Dual Action of White Light in the Photocontrol of Germination of Oryzopsis miliacea [1,2]

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The control of germination in *Oryzopsis miliacea* exhibits a dual action of white light, promotive on the one hand and inhibitory on the other. Thus, while a short-irradiation treatment was promotive under all temperature conditions, continuous irradiation was less promotive, or even inhibitory in certain temperatures (11). A similar phenomenon was observed in *Amaranthus fimbriatus* (13), *Atriplex dimorphostegia* (9), *Amaranthus blitoides* (7), and *Nigella damascena* (6). Seeds exhibiting such behavior have been considered by certain investigators as short-day types (1, 5), in accordance with the accepted definitions of the photoperiodically controlled flowering types.

White light was used in the previous work (11). In view of the widespread occurrence of the phytochrome pigment system in seeds (2, 14), it was decided to determine whether this pigment system was involved in this dual action of white light. The involvement of blue light in this phenomenon was also tested, since it is known to be active in the photocontrol of germination (4, 10).

Materials and Methods

Material used in this study was collected from a stand of *Oryzopsis miliacea* Asch. et Schw. in Eithanim (Judaean Hills) on July 1, 1961, and on July 1, 1962. This material was treated with 70% v/v H_2SO_4, as described earlier (11). The material from these 2 collections differed in its quantitative responses, but behaved in the same manner qualitatively.

The light sources were incandescent (tungsten-filament) lamps and/or cool-white fluorescent tubes. When the light source was mixed, three 40-w incandescent lamps and five 40-w fluorescent tubes were used. Separation of spectral regions was usually carried out by use of colored cellophane filters, after passing the light through a 1-cm-thick layer of $CuSO_4$ solution (0.2 of saturation), or through a similar layer of water. Transmittance of the filters used was measured with a Unicam Spectrophotometer in the range of 400 to 800 mμ (fig 1)[3]. Light intensity was measured by a Weston Illumination Meter Model 756.

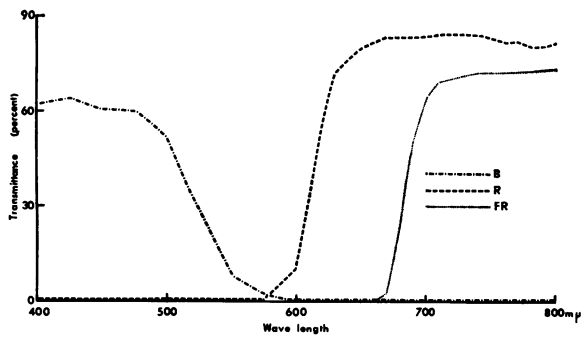

FIG. 1. Spectral properties of filter systems used in this work. B, blue system; R, red and far-red system; FR, far-red system.

Germination was tested in petri dishes of 5 or 9 cm diameter, containing 1 layer of Whatman No. 1 filter paper and 2.5 or 4 ml of double distilled water. In all dark treatments the dishes were enclosed in light-proof cans. Incubators controlled at ±1° were used. The results are given in mean germination percentages ± S.E. of 4 replicates of 75 to 125 seeds each.

Results

The Short-irradiation Effect. Irrespective of time of application, between 60 and 120 seconds of R was a saturating dose in the promotion of dark germination at 25° (fig 2). Similarly, 4 minutes of FR irradiation were sufficient to reverse completely the full promotion by R (table I). Consequently, 4 minutes R and 12 minutes FR were used, except when specified otherwise. The effects of R and FR were also mutually reversible, and the final germination percentage was determined by the last irradiation applied (table II). A short irradiation with FR, and continuous irradiation with white light reversed the promotion by R, and the degree of reversal became less with increasing duration of the dark interval between the promotive and inhibitory irradiations. When R was followed by continuous irradiation with white light, germination never exceeded that induced by R alone. When, on the other hand, R was followed by FR, after a sufficiently long dark interval,

[1] Received July 18, 1963.

[2] Supported by Research Grant FG-Is-115, from the United States Department of Agriculture.

