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Ecophysiology of germination in the aromatic plants thyme, savory and oregano (Labiatae)

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Abstract

Ecophysiological aspects of seed germination were investigated in the widely distributed Mediterranean-endemic, aromatic plants thyme (*Coridothymus capitatus*), savory (*Satureja thymbra*) and oregano (*Origanum vulgare* subsp. *hirtum*). Thyme seed germination is light indifferent, whereas oregano seeds have an absolute light requirement; their germination can be promoted even by green safelight or far-red light. In savory, a portion of the seeds germinates in the dark and germination can be either increased or decreased by the appropriate illumination. All three species show more germination at a relatively low temperature range, a Mediterranean characteristic, with an optimum around 15–20°C. The rate of germination is considerably higher in the tiny seeds of thyme and oregano than in the larger seeds of savory. In the latter species, germination is also dependent upon the age of the seeds; old seeds germinate to a higher percentage than fresh ones, as already observed by Theophrastus, possibly as a result of the volatilization of the essential oils present on the nutlet coat. Seeds of thyme, savory and oregano are dispersed within the persistent fruiting calyces and the seeds eventually germinate within it. Essential oils in the calyx strongly inhibit germination of the enclosed seeds; germination is much suppressed in thyme and to a lesser extent in savory and oregano. This diaspore dormancy caused by essential oils apparently is overcome under natural conditions by leaching of the inhibitors with rainwater. It is suggested that this dormancy operates as an adaptation strategy that delays germination by acting as a rain gauge. In this way, seed germination and subsequent seedling establishment are prevented during the early phase of the rainy period, which is usually interrupted by drought spells in the Mediterranean climate.

Keywords: *Coridothymus capitatus*, *Satureja thymbra*, *Origanum vulgare*, seed germination, essential oils, persistent calyx, phytochrome

Introduction

Aromatic and medicinal plants constitute a considerable portion of the flora and the vegetation of the Mediterranean Rim. In the so-called cradle of civilization of the Eastern Mediterranean region, in particular, aromatic and medicinal plants have been collected from the wild and also cultivated for several millennia. Theophrastus (4th century B.C.) in his Enquiry into Plants (*Historia Plantarum, HP*) compiled the accumulated botanical knowledge during Greek Classical Antiquity; seed germination holds an eminent position among the various aspects of cultivation of pot-herbs. A considerable number of aromatic plants are described (e.g. *HP* 6.2), including the three taxa investigated in the present study. A whole book (*HP* 7) is devoted to pot-herbs and similar wild-growing plants.

Thyme (*Coridothymus capitatus*) is a dwarf calcicole shrub and an important element of the xeromorphic phryganic vegetation. It is endemic in the Mediterranean Rim (including Portugal). It grows near the sea (0–700 m altitude) and, as indicated by Theophrastus (*HP* 6.2.4), 'the peculiarity about thyme is that it cannot grow in a region without a sea breeze'. Savory (*Satureja thymbra*) is a dwarf phryganic shrub endemic to the eastern Mediterranean (Sardinia to Israel). Oregano (*Origanum vulgare* subsp. *hirtum*, formerly *O. heracleoticum*) is a woody rhizomatous perennial. It also is a Mediterranean endemic, but with a Balkan dis-

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tribution, including Anatolia and Cyprus. These three plants are mainly used as oregano spice and as a high-content source of essential oils (Philianos *et al.*, 1982; Kokkini and Vokou, 1989; Bosabalidis, 1990; Kanias and Loukis, 1992; Kokkini *et al.*, 1991).

Several specific accounts of Theophrastus concern seed germination of aromatic plants. For example, there is a comment on the low germination rate ('savory and marjoram take more than thirty days to germinate' *HP* 7.1.3) as well as its enhancement in the older seeds of savory ('some plants germinate quicker from old seed, as ... savory, marjoram ..., unless the fresh seeds have been previously soaked in water or milk' *HP* 7.1.6). Furthermore, in contrast to savory, which produces sizable, germinable seed (*HP* 6.2.3), thyme is proclaimed to generate inconspicuous seeds (which 'cannot be discerned visually' *HP* 1.5.3), but are 'somehow mixed up with the flower for when the flower is sown plants come up from it' (*HP* 6.2.3).

Apart from certain general rules for laboratory germination (e.g. AOSA, 1981; Ellis *et al.*, 1985; ISTA, 1993), information is scarce concerning aromatic plants in general and the three taxa mentioned above in particular. In the context of the potential use of aromatic plants as alternative crops in marginal lands, the ecophysiology of seed germination was investigated in thyme, savory and oregano.

Materials and methods

Plant material

Seeds were collected from the wild, mostly in Crete. *Coridothymus capitatus* (L.) Reichenb. fil. (thyme); a carvacrol-rich chemotype collected at Theriso Gorge, Chania in August 1993 was used in most experiments while a second lot, from a thymol-rich population, was collected at Agia Irini, Chania, in September 1993 and was used in the experiments reported in Figure 8. *Satureja thymbra* L. (savory); three lots collected at Masouri, Kalymnos Island in July 1988, at Mournies, Chania in September 1991 and at Mouzouras, Chania in August 1993, respectively. *Origanum vulgare* L. subsp. *hirtum* (Link) Ietswaart (oregano) was collected at Mournies, Chania in October 1992. Nomenclature follows Greuter *et al.* (1986) and distribution data are based on both Flora Europaea (Tutin *et al.*, 1972) and Med-Checklist (Greuter *et al.*, 1986). The two thyme chemotypes have been identified by colleagues at the Mediterranean Agronomic Institute of Chania, Crete (H. Kargiolaki and M. Skoula).

