Studies on the Light Controlling Photoperiodic Induction of *Pharbitis Nil*. II. Effect of Far-red Light Preceding the Inductive Dark Period

by Atsushi TAKIMOTO* and Katsuhiko IKEDA*

滝本 敦*・池田勝彦*：アサガオの花芽形成を支配する光条件について，
II. 暗期前に与えた近赤外光の影響

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It has been reported in a previous paper that *Pharbitis* seedlings fail to flower if 8 hours of incandescent light of low intensity precedes the inductive dark period and that this flower inhibitory effect of the incandescent light is attributable to the action of the far-red light included in it¹⁾. Recently Nakayama reported a flower inhibitory effect of far-red light given just before the dark period in *Pharbitis* seedlings of a strain which differs from our material²⁾. A flower promoting effect of far-red light preceding the dark period was reported by Borthwick *et al.* in *Xanthium saccharatum*³⁾. In order to find the cause of these quite opposite results, the present investigation was undertaken.

Material and Methods

Seedlings of *Pharbitis Nil*, strain "Violet", were used as material. The experimental methods employed were similar to those reported in a previous paper¹⁾.

Experimental results

1) Effect of far-red light preceding the dark period upon flowering responses.

i) Plants were exposed to far-red light of 60 kiloerg/cm.²/sec. (700-1000 m μ) for various hours and subsequently given a 16-hour dark period, which is fully effective for floral induction.

Results represented in Table 1 indicate that the far-red light prevented floral initiation. Experiments were performed several times with similar results. The flower inhibitory effect of the far-red light increased with increasing duration of the irradiation and became striking with 8-hour irradiation.

ii) Plants were exposed to far-red light of 60 kiloerg/cm.²/sec. for various hours and subsequently given a 12-hour dark period, which is not so inductive as to bring

* Laboratory of Applied Botany, Faculty of Agriculture, Kyoto University, Kyoto, Japan.
京都大学農学部応用植物学研究室

Table 1. Effect of far-red light preceding a 16-hour dark period upon flower initiation of *Pharbitis* seedlings.Intensity of far-red light: 60 kiloerg/cm.²/sec.

(Treated on Nov. 26, and dissected on Dec. 23, 1957)

Treatment	No. of plants dissected	% of plants with flower buds	No. of flower buds per plant	% of plants with terminal flower bud
16hd	18	100	4.8	100
5'FR→16hd	22	100	3.5	31.8
1hFR→ "	30	93.3	2.1	0
2hFR→ "	42	95.2	2.2	0
4hFR→ "	38	97.4	2.3	0
8hFR→ "	38	8.0	0.1	0

5'FR→16hd: 16-hour dark period preceded by 5 minutes' far-red light.

1 hFR→16hd: 16-hour dark period preceded by 1-hour far-red light.

These abbreviations will be used hereafter.

about the maximum flowering responses. Experiments were repeated several times, and gave similar results in all cases. Some of the results are shown in Table 2. An unexpected result is the flower promoting effect of the far-red light of short

Table 2. Effect of far-red light preceding a 12-hour dark period upon flower initiation of *Pharbitis* seedlings.Intensity of far-red light: 60 kiloerg/cm.²/sec.

(Treated on May 9, and dissected on May 26, 1958)

Treatment	No. of plants dissected	% of plants with flower buds	No. of flower buds per plant	% of plants with terminal flower bud
12hd	21	14.3	0.1	0
30'FR→12hd	29	51.7	0.6	0
2hFR→ "	26	96.2	1.6	0
4hFR→ "	28	100	1.8	0
8hFR→ "	29	0	0	0

duration. When the duration of the far-red irradiation was less than 4 hours, flowering was promoted in all cases. But if the far-red irradiation was given for 8 hours it inhibited flowering completely. Why the far-red light of 4 hours or less inhibits flower initiation when followed by a 16-hour dark period, but promotes when followed by a 12-hour dark period will be discussed later.

iii) Plants were exposed to 8 hours of far-red light of various intensities and subsequently given a 16-hour dark period. Results are presented in Table 3. All plants which were not exposed to the far-red light initiated terminal flower buds, whereas the plants exposed to 8 hours of far-red light of 100-5000 erg/cm.²/sec. initiated no flower bud. Even with only 10 erg/cm.²/sec., flowering was inhibited heavily; that is, only 78 % of the plants initiated flower buds, and no plant initiated

Table 3. Effect of the intensity of far-red light preceding a 16-hour dark period upon flower initiation of *Pharbitis* seedlings. Far-red light of various intensities was given for 8 hours preceding the 16-hour dark period.

(Treated on June 17, and dissected on July 3, 1958)

Energy of far-red light in erg/cm. ² /sec.	No. of plants dissected	% of plants with flower buds	No. of flower buds per plant	% of plants with terminal flower bud
5000	40	0	0	0
1000	40	0	0	0
400	39	0	0	0
200	40	0	0	0
100	40	0	0	0
50	39	7.7	0.1	0
20	40	30.0	0.3	0
10	41	78.0	0.9	0
Control				
16bd	39	100	4.1	100
24bd	40	100	4.7	95.0

a terminal flower. Thus far-red light of very low intensity inhibits flowering if it precedes the inductive dark period.

2) Effect of red light preceding the inductive dark period.

Plants were exposed to red light of 3000 erg/cm.²/sec. for various hours, and subsequently given a 16- or 12-hour dark period. Results are shown in Table 4.

Table 4. Effect of red light preceding 12- and 16-hour dark periods upon flower initiation of *Pharbitis* seedlings.

Intensity of red light: 3000 erg/cm.²/sec.