[3] Abbreviations: B, blue light; R, red and far-red; FR, far-red radiant energy.

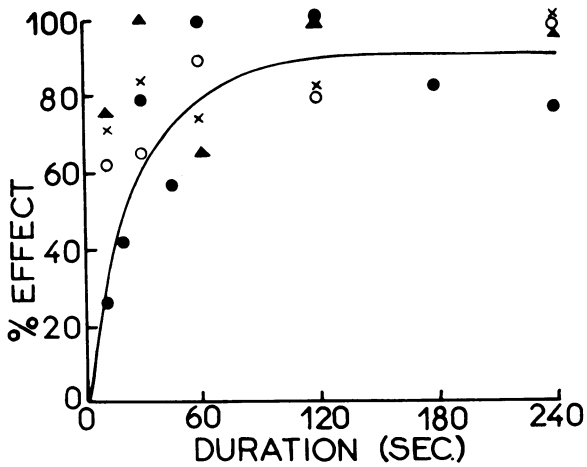

FIG. 2. Effectiveness of red radiant energy in the promotion of germination at 25°, as affected by duration of irradiation. Effect calculated as percent of maximal response. Results of 4 experiments. Incandescent light source, 250 ft-c at filter level. Irradiation applied after 9.5(●), 16(o), 12(▲) and 40(×) hours of dark incubation.

additional promotion occurred (table III). This increase may be due to a promotive effect of FR in later stages of incubation (cf fig 3B).

In some photoblastic seeds, short irradiations with blue light were found to reverse the promotive effects of R (3, 15). In seeds of *O. miliacea*, short irradiations of 10 or 30 minutes with B did not have any inhibitory effect if applied at different times during dark incubation, up to 96 hours. Similarly, 12 minute irradiations with B were also ineffective in modifying the promotive effect of R, when applied immediately after R, or after various dark intervals (up to 240 hr).

Changes in Sensitivity to Short Irradiations of Different Spectral Composition, as a Factor of Time of Incubation. The sensitivity towards R irradiations started after 45 minutes, and rose till the 15th hour reaching almost the maximal promotion by the 24th hour. Promotion by R remained high during the 96 hours of the experiment (cf table VI, ref 11). FR irradiation inhibited dark germination if applied during the first 8 hours, but became increasingly promotive up to the 48th hour and remained more or less constant up to the 96th hour (fig 3).

Table I

Reversal by Far-red of Red promotion

Irradiation treatment was applied 24 hours after start of incubation. Between the successive irradiations there were no dark intervals.

Irradiation (min)		Final germination % at 25°
Red	Far-red	
4	0	80 ± 2
4	4	33 ± 3
4	12	33 ± 2
4	36	34 ± 5
0	0	39 ± 5

Table III

Inhibition by a Short Irradiation with Far-red and by Continuous Irradiation with Unfiltered White Light, of Seeds Promoted by Red Light, as Affected by Duration of Intervening Dark Interval

Seeds incubating in darkness at 20° were irradiated after 48 hours for 4 minutes with red light from a fluorescent lamp of 300 ft-c intensity at filter level. The second irradiation was either 12 minutes of far-red light, or continuous irradiation with unfiltered light, in both cases from fluorescent and incandescent lamps. The intensity at filter level was 200 ft-c.

Dark interval between irradiation treatments (hrs)	Final germination %	
	Expt. I (Far-red)	Expt. II (continuous white light irradiation)
0	28 ± 5	12 ± 5
0.5	39 ± 2	10 ± 2
2.5	...	26 ± 3
4	48 ± 5	...
24	52 ± 6	22 ± 3
48	62 ± 4	40 ± 3
72	73 ± 5	56 ± 3
96	76 ± 6	62 ± 4
120	88 ± 3	64 ± 1
144	89 ± 3	62 ± 5
Controls = Red only uninterrupted darkness	72 ± 2	71 ± 6
	25 ± 5	5 ± 2

Table II

Mutual Repeated Reversibility of Promotion by Red and Inhibition by Far-red Irraditions in Control of Germination

Seeds incubated in darkness at 20° were irradiated after 24 hours with red light (R, for 4 minutes) and with far-red (FR, for 12 minutes). Successive irradiations were given without dark interval. The light source was incandescent lamps, providing 220 ft-c at filter level.