Seed weight was as follows: *C. capitatus*, 0.20 mg (first lot; mean weight of 20 nutlets: 3.94 ± 0.03 mg, n = 50) and 0.23 mg (second lot; mean weight of 20 nutlets: 4.68 ± 0.10 mg, n = 20); *S. thymbra*, 0.61 mg (1st lot, mean weight of 25 nutlets: 15.28 ± 0.20 mg, n = 25), 0.33 mg (2nd lot, mean weight of 20 nutlets: 6.67 ± 0.09 mg, n = 51) and 0.41 mg (3rd lot; mean weight of 20 nutlets: 8.21 ± 0.06 mg, n = 50); and *O. vulgare* subsp. *hirtum*, 61.4 μg (mean weight of 20 nutlets: 1.23 ± 0.02 mg, n = 50). The percentage of unsound seeds (revealed by dissection under a stereomicroscope) in *S. thymbra* was 62, 26 and *ca.* 10% in each of the three lots, respectively, but only about 10% in *C. capitatus* and *O. vulgare* subsp. *hirtum*. The number of nutlets per calyx was determined under a stereomicroscope. The thymol and carvacrol chemotypes of thyme showed a remarkable similarity (means of 1.8 ± 0.2 and 1.6 ± 0.2 seeds per calyx, n = 50, respectively); mean numbers for savory (3rd lot) and oregano were 2.4 ± 0.1 (n = 290) and 2.1 ± 0.1 (n = 100), respectively.

Germination conditions

Seed germination was carried out with nutlets (hereafter called seeds) and persistent calyces (containing up to 4 nutlets each). Seeds were extracted from their calyces manually by careful rubbing. Five replicates of 20 or 25 seeds or calyces were sown on moistened filter paper discs in Petri dishes. The criterion of germination was radicle protrusion, and after each count germinated seeds were discarded. The tests were terminated when no additional seeds germinated. A calyx was scored 'germinated' (and consequently discarded) when one or more of the seeds in it had germinated. T_{50} is the time needed for 50% of the final germination value, and is calculated by linear interpolation from the two germination values closest to median germination. At the end of each experiment ungerminated seeds were dissected and inspected for soundness under a stereomicroscope. Consequently, the data have been corrected for sound seeds. In experiments on the role of the calyx, a number of calyces were placed in the centre of the dish while the seeds were sown along a circle, so that the distance of each seed from the central source of essential oils was about 2 cm. Simulation of rain-mediated leaching of essential oils was carried out with 100 calyces immersed in distilled water in a 0.5-l beaker. The water was slowly stirred by a magnetic stirrer, at 15°C and under continuous white light.

For germination experiments in darkness, seeds or calyces were incubated within light-proof, metal containers in cabinets (Model BK 5060 EL, W.C. Heraeus GmbH, Germany) maintained at constant temperatures. Seed germination experiments under various light regimes were performed in temperature- and light-programmable growth benches (model GB48, Conviron, Canada) equipped with a lamp canopy of 48 incandescent bulbs (Sylvania 50A19, 50 W, 227 V) and 10 fluorescent tubes (Sylvania Cool White FR96T12/CW/VHO-235/1).

White light (W) had a value of ζ (660/730 nm photon ratio) equal to 1.119, establishing a calculated phytochrome photostationary state ratio ($\phi = [\mathrm{Pfr}]/[\mathrm{Ptot}]$) of 0.641. The total photon flux density in the visible range (400–800 nm) was 103.0 μmol m^{-2} s^{-1}. Using blue and red plexiglas filters, four types of light regimes were established: red (R), blue/far-red (B) and two types of 'canopy simulating' far-red rich light (FR I and FR II). For each of these four light sources, the values of ζ, ϕ and total flux density (μmol m^{-2} s^{-1}), respectively, were the following; R: 1.081, 0.593 and 45.2; B: 0.001, 0.095 and 20.9; FR I: 0.001, 0.062 and 13.6; FR II: 0.229, 0.320 and 20.7. The spectral distribution curves for the above light sources are presented elsewhere (Thanos and Doussi, 1995). Apart from a few cases where complete darkness is explicitly stated, most manipulations of imbibed seeds and calyces were carried out under a dim, green safelight (ω and total flux density were 0.322 and 0.8 μmol m^{-2} s^{-1}, respectively). This dim green light was obtained with one green fluorescent tube filtered with layers of green and orange plexiglas. Nearly 39% of the total amount of photons were emitted in the 'green' band 500–600 nm and 54% in the 'far-red' 700–800 nm, and only 6% in the 'red' 600–700 nm with less than 1% in the 'blue' 400–500 nm. Photon flux densities were measured with a spectroradiometer (ISCO SR, USA); calculations of flux densities and values of ζ and ϕ were made with a previously described software application (Thanos *et al.*, 1994).

Results

The effect of temperature on final, dark germination percentage of thyme seeds is illustrated in Figure 1. Almost all of the seeds germinated at 5–20°C, while germination was suppressed above 20°C. On the basis of the time to germination (T_{50} values), optimal temperature was 15°C where germination was completed in one week while at 5°C it took more than a month for the seeds to germinate. Seeds imbibing for a relatively long period at an inhibitory temperature could fully germinate upon subsequent transfer to the optimal temperature; nevertheless, seeds previously at 25°C completed their germination within 7 days while those pretreated at 30°C required more than 2 weeks.

