Glaucium flavum Seed Germination – an Ecophysiological Approach

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ABSTRACT

The yellow horned-poppy *Glaucium flavum* Crantz shows a final dark germination which is of characteristically 'mediterranean' type (maximal response at the temperature range 5–15 °C), though a considerable broadening is brought about, both by a red light pulse and a stratification treatment. Seeds imbibed in darkness at 25 °C for even a few hours are induced to develop a secondary dormancy (thermodormancy) which can be released by light and stratification. The well known time dependence of light sensitivity and the gradually imposed induction of light indifference at supraoptimal temperatures have also been shown. Seeds imbibed under regimes simulating those met naturally in Greece during November or April, do not germinate when illuminated with white light ($\zeta = 1{\cdot}26$). Full manifestation of germination occurs either in complete darkness or under various, red-enriched light conditions (ζ higher than 2·07). A partial promotion is observed with very low fluence rates of white light (in the order 10^{-3}–10^{-4} of daylight). The existence of a surface-avoiding seedling emergence mechanism based on light-inhibited seed germination was verified in a pot experiment under natural conditions, with seeds buried to various depths. Only those seeds buried at 0·5 cm germinate optimally and readily after the onset of the rainy season (November–December) although those at 1 and 2 cm also germinate to a considerable extent.

Key words: *Glaucium flavum*, yellow horned-poppy, seed germination, light, phytochrome, stratification, thermodormancy, seedling emergence.

INTRODUCTION

The yellow horned-poppy, *Glaucium flavum* Crantz, is a perennial or biennial herb, recognized by Theophrastus (*Enquiry into Plants*, IX, XII, 3) as a medicinal plant growing on rocky sites by the sea. The genus *Glaucium* (Papaveraceae) consists of nearly 20 species, chiefly of the Mediterranean region and also eastwards to Afghanistan (Meikle, 1977). *Glaucium flavum* occurs all along the Mediterranean shores, but also on the coasts of W. Europe and northwards up to Norway (Mowat, 1964; Eisikowitch, 1979/1980).

In sharp contrast to its wide distribution, there is a marked scarcity of information on the physiology of seed germination in the yellow horned-poppy, and only the requirement for stratification has been documented (Formanowiczowa and Kozlowski, 1976; Mermerska, 1984).

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The aim of the present study was to investigate in detail the germination characteristics of *G. flavum* seeds. Particular emphasis was given to the ecophysiological aspects in an attempt to gain insight into the possible role of the germination mechanisms revealed by laboratory experiments in the natural situation.

MATERIALS AND METHODS

Seeds of the yellow horned-poppy (*Glaucium flavum* Crantz) were collected in July 1986 from the ripe capsules of several plants growing in the sand-gravel seashore of K. Diminio (Northern Peloponnesus, Greece). The mean weight of 50 seeds (±s.e.) was found to be 0·0565±0·0005 g ($n = 10$), thus mean seed weight = 1·1 mg. The seeds were stored dusted with fungicide (Thiram) in light- and water proof plastic tins, both at room temperature (20±5 °C) and in the refrigerator (3±2 °C). No variation in germination characteristics was observed throughout the experimentation period.

Germination tests were performed in Petri

dishes (8 cm. diameter) lined with two filter papers and moistened with 3 ml of deionised water or appropriate mannitol (Merck) solution. For the stratification experiments the dishes were transferred to the refrigerator (in light-proof metal cans) immediately after onset of seed imbibition. Seed desiccation included an initial surface drying and afterwards seeds were left to dehydrate in air. The criterion of germination was visible radicle protrusion and measurements were taken daily, as a rule, though in certain cases only once or twice per week. After each count, the germinated seeds were discarded and the tests were considered finished when no additional seeds germinated. Each value is the mean from at least five samples of 50 seeds and ± numbers (in Tables) and vertical bars (in Figures) represent standard error (s.e.). 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 temperature controlled plant growth cabinets (Model BK 5060 EL, W.C. Heraeus GmbH, W. Germany) or chambers (Enviratrol, Conviron, Canada), where in all cases temperature was kept constant within ±0·5 °C. The growth chambers (experiments of Tables 4 and 5) were equipped with a white light source of an emission spectrum quite similar to natural daylight, with a ζ value equal to 1·26; ζ is defined as the R (660 nm):FR (730 nm) photon ratio (Smith, 1986). This source (light source A in Tables 4 and 5) consisted of four white fluorescent tubes (Sylvania, Cool White F48T12/CW/HO, 60 W) and four white incandescent bulbs (Osram 40 W). Light source B (Table 4) consisted of the four fluorescent tubes only. Various coloured and neutral (diffuse white) filters made of glass, Plexiglas and gelatine were used (Tables 4 and 5); certain characteristics of the light transmitted through these filters are appropriately indicated. A part of the experiment presented in Table 5 was carried out in a cabinet equipped with light source C, i.e. one white fluorescent (Philips TLD 18 W/33) and one white incandescent tube (Philips Philinea 6276 × 60 W). The broad band red and far-red light sources used for brief illumination (Table 3, Figs 1, 2 and 3) consisted of eight red fluorescent (Philips TL 20 W/18) and eight white incandescent tubes (Philips Philinea 6276 × 60 W), respectively, filtered through either one red (501) or one red (501) and two blue (627) sheets of Plexiglas filters, 3 mm thick each (Röhm GmbH,

