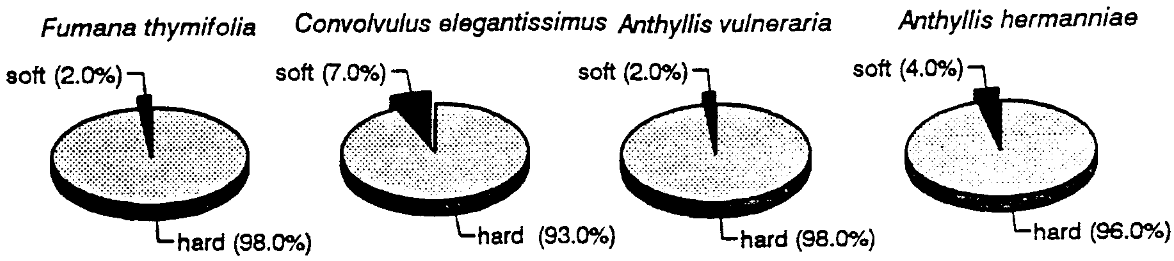

Fig. 1. The hard- and soft-coated seed fractions in the four seed populations studied.

(nearly 5%).

The mechanical scarification of the seed coat resulted, as expected, in an impressive enhancement of germination. Figure 2 shows the time course of germination of scarified *F. thymifolia* seeds in darkness. Except for the 5 °C where germination began after a week, in the rest five temperatures, germination started on the second day with quite impressive percentages. Germination was completed within 35 days and 15 °C is considered as the optimal temperature with a final germination level around 90%. No significant differences in the germinability were observed among the various temperatures with the exception of 5 and 30 °C where both the final germination percentage and the germination rate were decreased.

Figure 3 shows the time course of germination of scarified *C. elegantissimus* seeds in darkness. Except for 5 °C, where germination was significantly delayed, and 30 °C where final germination percentage was decreased, in the rest four temperatures germination began on the very first day and reached a final germination level of 100% within 10 days. Germination characteristics are impressively similar in these four temperatures.

Figure 4 shows the time course of germination of scarified *A. vulneraria* seeds in darkness. Here, germination was even

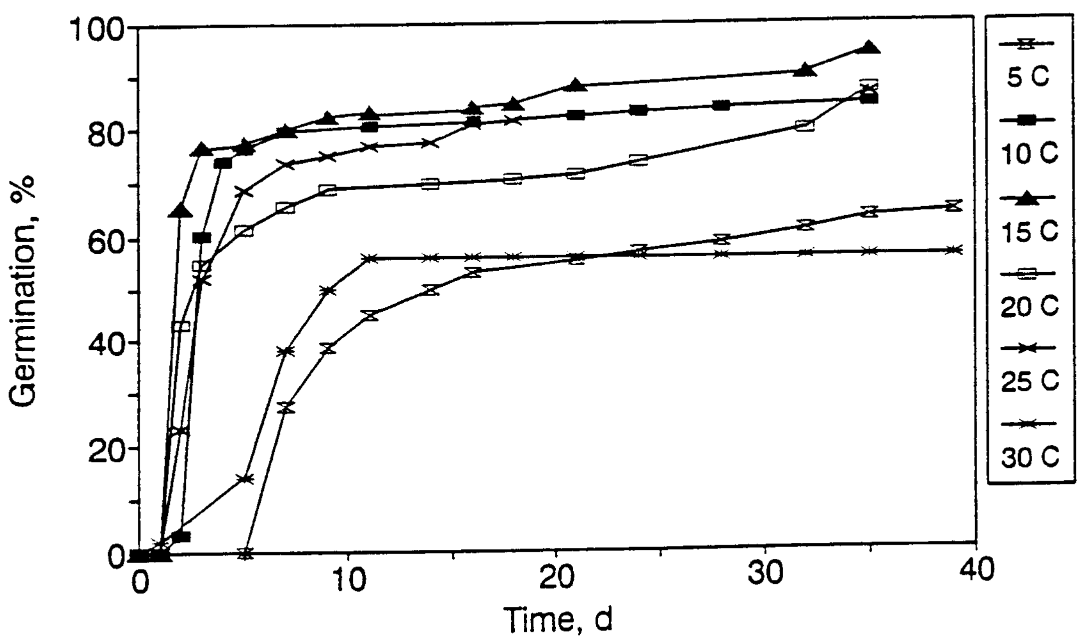

Fig. 2. Germination time course of scarified *Fumana thymifolia* seeds at various constant temperatures, in the dark.

faster than in the previous case: at 10, 15 and 20 °C it was completed in 4 days with a final level of 100%. At 5 °C germination, although at a lower rate reached nearly 100%. Finally, germination was fully inhibited at 30 °C.