Dark germination as a function of temperature in savory seeds (Fig. 2) was related to their age. The oldest seeds (Fig. 2A) germinated optimally at 5–25°C, while those of intermediate age (Fig. 2B) showed a considerable decrease at both ends of the temperature range, most markedly at 25°C. Freshly harvested seeds (Fig. 2C) were considerably slower to germinate than the other two at 5–10°C, while they were particularly dormant at higher temperatures. Nevertheless, seeds imbibing for long periods at inhibitory temperatures could still be induced to germinate by continuous white light at 15°C. Germination was completed within 20 days, in all four cases, with T_{50} values between 8 and 11 days.

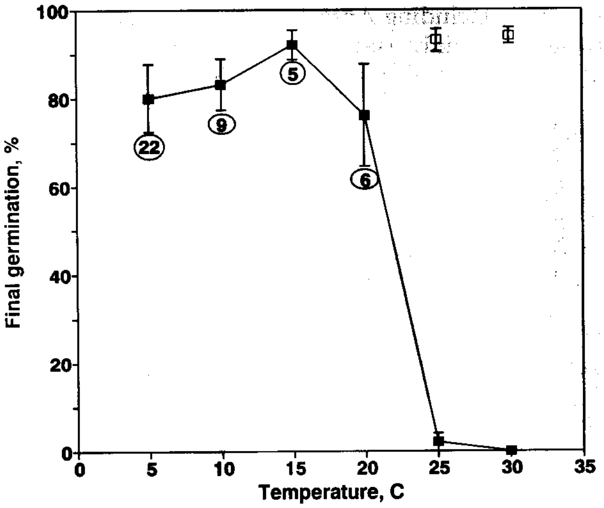

Figure 1. Germination of *Coridothymus capitatus* seeds in the dark as a function of temperature. Circled numbers are T_{50} in days. Final germination values are shown by solid squares connected with a straight line. Open squares represent subsequent germination for the ungerminated seed samples (same samples shown in solid squares) after eventual transfer to 15°C, under continuous white light. Vertical bars represent ± SE (standard error of the mean) values.

The minute seeds of oregano did not germinate in darkness at any temperature but did so after illumination with a green safelight when effects of temperature were revealed (Table 1).

When thyme, savory and oregano seeds were imbibed under various continuous light regimes (Fig. 3), different responses were obtained. In thyme, germination was particularly fast in all cases and, apart from a slight deviation in the time to germination (T_{50}

Table 1. Interaction between temperature and green safelight on germination of *Origanum vulgare* subsp. *hirtum* seeds. Seeds were imbibed in darkness and were checked for germination every other day under a dim, green safelight (T_{50} values correspond to the time required for half of final germination; SE: standard error of the mean)

Temperature (°C)	Final Germination (% ± SE)	T_{50} (days)
5	30.0 ± 5.0	35
10	39.0 ± 11.1	17
15	72.0 ± 5.6	10
20	72.0 ± 5.2	8
25	33.1 ± 5.1	15
30	0	—

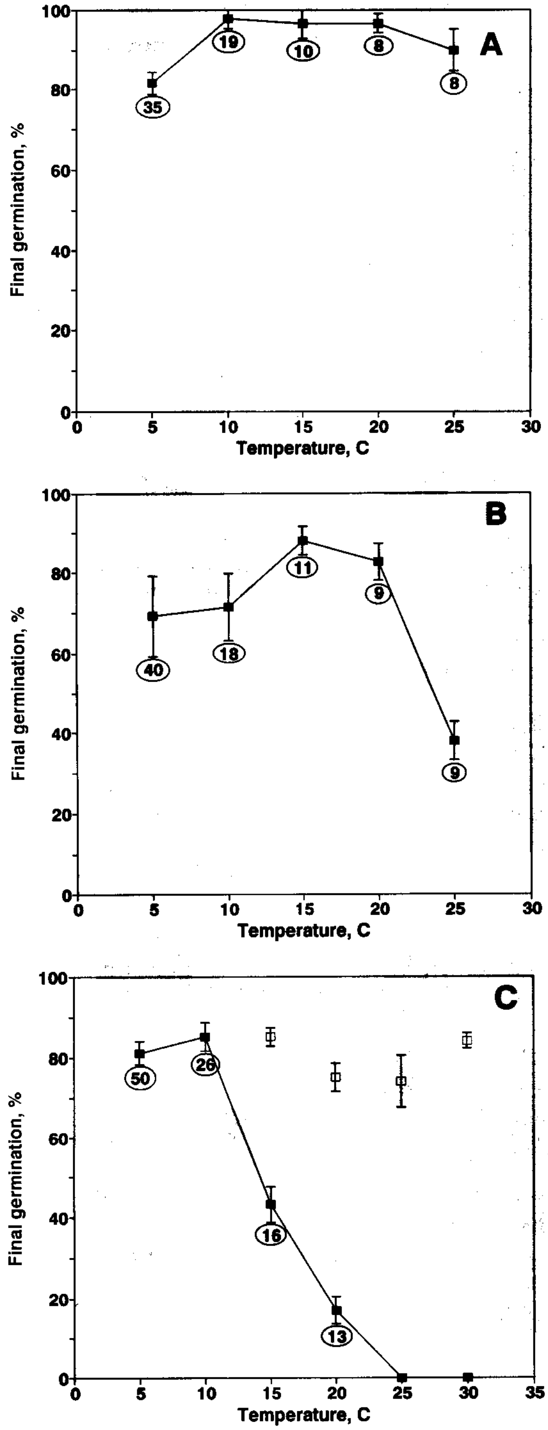

Figure 2. Final germination percentages of *Satureja thymbra* seeds in the dark as a function of temperature. Graphs **A**, **B**, and **C** refer to seed lots collected in 1988, 1991 and 1993, respectively, tested for germination 4 years, 1 year and 3 months after harvest, respectively. Circled numbers are T_{50} in days. Open squares (in C) represent final germination percentages for the ungerminated seed samples (same samples shown in solid squares) after their transfer to 15°C, under continuous white light. Vertical bars represent ± SE (standard error of the mean) values.

