Photoinhibition of Seed Germination in Mediterranean Maritime Plants

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Photoinhibition of seed germination was shown for Allium staticiforme, Brassica tournefortii, Cakile maritima and Otanthus maritimus, all plant species inhabiting sandy coasts of the Mediterranean Sea. Germination of A. staticiforme was found to be typically Mediterranean in regard to its temperature range (> 0-20 °C), while B. tournefortii germinated optimally at intermediate temperatures (15-25 °C). Light sensitivity was more pronounced in the latter species and 50% inhibition of seed germination was obtained with photon flux densities of approximately 0.1 and 0.015 mol m⁻² d⁻¹ in A. staticiforme and B. tournefortii, respectively. However, the slopes of the regression lines of germination plotted against the logarithm of white light flux density are similar in both species. From monthly experiments performed under fluctuating conditions of temperature and light, simulating the climate of Athens throughout the year, optimal germination response peaked in 'winter' conditions for A. staticiforme, while a bimodal pattern was observed for B. tournefortii (maxima at the warm ends of the rainy season). In contrast to the other plants, a fifth species tested, Crithmum maritimum, showed an absolute light requirement, probably related to the rocky habitats of the species; the optimum germination period coincided with the rainy season. Pot experiments with seeds of the five species buried at various depths confirmed that maximum emergence is favoured by shallow depths (0.5-1 cm). It is concluded that seed germination in maritime plants of the Mediterranean rim is mediated by a photoinhibition mechanism which can be considered an adaptation strategy against surface seedling establishment at the harsh, sandy or shingle, sea coast habitats.

Key words: Allium staticiforme, Brassica tournefortii, Cakile maritima, sea rocket, Crithmum maritimum, rock samphire, Otanthus maritimus, cotton-weed, seed germination, light, photoinhibition, phytochrome, seedling emergence.

INTRODUCTION

In a recent investigation on yellow horned-poppy, Glaucium flavum, a widely distributed maritime plant, a surfaceavoiding mechanism of seedling establishment based on photoinhibition of seed germination was clearly revealed for the first time (Thanos, Georghiou and Skarou, 1989). Such a light-mediated mechanism offers obvious adaptational advantages to plants inhabiting open habitats where harsh conditions, particularly regarding water economy, may prevail. Circumstantial evidence for the presence of this mechanism is already available for plants growing in deserts [Calligonum comosum (Koller, 1956), Atriplex dimorphostegia (Koller, 1957), Citrullus colocynthis (Koller et al., 1963) and Zygophyllum coccineum (Batanouny and Ziegler, 1971)], open chaparral [Phacelia tanacetifolia (Rollin, 1958), Eschscholzia californica (Goldthwaite et al., 1971), Limnanthes alba (Cole, 1974) and Nemophila menziesii (Cruden, 1974)], disturbed ground [Avena fatua (Cunning and Hay, 1958), Oryzopsis miliacea (Negbi and Koller, 1964), Amaranthus caudatus (Kendrick and Frankland, 1969), Sinapis arvensis (Bartley and Frankland, 1982), Bromus mollis and B. sterilis (Ellis, Hong and Roberts, 1986)] and sea coasts [Spinifex hirsutus (Harty and McDonald, 1972) and Pancratium maritimum (Keren and Evenari, 1974)].

The aim of the present study was to investigate the presence and properties of the light-inhibited germination in certain coastal species of the Mediterranean rim: Allium

staticiforme, Brassica tournefortii, Cakile maritima (sea rocket), Crithmum maritimum (rock samphire) and Otanthus maritimus (cotton-weed). These species cover a wide spectrum of attributes and belong to four families; two of the plants are annuals (B. tournefortii and C. maritima) and the rest perennials. They are all of Mediterranean origin although the distribution of three of them extends to the west European coasts, northwards to S.E. Ireland (O. maritimus), Scotland (C. maritimum) or Iceland (C. maritima) (Tutin et al., 1964-80). Distribution of B. tournefortii is mainly restricted to the southern and eastern parts of the Mediterranean rim, while extending eastward to the Caspian and Baluchistan (Meikle, 1977). Finally, A. staticiforme is endemic to Greece (southern Greece and Crete) (Tutin et al., 1964-80). All species are found mainly in sandy (and shingle) beaches with the exception of C. maritimum which usually inhabits maritime rocks (and cliffs) and is only rarely met on sand dunes. For three of the species there already exists some fragmentary information concerning light inhibition of seed germination [Barbour (1970a) and Batanouny (1974), for C. maritima and B. tournefortii, respectively] or even contradictory [Okusanya (1977) and Marchioni-Ortu and Bocchieri (1984) for C. maritimum].