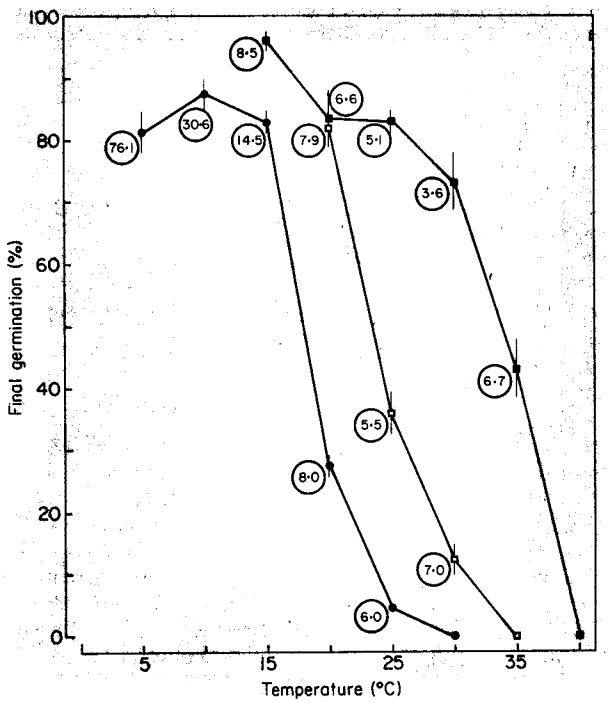

FIG. 1. Final germination of *Glaucium flavum* seeds as a function of temperature. Seeds were tested: untreated (●), illuminated with a short (15 mins red light (□) and stratified for 20 d (■). The R illumination was given 8, 4 and 4 h after onset of imbibition at 20, 25 and 30 °C, respectively. Vertical bars, 2 s.e. The circles enclose the corresponding T_{50} values.

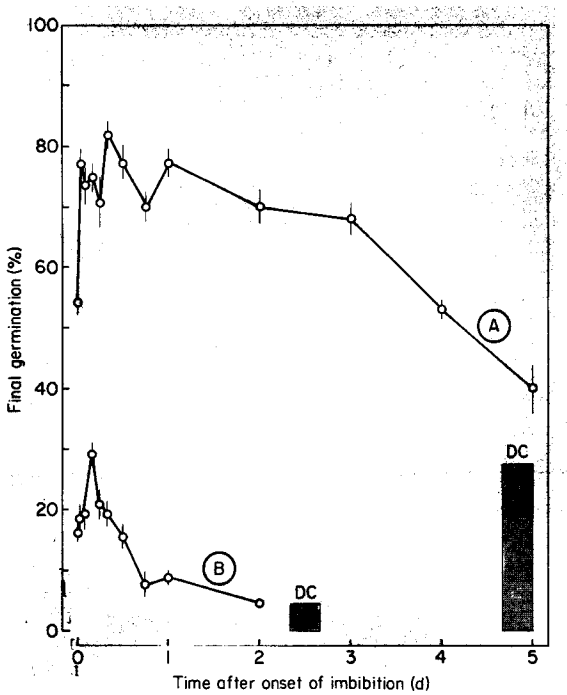

FIG. 2. Final seed germination of *Glaucium flavum* in response to a short (15 mins) red irradiation given after various periods of time from the onset of imbibition, at 20 and 25 °C (curves A and B, respectively). DC, corresponding dark controls, vertical bars, 2 s.e.