Figure 5 shows the time course of germination of scarified *A. hermanniae* seeds in darkness. Germination began around the 3rd day with the exception of 5 °C where germination started on the 11th day. Optimal temperature was 15 °C where germination was completed in 14 days time. At 10 and 20 °C germination reached a final level (100%) in 28 days while in 25 °C germination reached a level of nearly 100% in 35 days. Finally, 30 °C was fully inhibitory for germination. When all

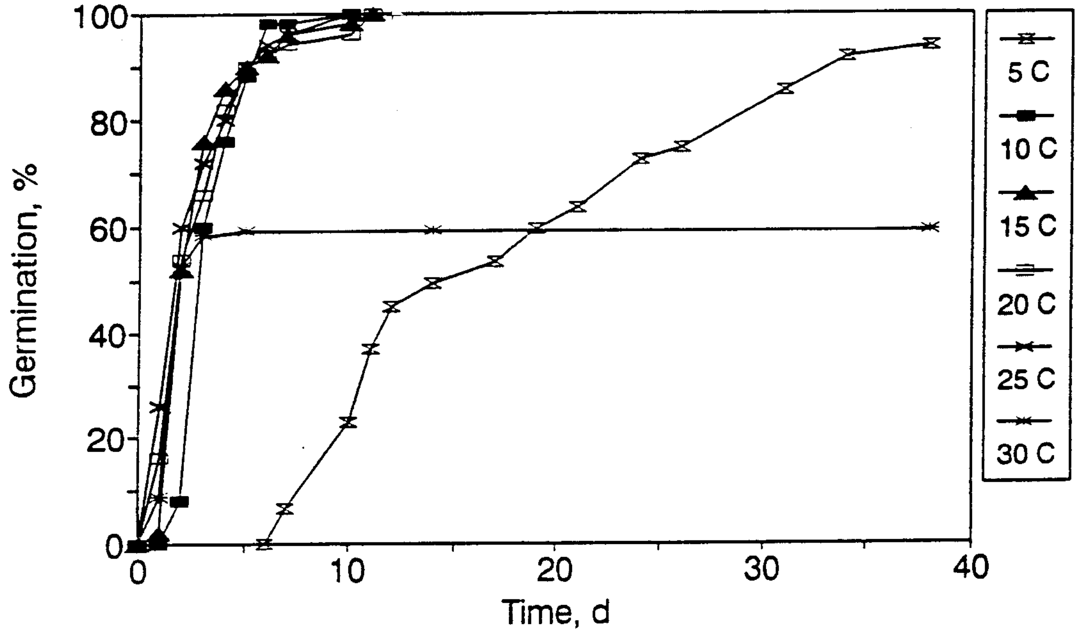

Fig. 3. Germination time course of scarified *Convolvulus elegantissimus* seeds at various constant temperatures, in the dark.

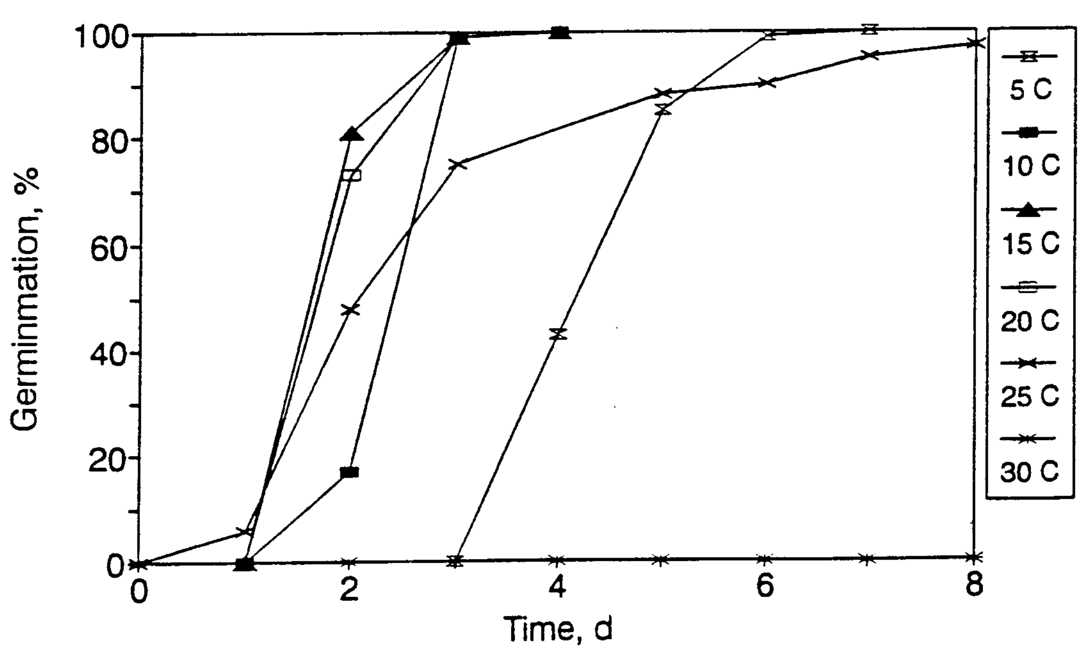

Fig. 4. Germination time course of scarified *Anthyllis vulneraria* seeds at various constant temperatures, in the dark.