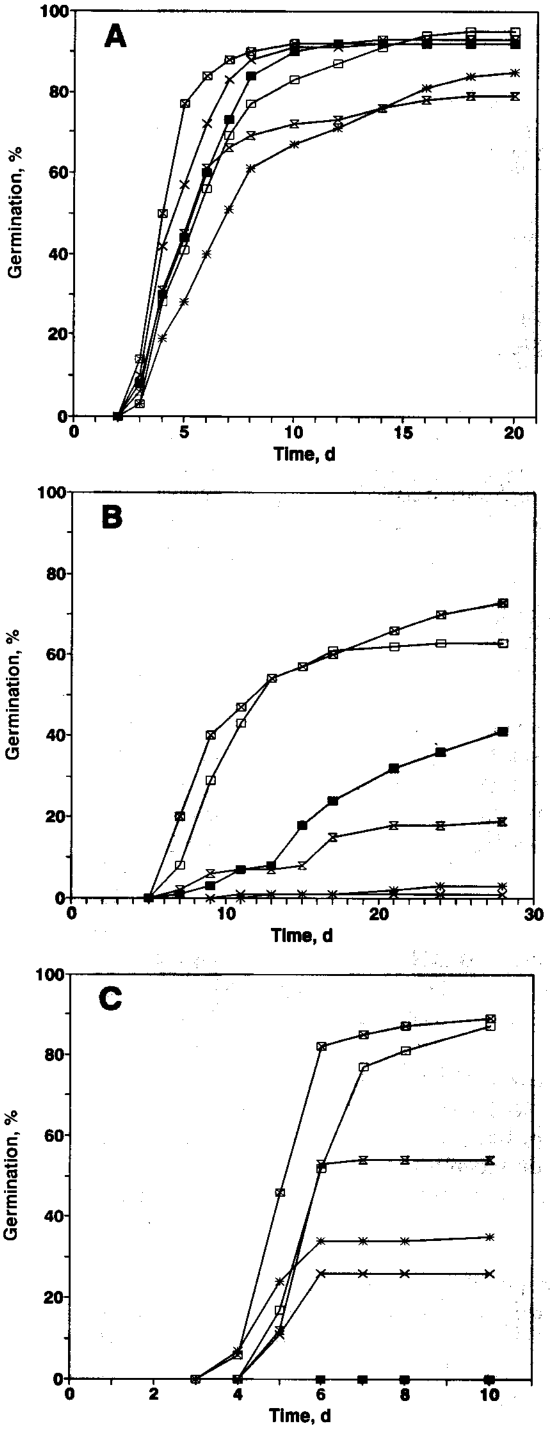

Figure 3. Time course of seed germination at 15°C and under various continuous light regimes (White light, □; Red: ☒; Blue/far-red: *; Far-Red I: ×; Far-Red II: ⧗; Darkness: ■). **A**: *Coridothymus capitatus*; **B**: *Satureja thymbra*; and **C**: *Origanum vulgare* subsp. *hirtum*.

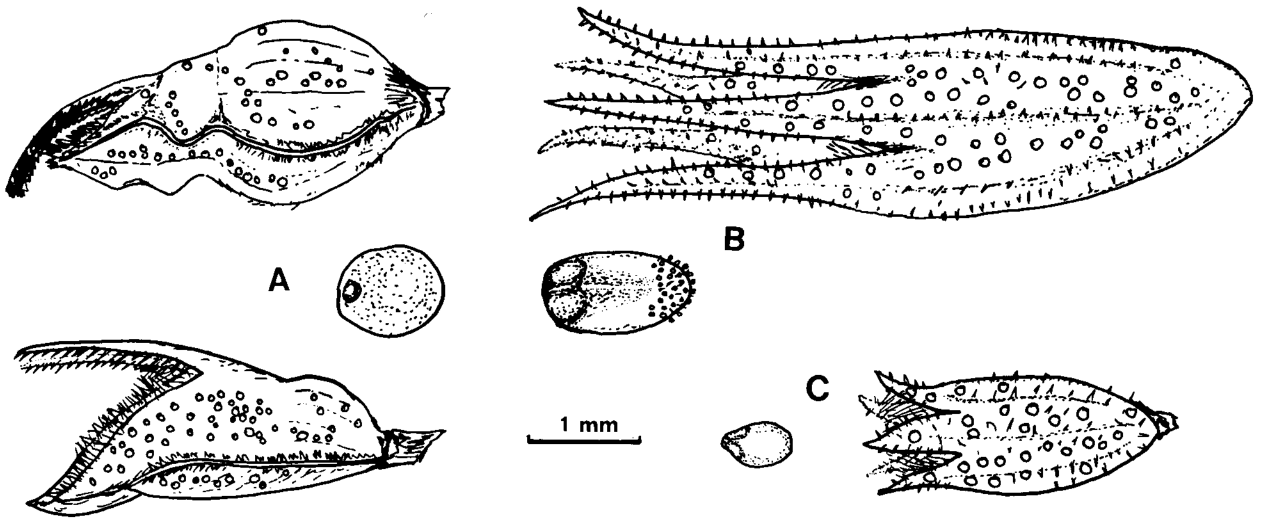

Figure 4. The seed and the dispersal unit (dry fruiting calyx) of *Coridothymus capitatus* (A), *Satureja thymbra* (B) and *Origanum vulgare* subsp. *hirtum* (C). The fruiting calyx of thyme (lateral view) is shown closed (upper) and opened (lower). Little 'bubbles' on the calyx surfaces (as well as the tiny ones at the posterior end of savory seed) portray the essential oil-containing heads of the secretory glands.