MATERIALS AND METHODS

Seeds of Allium staticiforme Sibth. & Sm. and Brassica tournefortii Gouan were collected in July 1988 from the

sandy beach of Schinias, Attica. Mericarps of Crithmum maritimum L. were collected in October 1988 from plants growing on maritime rocks in Mt Athos Peninsula (northern Greece). Upper and lower fruit (siliqua) segments of Cakile maritima Scop. were collected in September 1988, at the sand-gravel seashore of K. Diminio (northern Peloponnesus). Achenes of Otanthus maritimus (L.) Hoffmanns. & Link were collected in September 1988, at the sandy beach of Stavros, in Akrotiri, Chania (Crete). Mericarps of C. maritimum, fruit segments of C. maritima and achenes of O. maritimus are the actual dispersal units of these plants. Throughout the present work they were used without any removal of the surrounding fruit tissues but, for reasons of simplicity, they will be called seeds hereafter. The seeds were stored dusted with fungicide (Thiram) in light- and waterproof plastic tins, at room temperature $(20\pm5$ °C). The average seed (or fruit) weight was found to be: A. staticiforme 0.5, B. tournefortii 1.3, C. maritimum 3.1, C. maritima 35.6 (upper) and 44.2 (lower), and O. maritimus 0.8 mg. No variation in germination characteristics was observed during the experimentation period.

Germination tests were performed in Petri dishes (7 cm diameter) lined with two filter paper discs and moistened with 3 ml of deionized water. The criterion of germination was visible radicle protrusion and measurements were taken daily, or in certain cases once or twice weekly. After each count, the germinated seeds were discarded and the tests were considered finished when no additional seeds germinated. Each value is the mean of five samples of seeds (ten for *C. maritima*) \pm standard error (s.e.).

The experiments were performed in plant growth cabinets (Model BK 5060 EL, W. C. Heraeus GmbH, Germany). Continuous or diurnally alternating temperatures were maintained in all cases within ± 0.5 °C of the value set. Lighting in Fig. 2 was provided by a white light source with an emission spectrum quite similar to daylight. The source consisted of one white fluorescent (Philips TLD 18 W/33) and one white incandescent tube (Philips Philinea 6276 X. 60 W); the total flux density of the region 400-750 nm at the seed level was 2.4 W m⁻² and ζ was 1.0 [$\zeta = R(660 \text{ nm})/$ FR(730 nm) photon ratio, as defined by Smith (1986)]. For higher or lower flux densities (Fig. 3) either several tubes of both types or diffuse white plexiglas filters (four to ten sheets, each 3 mm thick) were added. In all these cases the value of ζ was maintained fairly constant (1.0–1.3). All manipulations of imbibed seeds were carried out under a dim green safelight and flux densities were measured with a spectroradiometer ISCO SR, USA (Thanos et al., 1989).

The germination experiments presented in Fig. 7 were carried out on two temperature- and light-programmable growth benches, model GB48 (Conviron, Canada) equipped with a lamp canopy of 48 incandescent bulbs (Sylvania 50A19, 50 W, 277 V) and 28 fluorescent tubes (Sylvania Cool White FR96T12/CW/VHO-235/1). Temperature and light programmes were changed every 10 d. The micro-processor was fed with the mean values for the particular 10-d period, pooled from the daily data furnished by the Greek Meteorological Service (EMY). These data were mean values of temperature for 3-h intervals, for each day of the year (period 1955–87), at the Meteorological Station

of Athens, Ellinikon. Therefore, temperature was programmed to change every 3 h. The lights were programmed to turn on 30 min before official sunrise and off 30 min after official sunset (means for the particular 10-d period). Both the quality and quantity of light were automatically adjusted several times during the 'day'. At 'dawn' and 'dusk' (16 incandescent bulbs on) the ζ value was 0.7 and the total flux density (400–750 nm) 1·2 W m⁻²; at 'mid-day' (48 incandescent bulbs and 20 fluorescent tubes on), ζ obtained its maximum value (2·1) as did total flux density (40 W m⁻²). Germination tests were performed in the simulated conditions for each month of the year, for *A. staticiforme*, *B. tournefortii* and *C. maritimum*.