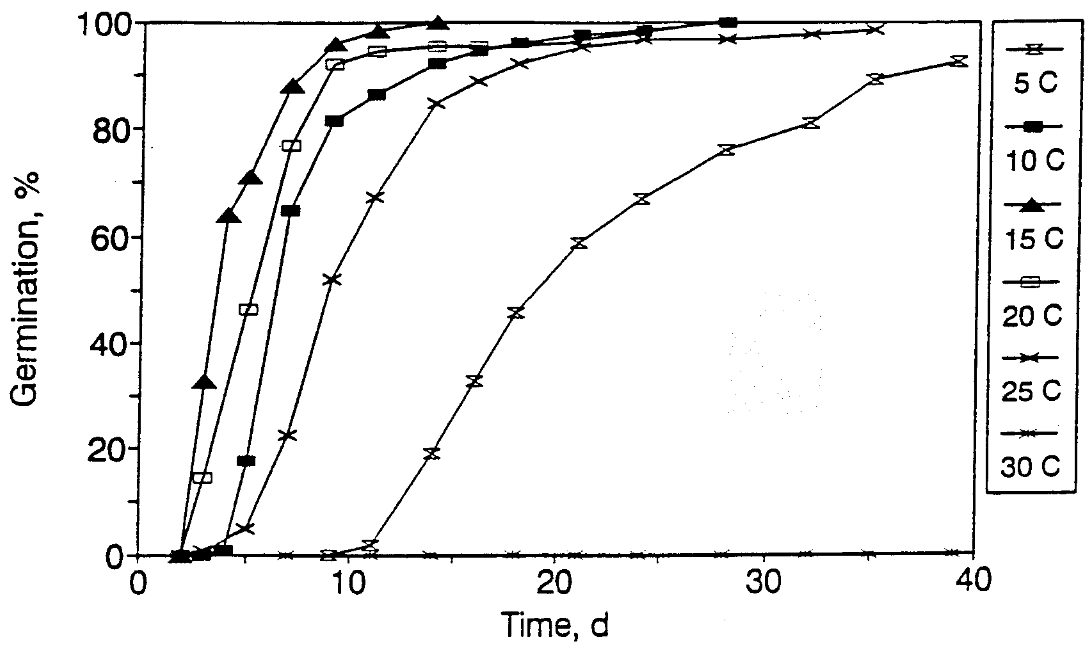

Fig. 5. Germination time course of scarified *Anthyllis hermanniae* seeds at various constant temperatures, in the dark.

ungerminated seeds were transferred from 30 °C to 15 °C no further germination was scored (data not shown), possibly as a result of seed senescence and/or necrosis.

In an attempt to investigate the germination mechanisms prevailing in nature, seeds of all species were imbibed under fluctuating conditions of temperature and light simulating those encountered during the start of the rainy season in Greece. Seeds were imbibed under either continuous darkness (D) or far-red light (FR) given during the "day" (Table I). The above experimental conditions simulate those experienced by seeds either when buried in the soil or while imbibing under dense plant canopy, respectively. As shown in table I even under the highly adverse, far-red illumination no suppression of germination was observed.

Table I. Germination of scarified seeds under "November" conditions of temperature and light. In all cases one sample of 10 seeds was used. Values represent number of germinated seeds.

Test period (days)	*F. thymifolia*		*C. elegantissimus*		*A. vulneraria*		*A. hermanniae*	
	D	FR	D	FR	D	FR	D	FR
1	9	8	3	1	0	0	0	0
2	10	9	10	8	0	2	0	0
4	10	10	10	10	8	10	6	2
7					10	10	8	8
10							10	10

DISCUSSION AND CONCLUSIONS

The major characteristic of the species studied in this work is seed coat hardness. Their seeds show a testa-imposed primary dormancy which is eventually released by mechanical scarification. The phenomenon of hardseededness is widespread and under natural conditions, the "softening" of the hard seed coat has been repeatedly suggested to result from either microbial degradation or weathering. However, there is only weak 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 realised 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. Thanos et al., 1989). Since all the plant species investigated in the present study are fire-followers, sometimes producing prolific dense stands, it is postulated that fire is the natural agent that induces germination. Moreover, it is concluded that once the hard seeds have been "softened", their germination is relatively opportunistic in regard to temperature and light. This is illustrated by their broad temperature range (5-25 °C), although all four species are Mediterranean, and by their ability to germinate under a "dense canopy" light, as well.

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