W. Germany). Total fluence rates at the regions 600–725 and 675–750 nm was 2 and 4 W m^{-2}, respectively. All manipulations of imbibed seeds were carried out under a dim green safelight (one green fluorescent tube F 15T8.G.6, 15 W Green-Photo, General Electric; two sheets of Plexiglas filter, 3 mm thick each, one red orange, 478, and one green, 700, Röhm GmbH, W. Germany; emission at 525–575 nm, maximum at 550 nm, total fluence rate 10 mW m^{-2}). Total fluence rates were estimated by integrating the spectral fluence rate curves constructed after the measurements taken with a spectroradiometer (ISCO SR, USA).

For the experiment described in Fig. 4, 30 small plastic pots (height 10 cm, diameter 8–9 cm) were filled (up to 8 cm. from the bottom) with dry sea sand. The majority of the sand particles had a diameter of 0·02–0·5 mm, the rest being considerably larger (0·5–2 mm); on wetting, the sand compacted to about 90% of its initial volume. In each pot, 25 seeds had been previously buried at various depths (0, 0·5, 1, 2, 4 and 6 cm), each depth represented by five pots. The pots were established on bare ground, in a well-protected place outdoors and received only diffuse daylight (the maximum value of which ranged from 15 to 30 W m^{-2}, at 400–750 nm, for an overcast or a sunny day, respectively). The pots were subjected only to natural fluctuations of environmental factors and the seedlings emerging from the surface of the sand were counted (and subsequently removed) twice per week. At the same dates the minimum and maximum air temperature as well as rainfall were also recorded.

RESULTS

The germinability of *G. flavum* seeds at various temperatures is shown in Fig. 1. Dark germination was restricted to temperatures below 20 °C, where it occurred at a very slow pace, especially at 5 °C. Both a short red light (R) and a 20 d chilling pre-treatment considerably expanded the temperature range of germination (by about 5 and 15 °C, respectively). When a short (30 min) pulse of diffuse daylight was given, instead of the R one, a significant promotion of germination at 20 and 25 °C was also obtained (data not shown), though the effect was reduced in comparison to the corresponding R light pulse.

When the seeds were imbibed in mannitol solutions at 15 °C, in darkness, a significant decrease of germinability was observed as a

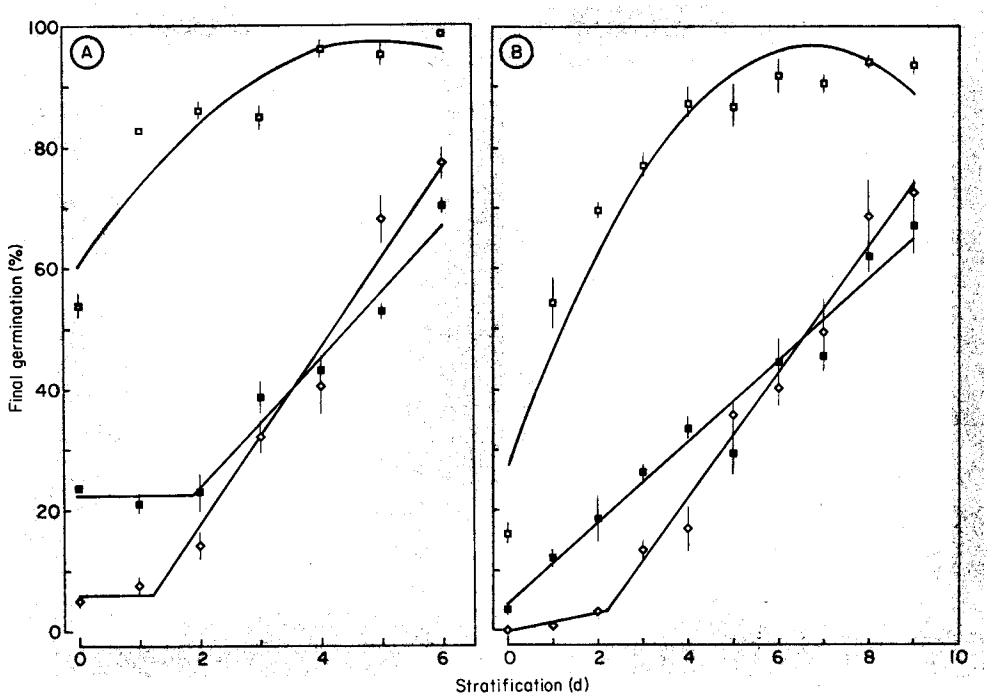

FIG. 3. The photosensitivity of stratified *Glaucium flavum* seeds at 20 A or 25 °C B. Final germination was scored after various stratification periods and in response to either a short (15 mins) red pulse (□) or a short red pulse followed by a short (15 mins) far-red one (◇). The irradiations were given immediately after seeds had been transferred to 20 or 25 °C. Seeds at time O had been left to imbibe for 30 mins at 20 or 25 °C, before being subjected to irradiations. DC (■), dark controls. Vertical bars, 2 s.e.