For the experiments performed outdoors (Table 1, Figs 4 and 5) the procedure described previously (Thanos et al., 1989) was followed. In addition to pots, Petri dishes (always kept moist) were also exposed to natural conditions; dark controls were placed in light-proof metal cans (as were other dark treatments). The experiments started on 1 Nov. 1988 and ended on 30 Mar. 1989. During this period the climatic conditions in Athens were very unusual. November and December 1988 were quite rainy and attained precipitation values nearly double that of their respective averages, although all of the rain was recorded in two distinct spells (approx. 100 mm from 15 Nov. to 28 Nov. and approx. 120 mm from 12 Dec. to 26 Dec.). Afterwards, January and February 1989 were practically rain-free (3 mm of rain each) and March 1989 drier than average (25 mm). The total of the 3 months (31 mm) was the lowest recorded during the last 50 years; the second lowest being 1977 (32 mm) and the third 1957 (48 mm).

RESULTS

The germinability of A. staticiforme and B. tournefortii seeds at various constant temperatures, in the dark, is



FIG. 1. Final seed germination of Allium staticiforme (\bullet) and Brassica tournefortii (\blacksquare) , in the dark, as a function of constant temperature. Vertical bars represent \pm s.e.



FIG. 2. The time courses of seed germination under a diurnally alternating temperature regime [11 h (20 °C)/13 h (13 °C)], in continuous darkness (solid symbols) or under white light (2.4 W m⁻²) during the warm period (open symbols). A, *Allium staticiforme*; B, *Brassica tournefortii*; C, *Crithmum maritimum*. Vertical bars represent ± s.e.

presented in Fig. 1. In the former species, full germination was sharply suppressed above 20 °C, while in the latter there was an optimum range at intermediate temperatures (15–25 °C), with certain germination 'tails' at both ends (10 and 30 °C). The rate of germination was much slower in A. staticiforme than in B. tournefortii seeds (data not shown); thus, at optimal temperatures, germination was completed after 10 and 4 d, respectively.

In the experiments shown in Fig. 2, seeds of A. staticiforme, B. tournefortii and C. maritimum were imbibed in diurnally alternating temperatures; white light was also added during the warm period. Both the duration of the photoperiod and the temperatures of 'day' and 'night' were chosen to simulate those naturally encountered at the beginning of the rainy season in Greece (late October early November). The quality of the white light was close to that of daylight but its flux density was only approx. 1% of the latter. Nevertheless, virtually total inhibition of germination was recorded for B. tournefortii (Fig. 2B) while a considerable decrease of both the final level and the rate of germination was shown by A. staticiforme seeds (Fig. 2A). On the other hand, C. maritimum seed germination was dramatically promoted by white light (Fig. 2C). The pace of germination was shown once more to be rather quick for B. tournefortii (in the range of several days) and comparatively slow for A. staticiforme and C. maritimum (in the order of 1-2 and 1-3 weeks, respectively).

As a consequence of the previous experiment, the white light flux density was varied and its effect on the inhibition of seed germination is presented in Fig. 3. The final germination percentages of *A. staticiforme* and *B. tournefortii* are plotted against the logarithms of the flux density. Although the probability levels for the regression curves are



FIG. 3. Final seed germination of *Allium staticiforme* (○) and *Brassica* tournefortii (□) as a function of the flux density of white light provided during the warm period of a diurnally alternating two-temperature regime [11 h (20 °C)/13 h (13 °C)]. The linear regressions are:

$$Y = 81.72 - 68.88X (r^2 = 0.78, \text{ d.f.} = 1, 0.10 < P < 0.25)$$

$$Y = -3.04 - 57.96X$$
 ($r^2 = 0.86$, d.f. = 2, 0.025 < P < 0.05)

for A. staticiforme and B. tournefortii, respectively. Closed symbols are corresponding controls in continuous darkness. Vertical bars represent \pm s.e.