Treatment	Germination %	Treatment	Germination %
Dark controls	13 ± 1		
R	50 ± 5	FR	8 ± 3
R → FR → R	44 ± 5	R → FR	7 ± 3
R → FR → R → FR → R	46 ± 3	R → FR → R → FR	15 ± 4
R → FR → R → FR → R → FR → R	45 ± 6	R → FR → R → FR → R → FR	13 ± 2

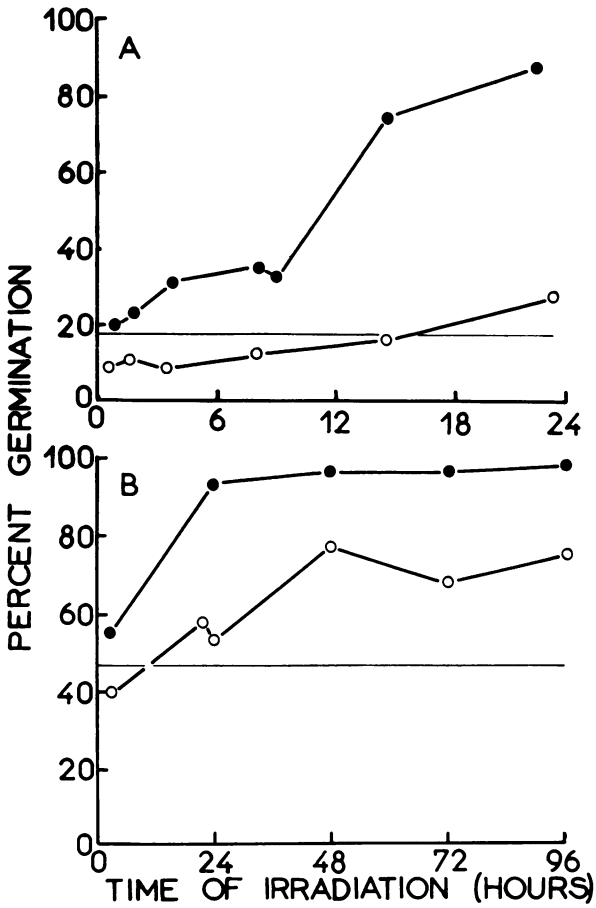

FIG. 3. The effects of single irradiations with red (●, 4 min), or far-red (o, 12 min) light on dark germination at 25°, as affected by time of application, during the first 24 hours (experiment A) and 96 hours (experiment B) of dark incubation. Incandescent light source, 220 ft-c at filter level. Fine horizontal line indicates level of controls in darkness throughout.

Further experiments showed that the incomplete inhibition of dark germination by FR during the first hours of incubation was not due to nonsaturation, since 30-minute irradiations were not more effective than 15-minute ones, when applied 20, 100, 180, and 220 minutes after the start of incubation.

Irradiations of 10 minutes with B alone, which were applied at various times during the first 96 hours of incubation in darkness were found ineffective.

The promotive effects of short irradiations with FR, when applied during the later hours of dark incubation, were not a result of impurities in the light transmitted by the FR filters. The increase in stimulation by short irradiations with FR, as duration of the preceding dark period increased, occurred also with pure FR light transmitted by interference filters. Moreover, this increase parallelled that of the stimulatory effect of short irradiations with R (table IV).