function of the osmotic potential. Thus in mannitol solutions of 0·1, 0·2, 0·3, 0·4 and 0·5M (with corresponding Ψ_s −0·248, −0·496, −0·744, −0·991 and −1·239 MPa), the final germination dropped to 47·4, 39·4, 19·6, 10·4 and 0·0%, respectively.

At the supraoptimal temperatures 20 and 25 °C, final germination could be considerably promoted by a short R illumination (Fig. 1). Nevertheless, this promotive effect depended upon the length of imbibition time elapsed since the onset of seed hydration. The photosensitivity curves showed a rapidly attained maximum (after 8 and 4 h, at 20 and 25 °C, respectively) and a subsequent gradual decline (Fig. 2). A chilling pre-treatment could also promote germinability at both temperatures, as already shown in Fig. 1. Nearly maximal germination was obtained with either 12 or 20 d of stratification for 20 and 25 °C, respectively, while at the same time a slight, gradual increase of germination rate was observed (Table 1). The promotion brought about by a 20 d chilling treatment persisted both through seed desiccation and a subsequent short storage period. In these two cases, an additional dramatic increase of germination rate was also recorded.

The combined action of light and stratification is shown in Fig. 3. When a R pulse was given immediately after transfer to either 20 or 25 °C, about 4 d of pre-chilling were sufficient to promote maximal germination. On the other hand, a far red (FR) pulse following the R one was fully inhibitory, even to levels below those of the dark controls for the first 2 and 4 d, respectively. The regression curves fitted to the R pulse data are parabolic:

$$Y = 59{\cdot}98 + 14{\cdot}80X - 1{\cdot}47X^2 \quad (r^2 = 0{\cdot}867)\,(20\ °C)$$

and

$$Y = 26{\cdot}91 + 20{\cdot}77X - 1{\cdot}54X^2 \quad (r^2 = 0{\cdot}933)\,(25\ °C).$$

when Y = final germination (%), and X = stratification time (d). The corresponding linear regression equations for D and R + FR germination data are, respectively:

$$Y = 1{\cdot}84 + 10{\cdot}92X \quad (r^2 = 0{\cdot}961)$$

and

$$Y = -12{\cdot}24 + 14{\cdot}87X \quad (r^2 = 0{\cdot}971)\,(20\ °C).$$

$$Y = 4{\cdot}24 + 6{\cdot}69X \quad (r^2 = 0{\cdot}962)$$

and

$$Y = -19{\cdot}42 + 10{\cdot}38X \quad (r^2 = 0{\cdot}979)\,(25\ °C).$$

A dramatic decrease of *G. flavum* germinability

TABLE 1. *Final dark germination and T_{50} values of* Glaucium flavum *seeds after various periods of stratification*

Stratification (days)	Germination temperature (°C)		
	15	20	25
0	92·0 ± 2·1* (15·4)†	32·4 ± 4·3 (8·7)	3·6 ± 1·6 (6·4)
4	92·8 ± 1·9 (11·8)	71·6 ± 2·7 (8·2)	37·6 ± 3·1 (7·4)
8	94·0 ± 2·4 (11·0)	76·8 ± 2·4 (8·0)	57·6 ± 2·2 (5·9)
12	91·6 ± 3·7 (10·4)	84·0 ± 3·9 (6·5)	63·6 ± 4·3 (5·8)
16	92·0 ± 1·5 (9·4)	86·4 ± 1·7 (6·0)	66·0 ± 3·4 (5·8)
20	96·0 ± 1·4 (8·5)	83·6 ± 4·5 (6·3)	83·2 ± 1·9 (5·1)
20 + D‡	—	—	86·0 ± 1·9) (2·9)
20 + D + S	—	—	82·0 ± 2·8 (3·1)

* Germination values are % ± s.e.