TABLE 1. Final seed germination (or seedling emergence)values (%±s.e.) of five maritime plant species exposed tonatural conditions (1 Nov. 1988–30 Mar. 1989)

	Petri dish		Pot	
	L/D	D	Surface	Buried
Allium staticiforme	86·8 ± 3·2	96·0±2·0	18.4 ± 1.2	95·6±2·9*
Brassica tournefortii	0.0 + 0.0	22.3 ± 5.1	0.0 ± 0.0	8·4 ± 3·3†
Cakile maritima (upper fruit segment)	0.0 ± 0.0	$33\cdot2\pm5\cdot1$	0.0 ± 0.0	3·0±1·9*
Cakile maritima (lower fruit segment)	0.0 ± 0.0	18·8±2·4	0.0 ± 0.0	$2.0 \pm 1.3*$
Crithmum maritimum	90.0 ± 3.3	0.8 ± 0.5	0.0 ± 0.0	5.6 ± 2.11
Otanthus maritimus	0.0 ± 0.0	7.6 ± 2.3	0.4 ± 0.4	24·8±12·9†

L/D, dishes exposed to diffuse daylight; D, continuous darkness.

* Buried 1 cm deep.

† Buried 0.5 cm deep.



FIG. 4. Final seedling emergence of Allium staticiforme (A) and Brassica tournefortii (B) buried beneath different depths of sand and exposed to natural conditions for 40 d (1 Nov.-10 Dec. 1988). Vertical bars represent \pm s.e.

not particularly low, their slopes are quite similar. On the other hand, the difference between the X-intercepts of the two lines is higher than one order of magnitude of flux density.

Table 1 shows the final levels of germination or emergence under natural conditions. Seed germination on the surface of the sand was fully inhibited, with the exception of A. *staticiforme* where some germination was observed. On the other hand, seedling emergence from buried seeds was complete only in the case of A. *staticiforme*; in O. *maritimus* and B. *tournefortii* a rather small fraction was observed,



FIG. 5. Germination time courses of Allium staticiforme seeds imbibing in Petri dishes but exposed to natural temperature conditions (1 Nov.-10 Dec. 1988), in the dark (\oplus) or under diffuse daylight (\bigcirc). Vertical bars represent \pm s.e.

while for the remaining plants a very poor percentage was recorded (though it must be noted that in the latter species, emergence was very late, i.e. by the end of December 1988). Germination in Petri dishes was more or less similar to that in pots with the exception of *A. staticiforme* and *C. maritimum* which germinated nearly optimally at daylight (L/D).

Seedling emergence, as a function of burial depth, for seeds of A. staticiforme and B. tournefortii is presented in Fig. 4. Germination at the surface of the sand was dramatically reduced and optimal emergence was observed at rather shallow depths $(0.5-2 \text{ cm} \text{ for the former and} approx. 0.5 \text{ cm} for the latter species})$. The time course of seed germination of A. staticiforme in Petri dishes exposed to natural conditions of light (diffuse daylight) and temperature (fluctuating daily between 5 and 18 °C) was considerably retarded in comparison to dark controls. Germination in the light started 1 week later than in darkness and was completed 3 weeks later (Fig. 5).

Figure 6 shows the mean climatic conditions of Athens, Ellinikon. Temperature data and relative lengths of 'day' and 'night' were used to simulate the average conditions of each 10-d period, all year long. Precipitation values have been also included to complement the insight into the simulated climate, particularly concerning the 'warm and dry' period. This xerothermic season covers a nearly halfyear long period, from April/May to September/October, and although moisture is fully supplied in the dishes, experimental germination of both *A. staticiforme* and *C. maritimum* is strikingly inhibited during these 'warm' months (Fig. 7A, C). Also in the case of *B. tournefortii*, dark germination during summer was markedly decreased in



FIG. 6. Climatic data for Athens, Ellinikon. Monthly precipitation values (---) are the means for the period 1951-90. Maximum and minimum air temperatures (for each 10-d period) are means for 1955-87. The duration of the daily skotoperiod (shaded area) was derived from sunrise and sunset official timetables (less 1 h for both dawn and dusk light).