Effects of Continuous Irradiation with White Light. The inhibitory effects of continuous irradiation with white light lasted only as long as the seeds were exposed to it. Moreover, when seeds were transferred from white light to darkness, germination was higher than in continuous darkness or in continuous irradiation with white light (table V). This indicated that white light promoted germination in all cases, but the expression of this promotive effect required darkness. This promotive effect of white light, which expresses itself in subsequent darkness, manifested itself also in many other experiments where the light source was incandescent and thus relatively high in FR. Thus, the FR present in white light did not prevent the latter from stimulating subsequent dark germination, though long irradiations with FR alone were extremely inhibitory (cf table X). Darkness requirement for expression of the promotive effects of long irradiations with white light was evident also from the following results. The promotive effects of a 24-hour light period were the same when given either from the start of imbibition or after 1 or 2 days of previous darkness, provided a dark period of 6 days followed the light period (table VI). The slight promotion by 7 days of white light (6 + 1), when started after 2 days in darkness, was probably due to the fact that by the time light was applied some of the dark germinating seeds were no longer susceptible to inhibition by continuous irradiation. These experiments were performed with

Table IV

Effects of a Single Irradiation with Red and Far-red Light, Transmitted by Interference Filters, on Dark Germination at 17°, as a Function of Time of Application

Interference filter*	Irradiated for 4 minutes on indicated hour of dark incubation	
	24	47
Red (664 mμ)	77 ± 4	92 ± 2
Far-red (736 mμ)	45 ± 4	62 ± 4
Nonirradiated controls	... 28 ± 2	...

* Balzers, Lichtenstein. Half width 10 mμ. Light source: 300-w slide projector.

Table V

Effects of Duration of Initial Irradiation with White Light on Subsequent Germination in Darkness

Seeds incubating at 20° were irradiated with unfiltered light from a fluorescent tube, providing 20 ft-c at dish level.

Initial duration of light (days)	Germination % 9 days after transfer to darkness
0	18 ± 1
1	54 ± 4
3	50 ± 2
6	48 ± 6
Controls: 15 days light	17 ± 3
15 days dark	22 ± 2

Table VI

Effects of 24 Hrs of White Light on Germination, as Affected by Duration of Initial Dark Period and by Subsequent Light or Dark

Seeds incubating in darkness at 22° were exposed at different times to unfiltered white light for 24 hours and were either returned to darkness, or remained in light for 6 more days. The light source was fluorescent tubes, which provided 75 ft-c at dish level.

Initial dark period (days)	Germination induced by 24 hours of irradiation when followed by	
	6 days light	6 days dark
0	37 ± 3	97 ± 1
1	27 ± 2	95 ± 1
2	45 ± 2	96 ± 1
Controls: 8 days in dark	... 39 ± 2	...

the whole seed population: the dark germinators as well as the light-requiring seeds. Isolation of the light-requiring seeds was made by removal of the seedlings which had germinated at 20° during 5 days incubation in darkness (about 45%). Of these seeds, 33 ± 3% germinated during 7 days exposure to continuous irradiation from a white fluorescent light source (100 ft-c at dish level) and 96 ± 1% germinated 6 days after a 24-hour exposure to irradiation from the same source. Controls in darkness for 12 days reached 47% germination.

The promotive effects of long irradiation with white light on subsequent germination in darkness could be entirely reversed by a short irradiation with FR, if applied immediately before transfer of the seeds from the white light to darkness. Moreover, the germination resulting from such a treatment was lower than that of controls in continuous darkness (table VII).

Table VII

Effects of Short Irradiation with Far-red light on the Germination Induced by a Preceding 48 hours of Irradiation with White Light

Seeds incubating at 21° in unfiltered white light for 48 hours were transferred to darkness, either immediately, or after 15 minutes exposure to far-red radiant energy. The light source was mixed, from fluorescent and incandescent lamps, which provided 100 ft-c at filter level.

Treatment	Experiment I	Experiment II
Controls continuously in darkness	15 ± 2	16 ± 2
48 hr irradiation → dark	30 ± 2	34 ± 4
48 hr irradiation → far-red → dark	2 ± 0	2 ± 1

Comparing the effects of a long and a short irradiation with white light on subsequent germination in darkness, showed that the course of germination after the latter treatment was parallel to, but consistently higher than after the former treatment (table VIII).