† T_{50} values (in parentheses) are given in days and refer only to the germination period after the stratification treatment.

‡ D, Desiccation in darkness at 25 °C for 3 d; S, storage in darkness at 25 °C for 20 d.

TABLE 2. *Final dark germination at 15 °C and T_{50} values of* Glaucium flavum *seeds after various periods of dark incubation (immediately after sowing) at 25 °C*

Incubation period at 25 °C	Final germination (% ± s.e.)	T_{50}* (days)
1 h	40·4 ± 1·7	12·8
2 h	40·4 ± 2·3	13·6
4 h	50·8 ± 4·8	10·4
8 h	35·2 ± 1·4	15·4
12 h	46·0 ± 4·0	16·9
1 d	35·2 ± 5·0	15·0
2 d	37·6 ± 5·2	16·8
3 d	18·0 ± 2·9	14·0
4 d	16·0 ± 3·4	12·3
5 d	17·6 ± 3·1	11·5
10 d	22·8 ± 5·8	7·3
10 d + D†	57·6 ± 3·7	9·8

* T_{50} refers only to the germination period at 15 °C.

† D, Desiccation in darkness at 25 °C for 3 d.

at 15 °C was observed when the seeds had been previously subjected to an initial imbibition period at 25 °C (Table 2). Even 1 h of dark incubation at 25 °C was largely inhibitory, whereas only a partial restoration of germinability was obtained by an intervening desiccation of seeds. This warm temperature effect was fully reversed by both a short R pulse and a rather long chilling treatment (Table 3).

When *G. flavum* seeds imbibed under light and temperature conditions simulating roughly those prevailing in nature during springtime (mid-April) in Greece, germinability was unexpectedly nil while the corresponding dark controls germinated to a maximal level (Table 4). Full manifestation of germination under white or coloured light was again possible with a relative enrichment in red light, resulting in an increase of ζ value to 2·07 or higher. A similar inhibition of germination by 'natural' light was also obtained under late autumn (late November) conditions, as shown in Table 5. By gradually decreasing the total fluence rate (without a substantial change of the ζ value) down to only 11 mW m^{-2}, germination was partially restored. When the ungerminated seeds of Table 5 were eventually transferred to complete darkness (at the same temperature regime), full germination was observed (data not shown) in those seeds previously illuminated with 'white' light, irrespective of the total fluence rate. On the other hand, seeds imbibed under 'blue' and 'green' light (which also contained considerable amounts of far red) germinated very poorly upon transfer to darkness.

The experiment illustrated by Fig. 4 lasted for

TABLE 3. *Final dark germination at 15 °C and T_{50} values of* Glaucium flavum *seeds after various pre-treatments*

Pretreatment	Final germination (% ± s.e.)	T_{50}* (days)
1 d (25 °C)	46·0 ± 4·9	16·6
1 d (25 °C) + R†	90·0 ± 3·1	13·1
1 d (25 °C) + R + FR	29·6 ± 4·1	14·8
1 d (25 °C) + 10 d (3 °C)	81·6 ± 3·8	11·7
1 d (25 °C) + 10 d (3 °C) + R	98·0 ± 1·3	10·3
1 d (25 °C) + 10 d (3 °C) + R + FR	84·4 ± 2·3	10·5
1 d (25 °C) + 20 d (3 °C)	95·0 ± 1·6	11·8

* T_{50} refers only to the germination period at 15 °C.
† R and FR, 15 mins of broad band red and far-red irradiation respectively, at 25 °C.

TABLE 4. *'Spring' final germination of* Glaucium flavum *seeds under various light conditions supplied during the warm period of a diurnally alternating two-temperature regime (14 h (20 °C) 10 h (15 °C))*

Light source*	Filter	Total fluence rate (400–750 nm) W m^{-2}	ζ	Final germination (% ± s.e.)	T_{50} (days)
A	—	15·9	1·26	0·0 ± 0·0	—
A	White glass	8·4	0·94	2·0 ± 0·8	—
A	Red gelatine	2·2	0·77	0·5 ± 0·5	—
A	Gray gelatine	4·3	0·50	0·0 ± 0·0	—
A	Blue glass	1·2	2·07	88·5 ± 1·9	10·0
B	—	7·5	5·86	96·5 ± 1·3	9·8
B	Red Plexiglas	0·6	4·68	87·5 ± 2·2	10·2
B	Blue Plexiglas	1·2	3·40	92·0 ± 1·4	10·2
Dark control				87·6 ± 3·1	11·1

* Light sources are described in Materials and Methods.