values ranged between 4 and 6 days), it was completed within 10 days. Nevertheless, no statistically significant differences were observed in the final germination values among the six light treatments (Fig. 3A). In savory (Fig. 3B), light was particularly important to germination: white and red light promoted, while blue/far-red and both far-red regimes inhibited germination. Both blue/far-red and far-red I (intense far-red) suppressed germination entirely; however when these seeds and those imbibing in darkness were subsequently transferred to continuous white light (data not presented), germination reached about 80% in 14 days. In oregano seeds (Fig. 3C), darkness was entirely inhibitory, while full induction of germination was obtained by red and white light. A gradually increasing amount of germination (in positive relationship to the ϕ values of the light regimes) resulted under far-red I, blue/far-red and far-red II. Rate of oregano seed germination was high, with a T_{50} around 5 days, irrespective of light conditions. When ungerminated seeds were eventually transferred to continuous white light (data not presented), full promotion of germination occurred within 15 days.

Dispersal of seeds in thyme, savory and oregano takes place within the persistent fruiting calyces, the opening of which is brought about by an increase in moisture (hygrochasy). Nevertheless, the seeds remain within the calyx where they eventually germinate (Fig. 4). The young roots and stems of the seedlings may either emerge through the 'collar' of the calyx, or in most cases pierce it at various points. In sharp contrast to isolated thyme seeds, germination within the calyx was sporadically spread over a very long period and it reached only a very low final amount (Fig. 5A); the slightly increased germination obtained under white illumination over complete darkness might be attributed to a partial removal of essential oils from the exposed dishes (while those in darkness were maintained within tightly closed metal containers). Note also that the percentages of 'germinating' calyces were clearly overestimated in comparison with seeds because each calyx was considered as one although it contained nearly two seeds on average. This was equally true in the following cases for savory and oregano. A notable delay of germination, as well as a considerable decrease of final germination was also obtained in savory (Fig. 5B) and oregano (Fig. 5C). Furthermore, a particularly strong induction of calyx 'germination' by white light was observed in both species, the germination in dark controls being virtually fully inhibited. This differential response was similar to the differences obtained in isolated seeds of these species.

When thyme seeds were imbibed in the presence of a gradually increasing number of thyme calyces within the same dish, a statistically significant delay of seed germination took place (Fig. 6). Although no inhibition of final germination amount was observed with up to 20 calyces, the higher the number of calyces present the slower the germination rate of nearby seeds; 20 calyces caused a delay of almost 5 days, and even one calyx per dish produced a certain effect.

To simulate the leaching action of rain, calyces of thyme, savory and oregano were continuously stirred in distilled water at 15°C under continuous white light. At the end of the treatment, the calyces were placed in dishes and left to germinate under the same conditions of temperature and light. Even 1 day of washing can

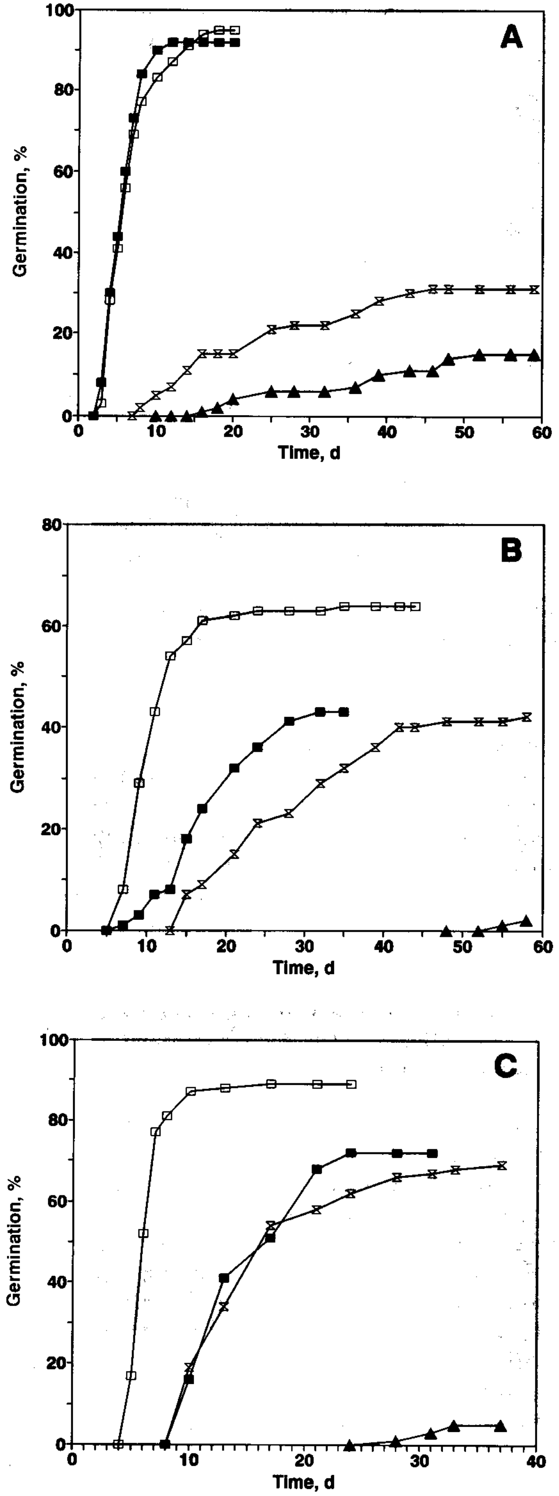

Figure 5. Time course of germination for isolated seeds (■, □) and seeds within calyces (▲, ⧖) at 15°C and under continuous white light (□, ⧖) or darkness (■, ▲). A: *Coridothymus capitatus*; B: *Satureja thymbra*; and C: *Origanum vulgare* subsp. *hirtum*. Seeds and calyces imbibing in darkness were inspected under dim safelight.