Inhibition by Continuous Irradiation of Seeds Promoted by Long Irradiation with White Light. Seeds whose dark germination was promoted by a preceding long irradiation with white light could be reinhibited by a subsequent continuous irradiation from the same source. Seeds were exposed to an initial 48-hour irradiation with unfiltered white light (mixed fluorescent and incandescent source, 100 ft-c at dish level), after which they were transferred to darkness for 24 and 48 hours, and returned to white light. Controls in light and darkness germinated up to 2 ± 1% and 27 ± 2%, respectively. Seeds exposed only to the initial 48-hour irradiation germinated up to 58 ± 2% in the subsequent dark period. When the second irradiation was separated from the initial one by 24 and 48 hours of darkness, germination reached 9 ± 1% and 20 ± 2%, respectively, in the second light period. At time of transfer to the second light period, the percentages in these 2 treatments were 4 ± 2 and 8 ± 1, respectively. It was clear that a return to light after less than 48 hours of intervening darkness inhibited germination of some of the seeds which had been induced by the first light period. The fact that germination continued even in the second light period, indicated that in the intervening dark period some of the induced seeds had reached a stage at which they could no longer be inhibited by light, but still required time for final expression of germination.

Effects of Continuous Irradiation with Separate Spectral Regions. Continuous irradiation with B was more inhibitory than with white light, while with R it was promotive (table IX). Continuous irradiation with FR was also more inhibitory than with white light. Very low energies of B and FR were already inhibitory (table X). Though B in tables IX and X contained some FR, further experi-

Table VIII

Comparative Effects of Short and Long Irradiation with White Light on Course of Subsequent Dark Germination

Seeds incubating at 20° were irradiated with unfiltered white light, either for 44 hours from the start of incubation, or for 10 minutes after 44 hours of darkness. Light source was mixed, from fluorescent and incandescent lamps, which provided 100 ft-c at dish level. Counted dishes were discarded.

Treatment	% germination on indicated day of incubation			
	3	5	7	9
44 hours light → dark	2 ± 2	32 ± 3	61 ± 5	61 ± 4
44 hours dark → 10 minutes light → dark	5 ± 2	43 ± 4	69 ± 2	77 ± 4
Controls continuously in dark	...	...	...	36 ± 5

Table IX

Effects of Continuous Irradiation with White, Red, and Blue Light on Germination

Type of irradiation*	Final germination %	
	20°	25°
White (unfiltered)	7 ± 3	10 ± 4
Blue (+ far-red**)	0	0
Red (+ far-red**)	76 ± 5	80 ± 1
Dark control	46 ± 3	10 ± 5

* Fluorescent source, 200 ft-c at 20°, 100 ft-c at 25°, measured at filter level.

** Far-red present only in small amount, since light source was fluorescent.

ments (cf table XII) showed that continuous irradiation with B alone was as inhibitory as with FR alone, thus indicating that the inhibitory activity of B does not depend on synergism with FR. The inhibitory effects of long irradiation with B are in contrast with the ineffectiveness of short irradiations with B.

Kadman-Zahavi (8) had found that a short irradiation with white light, given after long exposure to a mixture of FR and B, failed to induce complete germination in *Amaranthus retroflexus*. This effect was studied also with *O. miliacea*. Seeds which had not been pretreated with B were almost fully promoted by the short irradiation, while those pretreated with B were only partially promoted (about 50%),

Table X

Effects of Continuous Irradiation with Far-red and with a Mixture of Blue and Far-red Light of Different Intensities on Germination at 26°

Light intensity at filter level (ft-c)*	Germination % in	
	Far-red	Blue + far-red
100	2 ± 0	0
20	8 ± 0	1 ± 1
5	10 ± 2	6 ± 2
Dark controls	... 22 ± 3	...

* Light source: incandescent lamp.

Table XII

Inhibition by Blue and Far-red Irradiations of Subsequent Dark-germination as a Function of Duration of the Light Period

Seeds incubating at 20° were irradiated for various periods from the start of incubation, with filtered light from a source of mixed fluorescent and incandescent lamps, which delivered 100 ft-c at filter level.