110 d. At the beginning (October 31) the official daylength was 10 h 39 min; it gradually decreased afterwards down to 9 h 29 min (on December 22) and increased again up to 10 h 53 min (on February 18). However, the actual daylength was extended by about 1 h of twilight, at both ends of each photoperiod. Rainfall (Fig. 4B) occurred throughout the experimentation period (though November was by far the wettest month) amounting to 281·1 mm precipitation, which is normal for Athens. The air temperature ranged from 3 to 19 °C and the half-weekly fluctuations were, on average, about 6–7 °C (Fig. 4B). Seedling emergence is presented in six separate time courses, each corresponding to a depth of burial (Fig. 4A). Nearly 25 d after the start of the experiment, no seedlings had emerged, while the dark controls imbibing in Petri dishes had already reached almost 100% germination. Shortly afterwards, by the end of November, a rather massive emergence began, and continued quite steadily until about the end of December, when it reached, in most of the curves, its highest level. During the second half of the experiment, from January and onwards, few additional records of seedling emergence were observed. Final emergence levels clearly showed a peaked, and somewhat skewed pattern (Fig. 4C). Although surface germination was minimal a quite abrupt maximum of emergence was scored at a 0·5 cm depth of burial. For seeds buried deeper, seedling emergence was progressively reduced, down to a minimal level at 6 cm deep. Consistently enough, seeds imbibed in Petri dishes alongside the pots (LC in Fig. 4A) germinated only to a very low final level.

DISCUSSION

The temperature range for the germination of *G. flavum* seeds in darkness (Fig. 1) is typically

TABLE 5. *'Late autumn' final germination of* Glaucium flavum *seeds under various light conditions supplied during the warm period of a diurnally alternating two-temperature regime (10·5 h (15 °C)/ 13·5 h (10 °C))*

Light source*	Filter	Total fluence rate (400–750 nm) W m^{-2}	ζ	Final germination (% ± s.e.)	T_{50} (days)
A	—	15·9	1·26	0·0 ± 0·0	—
A	6 mm white Plexiglas	7·8	1·25	0·8 ± 0·8	—
A	12 mm white Plexiglas	3·8	1·28	2·0 ± 0·0	—
A	18 mm white Plexiglas	1·9	1·30	4·8 ± 1·0	—
C	—	3·1	1·00	1·6 ± 0·4	—
C	Blue Plexiglas	0·4	0·02	0·0 ± 0·0	—
C	Green Plexiglas	0·5	0·02	0·4 ± 0·4	—
C	30 mm white Plexiglas	0·525	1·21	8·4 ± 0·7	16·0
C	Dark grey gelatine	0·250	0·93	9·6 ± 1·5	17·4
C	45 mm white Plexiglas	0·090	1·40	21·6 ± 3·2	14·0
C	6 mm white Plexiglass + 1 dark grey gelatine	0·050	0·85	23·2 ± 3·4	16·0
C	6 mm white Plexiglas + 2 dark grey gelatine	0·011	1·36	47·6 ± 3·2	14·8
Dark control				97·6 ± 1·0	24·0

* Light sources are described in Materials and Methods. White Plexiglas filters were multiple layers of 3 mm sheets.

Mediterranean (Thompson, 1973) and this is consistent with the probable origin of the species (Meikle, 1977). Work based on seeds of various Polish provenances (Formanowiczowa and Kozlowski, 1976; Mermerska, 1984) has shown a similar temperature range, but it would be interesting to conduct a more extensive survey of germination characteristics and mechanisms using seeds collected from other parts of Europe.

The ability of *G. flavum* seeds to germinate in mannitol osmotica was found to be weak. This supports the view that the mainly littoral distribution of the species should be considered as the result of its poor capacity for competition against inland species rather than as a halophytic adaptation (Eisikowitch, 1979/1980).