comparison to spring or autumn (Fig. 7B). While exposure to light was an obvious and absolute requirement for *C. maritimum* seed germination (Fig. 7C), the opposite held true for *A. staticiforme* and *B. tournefortii*. Germination of the former was practically complete in both light/dark and continuous darkness during the cool season (November to March) while during the 'marginal' months (April, May and October) germination was strongly suppressed by light. A marked inhibition by light was also observed for *B.* tournefortii seeds, though in this case it was considerably higher during the cooler months and only slight during 'summertime'. It must also be noted that germination of the latter species was generally higher at intermediate temperatures (April to June and September to November) than at cooler or warmer ones.

DISCUSSION

The temperature range for the germination of A. staticiforme seeds in darkness (Fig. 1) is typically Mediterranean (Thompson, 1973) and is consistent with the species origin. The same conclusion may be reached indirectly for C. maritimum seed germination under alternating light and darkness (Fig. 7C). On the other hand, the temperature dependence of B. tournefortii germination (Fig. 1) seems adapted to warmer climates and this may be related to its southward- and eastward-shifted distribution. For C. maritima and O. maritimus, it was not possible to obtain the corresponding germination vs. temperature curves; neither species germinated readily and they may require a stratification treatment. The fact that virtually no C. maritima seeds germinated in sand can be attributed to the drought which prevailed from January 1989 onwards (cf. Materials and Methods); according to Barbour (1970b), Ignaciuk and Lee (1980) and Hocking (1982), these seeds require a chilling period and simultaneous leaching of inhibitors and/or salt present in the seed coats and the surrounding fruit tissues. Nevertheless, further research is needed on both C. maritima and O. maritimus to clarify the relative importance of the mechanism of photoinhibition in their overall seed germination ecophysiology.

The major conclusion of this study is that seed germination in four of the species investigated is negatively photo-



FIG. 7. Final seed germination of Allium staticiforme (A), Brassica tournefortii (B) and Crithmum maritimum (C) as a function of various temperature and light conditions, simulating those prevailing naturally, throughout the year, in Athens, Ellinikon (Fig. 6). Shaded bars are controls in continuous darkness. Vertical lines represent s.e.

sensitive. This was shown clearly for A. staticiforme and B. tournefortii and rather indirectly for C. maritima and O. maritimus. Certain discrepancies of the experimental results are discussed below. Germination of A. staticiforme seeds in Petri dishes, in L/D (Table 1 and Fig. 5) was encouraged by both low light levels and cool temperatures (compare also with the winter months in Fig. 7A). However, it must be kept in mind that flux density values used in the pot experiments (Table 1) and in the simulated climate (Fig. 7) are about one-tenth those of naturally prevailing ones. Therefore, it is postulated that seed germination of A. staticiforme would be considerably suppressed by light in nature, although cool temperatures act antagonistically. The slow rate of germination is an additional factor in support of the previous conclusion, since moisture availability may not be continuous (as in the dishes), and this would seem to be the explanation for the reduced level of germination on the surface of the sand (Table 1). With regard to the low germinability of B. tournefortii seeds in darkness, both in the sand and in the dishes (Table 1), it is possible that this reduction may be attributed to the rather low temperatures met during the experimentation period. This is supported by the results of Figs 1 and 7B and leads to the construction of a bimodal germinability curve, i.e. optimal season for germination in nature is both at the start (October/November) and at the end (April/May) of the rainy period (in contrast to A. staticiforme which seems to germinate best in the coolest months of the year). Although theoretically possible, summer germination of B. tournefortii on a beach is, of course, highly improbable, but it can occur under artificially irrigated conditions. This postulation fits well with the account given by Batanouny (1974), which states that, besides inhabiting sand dunes, B. tournefortii is also an ephemeral weed of barley fields in Egypt.

In *C. maritimum*, the non-germinability of seeds sown on the sand surface may be attributed to reduced moisture availability in conjunction with the very slow germination speed of the species. The absolute light requirement of germination shown by the seeds used in the present work is in agreement with the preliminary observations of Okusanya (1977) but differs strikingly from those reported by Marchioni-Ortu and Bocchieri (1984). However, in the latter study seeds were collected from plants growing on the Sardinian sandy coasts. It is evident that further investigation is necessary before the identification of two different ecotypes, within the particular species, can be made on the basis of their contrasting seed ecophysiological behaviour.