Days initial irradiation	Germination % after irradiation with	
	Blue	Far-red
1	11 ± 1	6 ± 2
2	3 ± 2	1 ± 0
3	1 ± 0	2 ± 0
4	0	2 ± 0
Dark Control	.... 18 ± 3	....

in comparison with B pretreated seeds which were not exposed to a short irradiation (table XI). Similar results were obtained with seeds exposed to FR for 3 days. When these seeds were exposed to 15 minutes of white light on the 7th day (after 4 more days in darkness), 40 ± 3% of them germinated. FR irradiated seeds which were not exposed to a subsequent short irradiation gave 4 ± 0% germination, and those which were not exposed to FR, but only to a comparable short irradiation, germinated 88 ± 3%.

The effectiveness of B, or FR, as a function of duration of application, in inhibiting dark germination was studied. Two days of irradiation with either B or FR inhibited practically all germination (Table XII).

On the basis of these experiments it appears as if continuous irradiation with FR and with B were inhibiting the dark-germinating seeds. Continuous FR irradiation did not promote any of the light-requiring seeds. Thus, seeds incubating in darkness for 5 and 11 days germinated 16 ± 3% and 12 ± 1%, respectively, while seeds exposed to FR radiant energy (from a mixed fluorescent and incandescent light source, 150 ft-c at filter level) for 6 days, after 5 days in darkness, germinated 17 ± 2%.

Table XI

Promotion by a Short Irradiation with White Light, of Seeds Previously Inhibited by Darkness or by Long Irradiation with Blue Light

Seeds which had not germinated after 5 days exposure to blue light, or to darkness (remaining from experiment summarized in table IX) were irradiated for 15 minutes with unfiltered white light from a fluorescent lamp (200 ft-c at dish level) and returned to darkness.

Treatment	Germination %	
	20° 2 days after irradiation	25° 3 days after irradiation
5 days dark → short irradiation → dark	95 ± 1	97 ± 2
5 days blue (+ far-red*) → short irradiation → dark	51 ± 5	49 ± 3
5 days blue (+far-red*) → dark	0	0

* FR present only in small amounts, since light source was fluorescent.

This contrasted with the effects of a short irradiation with FR, which promoted germination of such seeds, when applied during the later stages of dark incubation (cf fig 3B).

Discussion

The results in tables I, II, and III and figure 2 prove the existence of the phytochrome pigment system in seeds of *O. miliacea*, and show clearly that this pigment system is responsible for the stimulating effects of a short irradiation with white light. Presumably, the balance of the phytochrome remains in the promotive P_{fr} [The symbols P_{fr} and P_r represent the 2 forms of phytochrome, according to the accepted terminology (2, 14).] form when the white light is extinguished.

Response to a short irradiation with R increases with progress of incubation in darkness (fig 3, table IV). Obviously, such an irradiation acts only on the light-requiring fraction of the seed population. Therefore, the increase in response with time may be due to gradual activation of the P_r system from an inactive form or precursor. The response to a short irradiation with FR, on the other hand, changes from inhibition in the early hours to promotion in the later hours of dark incubation. The inhibition by a short irradiation with FR is obviously related only to the dark-germinating seeds. Thus it must be the light-requiring fraction of the seed population which is promoted by FR. These considerations point to the conclusion that the spectral region in which P_r absorbs is sufficiently wide to include part of the region in which our FR filters transmit (fig 1, table IV), and that in addition the equilibrium state favors P_{fr}. The phytochrome in the dark germinators is in the P_{fr} form (2, 14). During the early hours of incubation, relatively little P_r has been activated in the light requirers. Consequently, a short irradiation with FR will inhibit more dark germinators than it will promote light requirers. The situation changes with advancing incubation, inasmuch as more and more of the dark germinators will have started the light-irreversible terminal process of germination, and more and more light requirers will have developed P_r and will have consequently increased their promotive response to the FR absorbed by the P_r.