Both the temperature range and the enhancement of germination by chilling and phytochrome activation (and its dependence upon imbibition time) match well the corresponding characteristics of the extensively investigated *Lactuca sativa* cv. Grand Rapids achenes. In addition, the effect of high temperature on the subsequent germination of *G. flavum* seeds at a favourable, lower temperature (Tables 2 and 3) is similar to the so called thermodormancy, also found in Grand Rapids achenes (Bewley and Black, 1982). Though in *Lactuca* a rather higher (30–35 °C) temperature is usually necessary to induce secondary dormancy, this was effectively overcome in both *Lactuca* and *Glaucium* by both stratification and phytochrome activation. The overall ecological importance of this type of secondary dormancy is still not clear. A marked difference in the seed germination properties of these two species, is shown by the considerably slower germination rate of *G. flavum* compared to that of *L. sativa*. The prolonged imbibition period prior to germination of *G. flavum* might be of ecological value, by preventing response to brief periods of rain which often occur at the beginning of the wet season in Mediterranean climates, thus ensuring that germination and establishment occur well into the wet season, in late autumn.

Seeds in which germination is either promoted by or is indifferent to light tend to show optimal seedling emergence from seeds buried in the top few mm of the soil, being progressively less from deeper seeds (e.g. Frankland and Poo, 1980; Bewley and Black, 1982). Recent work has shown that in most of the species studied, seed germination was generally unaffected by light below 4–6 mm of sand (Bliss and Smith, 1985). 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).