Despite the different sensitivity of A. staticiforme and B. tournefortii seeds towards white light (Fig. 3), the estimated slopes are statistically similar. Furthermore, it is interesting to note that in the corresponding curves for Amaranthus caudatus (Bliss and Smith, 1985) and Matthiola tricuspidata (C. A. Thanos, K. Georghiou and P. Delipetrou, unpubl. data) the slopes are also approx. 50 or, in other words, inhibition is brought about by approx. two orders of magnitude of flux density. For 50% inhibition of seed germination in Glaucium flavum, white light of a total daily dose (in the visible range of the spectrum) of as little as 0.002 mol m⁻² d⁻¹ is required (Thanos et al., 1989). Next, in descending order of sensitivity, come (in mol m⁻² d⁻¹):

Bromus sterilis 0.01 (Ellis et al., 1986), Brassica tournefortii 0.015 (this study), Allium staticiforme 0.1 (this study), Bromus mollis 0.5 (Ellis et al., 1986), Amaranthus caudatus 2.2 (Bliss and Smith, 1985), Lactuca sativa (two cultivars) approx. 5 (Ellis, Hong and Roberts, 1989) and Matthiola tricuspidata 6.6 (Thanos, Georghiou and Delipetrou, unpubl. data). It should be noted that the above values are not easily comparable due to differences in the quality of the white light used. Nevertheless, it is evident that among the plant species tested, there exist quite different levels of sensitivity towards light. This fact may be the result of diversity in: (a) optical properties of seed (and fruit) tissues; (b) functional properties of the photoreceptor(s) involved; and (c) adaptation strategies to various light environments including those caused by the season of the year and the depth of burial. With regard to the nature of the photoreceptor(s), it is generally believed that the inhibitory effect of prolonged white light is mediated through the phytochrome system and is due, according to the explanation furnished by Bartley and Frankland (1982), to the particularly high rates of interconversion ('cycling') of phytochrome molecules under high flux densities (although the inhibitory densities in certain cases, e.g. Glaucium flavum and Bromus sterilis, are markedly low).

The experiments with buried seeds confirmed the conclusion previously reached on many occasions-that seedling emergence is optimal from shallow depths, usually around 1 cm. Moreover, it is generally agreed that physiologically and ecologically significant amounts of light rarely penetrate more than 4-5 mm through soil (Tester and Morris, 1987; Mandolli et al., 1990). In a number of ecological studies where the germination response to light was not investigated, virtually all seeds of Cynoglossum officinale (Boorman and Fuller, 1984), Ammophila breviligulata (Maun and Lapierre, 1986) and Agropvron psammophilum (Zhang and Maun, 1990) germinated when buried at shallow depths (2-4 cm) of sand. On the other hand, seeds sown on the surface showed very poor germination, but this effect was attributed to evaporation stress rather than to excess light or temperature fluctuations (Maun and Riach, 1981); this factor also seems to be responsible for the nongermination of the light-requiring seeds of Senecio jacobaea on the sand surface (Van der Meijden and Van der Waals-Kooi, 1979).

The phenomenon of light-inhibited seed germination has been observed many times and in numerous plants, though with very diverse illumination regimes (Toole, 1973). The possible survival value of photoinhibition of seed germination has been postulated long ago by Koller (1964), particularly for a number of desert plants. Nevertheless, this light-mediated germination mechanism has not generally been attributed the special ecological function it may have, in contrast to the other two, already well established environmental roles of light in seed germination, i.e. promotion by light through soil disturbance and inhibition by light filtered through the leaf canopy (Frankland and Taylorson, 1983).