Continuous irradiation with white light is inhibitory, reducing germination below that of the dark controls. The spectral analysis of the effects of continuous white light (tables IX–XII) has shown that continuous irradiation with FR or B is completely inhibitory, while R is always promotive (tables IX, X, XII). Yet long irradiation with white light becomes as promotive as short irradiation (in comparison to nonirradiated controls), when followed by darkness (tables V, VI, VIII). A short irradiation with FR completely reverses the promotion of dark germination induced by a preceding long irradiation with white light (table VII). It thus appears that when the seeds are transferred to darkness from continuous irradiation with white light, the balance of phytochrome remains in the promotive P_{fr} form as is the case with the short irradiation with white light. It seems likely that the continuous presence of R with the B and FR in white light maintains the P_{fr} form of phytochrome, while continuous presence of B and FR prevents P_{fr} from initiating the light-independent terminal process of germination.

The promotion of dark germination by a preceding light period can also be reversed by a return to continuous light (table III). It seems likely that both inhibitions act on seeds in which the phytochrome is in the P_{fr} form. However, the reversal by short FR seems to differ from the one by long white light (which is presumably due to its B and FR content). It is likely that the former operates merely by transforming P_{fr} back into the inactive P_r, while the latter causes a more profound inhibition, as is evident from the incomplete repromotion by a short irradiation (table XI). The nature of this difference is being investigated.

Three of these phenomena indicate the participation of an additional pigment system in the photocontrol of germination in *O. miliacea*. First, continuous FR is entirely ineffective in promoting germination of the light-requiring fraction, while a short irradiation with FR becomes more and more promotive with progress of incubation (fig 3). The dark germinators, however, are inhibited by both types of FR treatment. Secondly, short irradiations with B have no discernible effects on germination, while long ones are highly inhibitory to seeds whose phytochrome is in the P_{fr} form. Lastly, the inhibitory responses to continuous FR bear a striking resemblance to those of continuous irradiation with B (table XII). Though a comprehensive study of the action spectrum of these inhibitory irradiations was not carried out, it is suggested that the additional pigment system is similar to the high energy B-FR system postulated by Mohr (12). In the present case, the B-FR system operates antagonistically to the phytochrome system, blocking the activity of P_{fr}. This is similar to the antagonistic action of the 2 pigment systems in the formation and straightening of the plumular hook of the lettuce seedling (12).

Summary

Germination of seeds of *Oryzopsis miliacea* Asch. et Schw. is inhibited by continuous light and promoted by a short irradiation. This dual action of light was investigated by spectral and kinetic analysis.

The promotive effects of short irradiations operate through the phytochrome system, the equilibrium favoring the promotive far-red absorbing form of the pigment (P_{fr}). However, the response to short irradiations with far-red light changed from inhibition in the early hours of incubation, to promotion in the later hours. Whereas the inhibitory short irradiations with far-red light were acting on the dark-germinating fraction of the seed population, the promotive ones were acting on the light-requiring

fraction, in which the red-absorbing form of the pigment (P_r) was being gradually activated. This stimulating effect of far-red radiant energy is attributable to a probable wide absorption of P_r, which could be activated by part of the light transmitted by the far-red filters used.

The inhibitory effects of continuous irradiation with white light were traced to the presence in it of the blue and far-red regions. Continuous irradiation with blue and far-red light prevented subsequent germination in darkness, while continuous irradiation with white light prevented germination only as long as it was applied, and caused promotion if followed by darkness. This promotion could be reversed by a short irradiation with far-red light as well as by continuous white irradiation. This indicates the possibility that presence of red in white light is preventing the inhibition induced by its blue or far-red spectral regions, leaving most of the phytochrome system in the P_{fr} form. At the same time, presence of blue and far-red in the white light is preventing the realization of the promotive action of P_{fr}.

It is suggested that an additional pigment system is participating in the photo-control of germination in this species, namely the high-energy blue-far-red system.

Acknowledgments

The authors wish to express their gratitude to Mrs. B. Tamari and Miss E. Rushkin for their technical assistance. Thanks are also due to Prof. M. Evenari for his stimulating discussion and criticism.

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