The seeds of the psammophyte *Artemisia mono-*

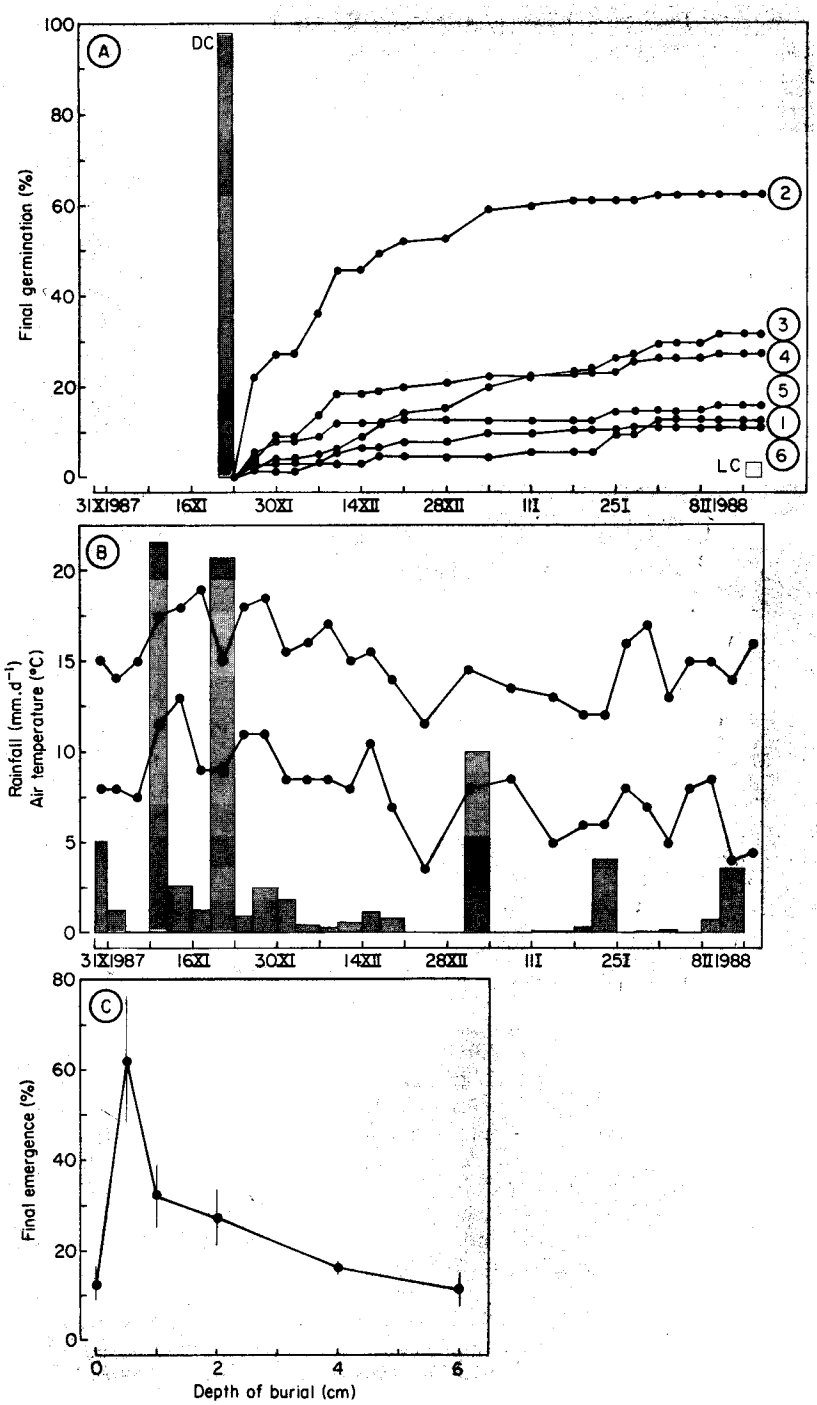

FIG. 4 (A). The time course of *Glaucium flavum* seedling emergence from seeds buried at different depths. Curves 1–6 correspond to depths of 0, 0·5, 1, 2, 4 and 6 cm. DC and LC bars represent final germination level for seeds imbibed in Petri dishes and kept alongside the pots, either in complete darkness or exposed to natural light alternation, respectively. (B) Air temperature (fluctuations of minimum and maximum values) and rainfall data (histogram) recorded for the whole experimentation period. (C) Final germination levels of *Glaucium flavum* seeds buried beneath different depths of sand and exposed to natural conditions for 100 d. Vertical bars, 2 s.e.

sperma have an absolute light requirement which prevents germination at depth. On the other hand, it has been suggested that the surface of the sand, where light is available, might present great hazards for newly germinated seedlings, due to rapid evaporation and large temperature fluctuations. Thus it was presumed that germination of shallowly buried seeds would be strongly favoured (Koller, Sachs and Negbi, 1964). This has been shown to occur in the light requiring achenes of *Senecio jacobaea* sand-dune populations. A thin covering of sand (1–2 mm) strongly stimulated germination compared to uncovered achenes, a sand layer of more than 4 mm imposed an enforced dormancy (Van der Meijden and Van der Waals-Kooi, 1979). In *G. flavum*, partial germination occurred when the total fluence rate was about 10 mW m^{-2} (Table 5), this value being less than 10^{-3} of the daylight actually experienced at the surface of the sand (experiment of Fig. 4). A sand layer of 5 mm was found to transmit about 10^{-4} of the incident light and it seems that when reduced to 10^{-3}–10^{-4} of daylight fluence rate, light was no more inhibitory to seed germination.

The dual action of white light ('daylight') on seed germination of the yellow horned-poppy is of particular interest. A short pulse (30 mins) of daylight could promote germination at supra-optimal temperatures (20 and 25 °C) considerably. On the other hand, daylight was completely inhibitory when given for either 14 or 10·5 h daily, during the warmer periods of the two-temperature regimes used (20/15 and 15/10 °C, respectively). Moreover, the prolonged irradiation effect was clearly shown to be both wavelength and fluence rate dependent (Tables 4 and 5). This differential white light action has been attributed to both the establishment of a particular amount of phytochrome in its active, P_{fr}, form and the rate of 'cycling' between P_r and P_{fr} forms (Bartley and Frankland, 1982).

In the present work, a surface-avoiding mechanism based on light-inhibited seed germination is clearly revealed for the first time (Tables 4 and 5, Fig. 4). This type of mechanism had been previously suggested from indirect evidence, such as that seed germination in *Nemophila menziesii* normally occurred at or just below the soil surface (Cruden, 1974), and that daylight inhibited seed germination in certain genetically nondormant lines of wild oats, (Sawhney, Hsiao and Quick, 1986). A third indirect piece of evidence was provided by Thompson, Grime and Mason (1977) who showed that when seeds of *Agropyron repens* and *Poa pratensis* were exposed to rather large daily fluctuations of temperature, dark germination was higher than in light and this fact led to the postulation of a mechanism that delays germination until after burial of seeds in the soil.

Seed germination at the soil surface is completely inhibited by daylight though no dormancy is eventually imposed; thus, seed germination occurs readily on subsequent cover. In contrast, when seeds imbibe at the soil surface under a dense leaf shade, secondary dormancy is enforced. Germination and eventual seedling establishment are strongly promoted by shallow burial and a possible reason why the coarse-sandy and shingle habitats frequently colonized by yellow horned-poppies are preferred may be because the cracks existing at the soil surface provide safe germination sites. The light-mediated surface-avoiding mechanism is of evident adaptational value, especially in the seashore or sandy habitats, for the successful seedling establishment of yellow horned-poppy.

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