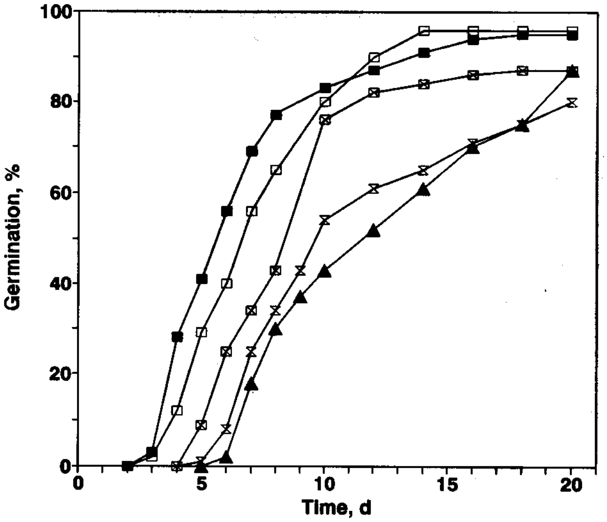

Figure 6. Time course of germination for *Coridothymus capitatus* seeds at 15°C under continuous white light, in the presence of 1 (□), 5 (⊠), 10 (⧖) and 20 (▲) thyme calyces per Petri dish. Controls (no calyces within the dishes): ■.

increase dramatically both the rate and the final percentage of germination in thyme and savory (Figs 7A and 7B, respectively). In oregano, germination enhancement was much less; washing the calyces for 3 days decreased time to germination only slightly (Fig. 7C).

When seeds of the two carvacrol- and thymol-rich chemotypes of thyme were reciprocally incubated in the presence of calyces of either of the two chemotypes, full germination was attained in all four combinations of seeds and calyces (Fig. 8). Moreover, for each one of the two seed lots used, a set of two, almost identical, curves was obtained (Fig. 8).

Discussion

Dark germination as a function of temperature in isolated thyme seeds seems to be typically Mediterranean (Thompson, 1970; Thanos, 1993). Virtually germination of all seeds took place at relatively low temperatures (5–20°C), with an optimum at 15°C. Although the rate of germination was somewhat slower than those previously reported (Argyris, 1977; Vokou, 1983), it was still relatively rapid for Mediterranean plants (Thanos, unpublished). Continuous illumination under various light regimes revealed no differences in the germination behaviour of thyme seeds; thus, it may be concluded that thyme seeds are totally indifferent to light, unexpected in such a tiny-seeded species.