Light-promoted seed germination in maritime plants has been demonstrated in *Plantago maritima* (Arnold, 1973), *Senecio jacobaea* (Van der Meijden and Van der Waals-

Kooi, 1979) and Ammophila arenaria (Van der Putten, 1990). Nevertheless, this response may be related to the fact that the seeds had been collected from plants growing in areas with temperate climates, considerably cooler and wetter than the Mediterranean (the former species collected in England and the latter two in the Netherlands). On the other hand, the presence of the photoinhibition mechanism of seed germination has been verified in all seven species of Mediterranean maritime plants tested: Pancratium maritimum (Keren and Evenari, 1974), Glaucium flavum (Thanos et al., 1989), the four species of this study, and Matthiola tricuspidata (C. A. Thanos, K. Georghiou and P. Delipetrou, unpubl. data). The exception of C. maritimum can be attributed to its particular habitat (rocks and cliffs). It is postulated that light requirement in this case might represent a mechanism to avoid seedling establishment in very deep fissures, even though its rather large seed could possibly support early development.

LITERATURE CITED

- ARNOLD, S. M., 1973. Interactions of light and temperature on the germination of *Plantago maritima* L. New Phytologist 72, 585–593.
- BARBOUR, M. G., 1970a. Germination and early growth of the strand plant Cakile maritima. Bulletin of the Torrey Botanical Club 97, 13-22.
- —, 1970b. Seedling ecology of Cakile maritima along the California coast. Bulletin of the Torrey Botanical Club 97, 280–289.
- BARTLEY, M. R. and FRANKLAND, B., 1982. Analysis of the dual role of phytochrome in the photoinhibition of seed germination. *Nature* 300, 750–752.
- BATANOUNY, K. H., 1974. Breaking dormancy by GA₃ in negatively photoblastic seeds of *Brassica tournefortii* Gouan. *Biochemie und Physiologie der Pflanzen* 165, 233–238.
- and ZIEGLER, H., 1971. Eco-physiological studies on desert plants.
 II. Germination of Zygophyllum coccineum L. seeds under different conditions. Oecologia 8, 52–63.
- BLISS, D. and SMITH, H., 1985. Penetration of light into soil and its role in the control of seed germination. *Plant, Cell and Environment* 8, 475–483.
- BOORMAN, L. A. and FULLER, R. M., 1984. The comparative ecology of two sand dune biennials: Lactuca virosa L. and Cynoglossum officinale L. The New Phytologist 96, 609-629.
- COLE, D. F., 1974. Effects of light and temperature on germination of two accessions of *Limnanthes alba* seed. *Economic Botany* 28, 155-159.
- CRUDEN, R. W., 1974. The adaptive nature of seed germination in Nemophila menziesii aggr. Ecology 55, 1295-1305.
- CUMMING, B. G., and HAY, J. R., 1958. Light and dormancy in wild oats (Avena fatua L.). Nature 182, 609-610.
- ELLIS, R. H., HONG, T. D. and ROBERTS, E. H., 1986. The response of seeds of *Bromus sterilis* L. and *Bromus mollis* L. to white light of varying photon flux density and photoperiod. *The New Phytologist* 104, 485–496.
- —, and —, 1989. Response of seed germination in three genera of Compositae to white light of varying photon flux density and photoperiod. *Journal of Experimental Botany* 40, 13–22.
- FRANKLAND, B. and TAYLORSON, R., 1983. Light control of seed germination. In *Encyclopedia of Plant Physiology, New Series, vol.* 16A, Photomorphogenesis eds. W. Shropshire Jr and H. Mohr, pp. 428–456. Springer-Verlag, Berlin.
- GOLDTHWAITE, J. J., BRISTOL, J. C., GENTILE, A. C. and KLEIN, R. M., 1971. Light-suppressed germination of California poppy seed. *Canadian Journal of Botany* **49**, 1655–1659.

HARTY, R. L. and MCDONALD, T. J., 1972. Germination behaviour in

beach spinifex (Spinifex hirsutus Labill.). Australian Journal of Botany 20, 241-251.