Savory seed germinability as a function of tem-

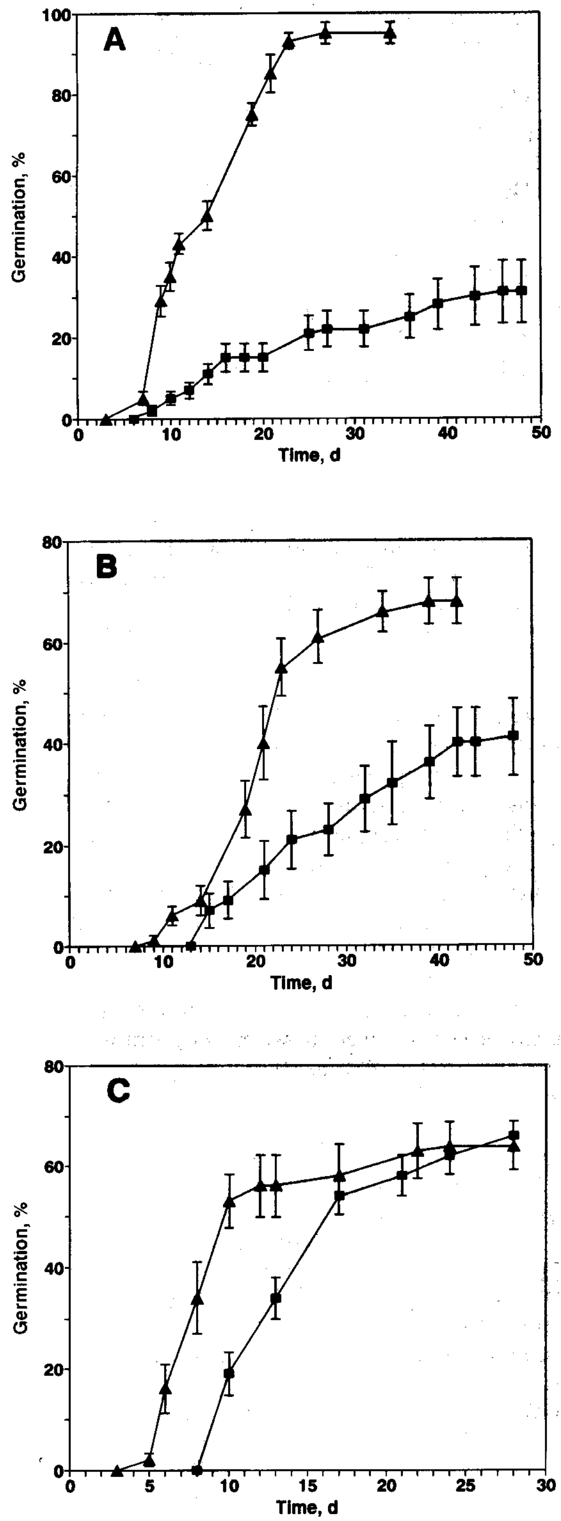

Figure 7. Time course of germination of *Coridothymus capitatus* (**A**) *Satureja thymbra* (**B**) and *Origanum vulgare* subsp. *hirtum* (**C**) seeds within calyces at 15°C under continuous white light. Calyces previously soaked in distilled water (for 1, 1 and 3 days, respectively): ▲; controls: ■.

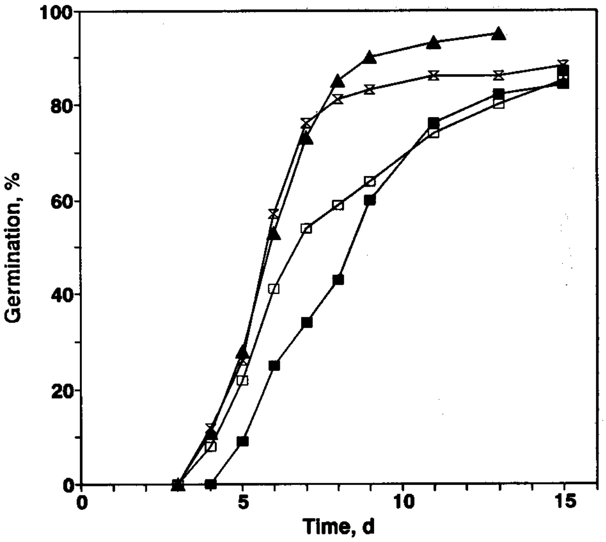

Figure 8. Time course of seed germination in two chemotypes of *Coridothymus capitatus* (thymol-type: ▲, ⧖; carvacrol-type: ■, □) at 15°C, under continuous white light in the presence of 10 calyces per dish of each chemotype (thymol-rich calyces: ▲, □; carvacrol-rich calyces: ⧖, ■).

perature seems to depend upon the age of the seed, as Theophrastus had already noticed two millennia ago. In particular, freshly harvested seeds were deeply dormant at higher temperatures, but they could be induced to germinate by continuous white light. Moreover, the relatively slow germination rates also depended upon the age of the seeds. Light was important for savory seed germination. Under white or red light, which establish calculated ϕ values of 0.6, approximately 70% germination occurred, whereas there was only 20% germination in seeds treated with FRII ($\phi = 0.32$). Since germination in darkness was about 40% ϕ in 'dark' seeds must be between 0.32 and 0.6. Light which establishes ϕ below 0.01 (similar to that under dense leaf canopies) is understandably inhibitory of germination (B and FRI in Fig. 3B). The partial dormancy in fresh savory seeds may be caused by essential oils, which are either present on the nutlet coats or are simply diffused within the seed from the surrounding calyx tissues. In a micromorphological study of certain representatives of the tribe Saturejeae, Husain *et al.* (1990) found both trichomes and sessile oil glands at the posterior end of the nutlets of *Satureja horvatii* and *S. pillosa* (but not in *S. montana*, *S. subspicata* and *S. cuneifolia*). A similar, preliminary observation has been made on *S. thymbra* under a stereomicroscope (*cf.* Fig. 4B) and this may explain the statement by Theophrastus that older seeds germinate better: the essential oils present on the nutlet coat suppress germination until they are volatilized.

Germination of the minute seeds of oregano was clearly light-requiring. Even a few short exposures to a dim, green safelight strongly promoted germination, suggesting a very low threshold level of photosensitivity. A similar response has previously been reported in several cases, e.g. in *Stellaria media* seeds (Baskin and Baskin, 1979). Full induction of oregano seed germination was obtained by red and white light, and even the far-red light partially promoted germination. Thus, in oregano seeds imbibing under complete darkness the established ϕ is presumably below 0.06 (the level established by far-red I). The rate of germination of illuminated oregano seeds was remarkably high, similar to that of thyme seeds.

Origanum vulgare is a taxonomically difficult and variable species with several subspecies (Kokkini *et al.*, 1991). Previous experiments on seed germination of oregano subspecies (unspecified but assumed to be different to the one used in the present study) have reached contradictory conclusions. Thus, oregano seeds were believed to germinate equally well in darkness or under white light (Macchia *et al.*, 1983; Grime *et al.*, 1988). In addition, only a partial suppression of germination was obtained when seeds imbibed under a layer of leaves (Silvertown, 1980) or bryophytes (van Tooren, 1990). However, in agreement with the results of the present study, when experiments were performed in complete darkness, germination was almost nil (Pons, 1991a). A red light pulse induced full germination, and even a far-red one promoted germination to around 40%. Upon successive illuminations, the final irradiation determined the level of germination, a proof for phytochrome mediation (Pons, 1991a,b).

In neither of the three species used in the present study, was any secondary dormancy found to be imposed by light or high temperatures. Absence of secondary dormancy (photodormancy) induction was noted in savory and oregano seeds, which germinated promptly under favourable light conditions and irrespective of a previous adverse light pretreatment; in thyme seeds no thermodormancy was induced.

Seed dispersal in thyme, savory and oregano takes place within the persistent fruiting calyces (Stopp, 1952), the opening of which is brought about by increased moisture. Nevertheless, despite opening of the calyx the seeds remain inside and eventually germinate within it (Thanos, 1993). On the other hand, the presence of the essential oils in the calyx tissues strongly inhibits germination of the enclosed seeds, as shown in the present work and by deductions from numerous previous reports (e.g. Vokou and Margaris, 1986). Seed germination within the calyx was dramatically suppressed in thyme and to a lesser extent in savory and oregano. It was, moreover, spread over a very long period. Therefore, this diaspore dormancy caused by the essential oil is suggested to be relieved under natural conditions by leaching with rainwater. This hypothesis is supported by the spectacular enhancement of germination by a rain-simulating treatment of calyces. Nevertheless, actual field observation and documentation need to be performed before reaching a final conclusion. The concept of a rain gauge was initially postulated by Went (1955) for seeds of desert annuals, which germinate when enough rain has fallen to leach out the inhibitors contained in the seed coverings. However, little evidence for breaking of seed dormancy by leaching of chemical inhibitors has been produced in the meantime, and this interesting hypothesis has not been proved under field conditions.

Seedlings of thyme are minute and very difficult to count under natural conditions. However, Argyris (1977) found that emergence takes place almost exclusively during November and December, with a certain delay in respect to the onset of the rainy season. The number of seedlings recorded was much lower than the estimated seed density. It still has not been resolved as to whether limited seedling emergence should be attributed to high mortality of seedlings or to an enforced dormancy. Similarly to its eastern Mediterranean counterpart, *Coridothymus capitatus*, postfire recolonization by *Thymus vulgaris* takes place through both resprouting and reseeding (Belhassen *et al.*, 1987). Furthermore, seeds of *T. vulgaris* can withstand temperatures up to 100°C, although they are not hardseeded. Therefore, it might be worth testing the possibility that thyme seeds are able to form either a transient or a short-lived persistent soil seed bank, as a result of their tiny size and presence of essential oils.

One noteworthy characteristic of certain types of Mediterranean vegetation (chaparral and coastal sage in California, phrygana in East Mediterranean) is either the depauperate herbaceous vegetation under the chaparral canopy (McPherson and Muller, 1969) or the bare zones around the dominant, aromatic shrubs, e.g. *Salvia leucophylla*, *Artemisia californica* (Muller *et al.*, 1964) and *Coridothymus capitatus* (Vokou, 1983; Katz *et al.*, 1987), respectively. This scarcity of vegetation has been attributed, *inter alia*, to toxins produced by the leaves of the established mature plants, which in this way prevent new germination and growth. Allelopathy was also suggested in the case of the essential oils produced by aromatic, phryganic shrubs (e.g. Vokou, 1983; Katz *et al.*, 1987; Friedman, 1995). On the other hand, allelopathy, or chemical inhibition by the shrub canopy, was considered an unlikely explanation of vegetation suppression (Keeley and Keeley, 1989). Despite the voluminous laboratory evidence, the ecological significance of allelochemicals is still strongly questionable (e.g. Friedman, 1995).

The major constituent of the essential oil in all three plants studied in the present work is carvacrol (Kokkini and Vokou, 1989), although several cases of populations (or chemotypes) rich in thymol (the isomer of carvacrol) have been reported. The effects of the individual constituents of thyme essential oil (thymol was not included) have been previously tested and carvacrol was found among the most inhibitory substances (Vokou, 1983). The experimental protocol of the present study was adopted in order to delay (instead of inhibit) germination and in this way to reveal any differences that might exist in seed germination behaviour and/or inhibitory effect of the essential oils, between the carvacrol and thymol chemotypes. The results obtained revealed no inter-chemotype differences in either seed germinability or inhibitory effect of the calyces. Thus, it may be concluded that thymol and carvacrol isomers are equally effective in thyme seed autopathy. A similar conclusion was recently reached for *Thymus vulgaris;* thymol and carvacrol (either in pure form or in crushed leaves of the corresponding chemotypes) were equally inhibitory on seed germination of both *Brachypodium phoenicoides* and thyme itself (Tarayre *et al.*, 1995).

Inhibition of seed germination by its own essential oil in *Coridothymus capitatus* is an example of autopathy (Vokou, 1983) and not autotoxicity (as referred to by Friedman, 1995), since no toxic effect remains after removal of the essential oils. This autopathic effect has been suggested to be a mechanism of self- regulating the density of thyme plants in the field (Vokou, 1992). Since the calyces are quite rich in essential oils known to inhibit both germination and radicle growth, the dispersal of seeds within their calyces (a fact not appreciated by Argyris, 1977 and Vokou, 1983) delays germination until the leaching of the essential oils. We suggest that such a device is an ecological adaptation to the unpredictable rainfall pattern during the early part of the rainy period in the Mediterranean climate. It ensures the delay of germination until well within the wet season. Such a delay is a common trait among Mediterranean plants and is illustrated by low germination rates, which may be attributed to the properties of either the seed coat or the embryo. Therefore, in this way seed germination and subsequent seedling establishment are secured against the dry spells frequently encountered during the early phase of the rainy period in the Mediterranean climate. Recent results on *Thymus vulgaris* support this postulation: the observed waning of the inhibitory effect of essential oils over time would imply that if such an effect really occurs in the field it would only be of a temporary character and thus represent a 'temporary inhibition' adaptation to the Mediterranean climate (Tarayre *et al.*, 1995).

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