- HOCKING, P. J., 1982. Salt and mineral nutrient levels in fruits of two strand species *Cakile maritima* and *Arctotheca populifolia*, with special reference to the effect of salt on germination of *Cakile*. *Annals of Botany* **50**, 335–343.
- IGNACIUK, R. and LEE, J. A., 1980. The germination of four annual strand-line species. *The New Phytologist* 84, 581-591.
- KENDRICK, R. E. and FRANKLAND, B., 1969. Photocontrol of germination in Amaranthus caudatus. Planta 85, 326-339.
- KEREN, A. and EVENARI, M., 1974. Some ecological aspects of distribution and germination of *Pancratium maritimum L. Israel Journal of Botany* 23, 202–215.
- KOLLER, D., 1956. Germination-regulating mechanisms in some desert seeds. III. Calligonum comosum L'Her. Ecology 37, 430–433.
- —, 1957. Germination-regulating mechanisms in some desert seeds. IV. Atriplex dimorphostegia Kar. et Kir. Ecology 38, 1–13.
- —, 1964. The survival value of germination-regulating mechanisms in the field. Herbage Abstracts 34, 1–7.
- —, POLJAKOFF-MAYBER, A., BERG, A. and DISKIN, T., 1963. Germination-regulating mechanisms in Citrullus colocynthis. American Journal of Botany 50, 597-603.
- MANDOLLI, D. F., FORD, G. A., WALDRON, L. J., NEMSON, J. A. and BRIGGS, W. R., 1990. Some spectral properties of several soil types: implications for photomorphogenesis. *Plant, Cell and Environment* 13, 287-294.
- MARCHIONI-ORTU, A. and BOCCHIERI, E., 1984. A study of the germination responses of a Sardinian population of sea fennel (*Crithmum maritimum*). *Canadian Journal of Botany* 62, 1832–1835.
- MAUN, M. A. and LAPIERRE, J., 1986. Effects of burial by sand on seed germination and seedling emergence of four dune species. *American Journal of Botany* 73, 450–455.
- and RIACH, S., 1981. Morphology of caryopses, seedlings and seedling emergence of the grass *Calamovilfa longifolia* from various depths in sand. *Oecologia* 49, 137–142.
- MEIKLE, R. D., 1977. Flora of Cyprus, Vol. 1, 832 pp. The Bentham-Moxon Trust, Kew.
- NEGBI, M. and KOLLER, D., 1964. Dual action of white light in the photocontrol of germination of Oryzopsis miliacea. Plant Physiology 39, 247-253.
- OKUSANYA, O. T., 1977. The effect of sea water and temperature on the germination behaviour of *Crithmum maritimum*. *Physiologia Plantarum* **41**, 265–267.
- ROLLIN, P., 1958. Action qualitative de la lumière sur la germination des graines de Phacelia tanacetifolia. Comptes Rendus de l'Académie des Sciences, Paris, Série D 247, 1484–1487.
- SMITH, H., 1986. The perception of light quality. In Photomorphogenesis in Plants, eds R. E. Kendrick and G. H. M. Kronenberg, pp. 187–217. Martinus Nijhoff, Dordrecht.
- TESTER, M. and MORRIS, C., 1987. The penetration of light through soil. *Plant, Cell and Environment* 10, 281-286.
- THANOS, C. A., GEORGHIOU, K. and SKAROU, F., 1989. Glaucium flavum seed germination—an ecophysiological approach. Annals of Botany 63, 121–130.
- THOMPSON, P. A., 1973. Geographical adaptation of seeds. In Seed Ecology, ed. W. Heydecker, pp. 31–58. Butterworths, London.
- TOOLE, V. K., 1973. Effects of light, temperature and their interactions on the germination of seeds. Seed Science and Technology 1, 339-396.
- TUTIN, T. G., HEYWOOD, V. H., BURGES, N. A., VALENTINE, D. H., WALTERS, S. M. and WEBB, D. A., 1964–80. Flora Europaea, Vols. 1-5. Cambridge University Press, Cambridge.
- VAN DER MEIJDEN, E. and VAN DER WAALS-KOOI, R. E., 1979. The population ecology of *Senecio jacobaea* in a sand dune system. I. Reproductive strategy and the biennial habit. *Journal of Ecology* 67, 131–153.
- VAN DER PUTTEN, W. H., 1990. Establishment of Ammophila arenaria (Marram grass) from culms, seeds and rhizomes. Journal of Applied Ecology 27, 188–199.
- ZHANG, J. and MAUN, M. A., 1990. Effects of sand burial on seed germination, seedling emergence, survival, and growth of Agropyron psammophilum. Canadian Journal of Botany 68, 304-310.