(Treated on Jan. 15, and dissected on Feb. 7, 1958)

Treatment	No. of plants dissected	% of plants with flower buds	No. of flower buds per plant	% of plants with terminal flower bud
16bd	22	100	3.9	77.3
1'R→16bd	21	100	4.4	100
5'R→ "	21	100	4.4	90.5
30'R→ "	20	100	3.9	60.0
2hR→ "	21	100	4.2	66.7
4hR→ "	20	100	4.4	95.0
12bd	18	50.0	0.5	0
1'R→12bd	21	38.1	0.5	0
5'R→ "	23	8.7	0.1	0
30'R→ "	20	30.0	0.3	0
2hR→ "	20	65.0	0.8	0
4hR→ "	22	77.3	1.0	0

R: red light

The red light has little effect on floral initiation whether a 16- or 12-hour dark period follows. Similar results were obtained in several repetitions of the experiment.

3) Reversible effect of red light on the flower inhibitory effect of far-red light preceding the inductive dark period.

Plants were exposed to far-red light of 60 kiloerg/cm.²/sec. for 8 hours and subsequently given 0, 1, 5, 30 and 120 minutes of red light of 3000 erg/cm.²/sec. followed by a 16-hour dark period.

Table 5. Reversible effect of red light upon flower inhibition of far-red light preceding the inductive dark period.

Intensity of far-red light (FR): 60 kiloerg/cm.²/sec.

Intensity of red light (R): 3000 erg/cm.²/sec.

(Treated on Apr. 18, and dissected on May 7, 1958)

Treatment	No. of plants dissected	% of plants with flower buds	No. of flower buds per plant	% of plants with terminal flower bud
16hd	20	100	4.8	100
8hFR—→16hd	21	9.5	0.1	0
" →1'R→ "	20	70.0	1.0	0
" →5'R→ "	19	100	2.9	15.8
" →30'R→ "	18	100	2.6	5.6
" →2hR→ "	14	92.9	2.1	7.1

As shown in Table 5, the red light can reverse the flower inhibitory effect of the far-red light, but not completely. As little as 1 minute of red light is effective to some extent. As has been reported in a previous paper, a similar reversible effect of red light was observed for the flower inhibitory effect of incandescent light of low intensity preceding the inductive dark period¹⁾.

4) Effect of incandescent light of low intensity preceding the inductive dark period.

From the experiments mentioned above and those reported previously¹⁾, it is noticed that the flower inhibitory effect of far-red light of high intensity bears a remarkable similarity to that of incandescent light of low intensity (10 lux) when followed by a 16-hour dark period. To make more detailed comparisons between them, the following experiments were done.

i) One group of the plants was exposed to far-red light of 60 kiloerg/cm.²/sec. for 5 min., 30 min., 2 hr., 4 hr. and 8 hr., another group exposed to incandescent light of 10 lux for the same durations, and subsequently both groups were given a 16-hour dark period. Results are shown in Table 6. Both far-red and incandescent light inhibited flowering but the former more heavily so than the latter. Both lights, however, inhibited flowering completely when administered for 8 hours.

ii) Low intensity incandescent light (10 lux) was given to plants for 2, 4, 8,

Table 6. Similarity of the far-red and the incandescent light of low intensity with respect to their flower inhibitory effect when followed by an inductive dark period in *Pharbitis* seedlings.

Intensity of far-red light (FR): 60 kiloerg/cm.²/sec.

Intensity of incandescent light (IL): 10 lux.

(Treated on Apr. 22, and dissected on May 10, 1958)

Treatment	No. of plants dissected	% of plants with flower buds	No. of flower buds per plant	% of plants with terminal flower bud
16bd	37	100	5.4	100
5'FR—16bd	38	89.5	2.1	5.3
30'FR—→ "	34	91.2	2.1	8.8
2bFR—→ "	37	48.6	0.8	0
4bFR—→ "	37	43.2	0.5	0
8bFR—→ "	34	0	0	0
5'IL—→ "	35	100	5.5	94.3
30'IL—→ "	38	100	4.6	71.1
2bIL—→ "	36	100	5.0	86.1
4bIL—→ "	36	97.2	3.3	33.3
8bIL—→ "	35	0	0	0

12, 16 and 24 hours and followed by 12-hour darkness in one group, and by 16-hour darkness in another one. Results presented in Table 7 show the remarkable flower-promoting effect of the incandescent light given for 4 hours or less preceding the

Table 7. Effect of incandescent light of 10 lux (IL) preceding 16- and 12-hour dark periods upon flower initiation of *Pharbitis* seedlings.

(Treated on May 3, and dissected on May 19, 1958)

Treatment	No. of plants dissected	% of plants with flower buds	No. of flower buds per plant	% of plants with terminal flower bud
16bd	39	100	3.7	100
2bIL—→ 16bd	40	100	4.2	100
4bIL—→ "	40	100	4.0	100
8bIL—→ "	39	94.9	1.6	0
12bIL—→ "	37	89.2	1.3	0
16bIL—→ "	37	81.1	1.0	0
24bIL—→ "	39	79.5	1.1	0
12bd	40	47.5	0.6	0
2bIL—→ 12bd	37	100	4.6	43.2
4bIL—→ "	38	100	4.4	78.9
8bIL—→ "	39	2.6	0.0	0
12bIL—→ "	40	0	0	0
16bIL—→ "	39	0	0	0
24 _b IL—→ "	40	0	0	0

12 hour dark period. This phenomenon had also been observed with the far-red light of 60 kiloerg/cm.²/sec. but with less flower promotion (cf. Table 2). When the low-intensity incandescent light was given for 8 hours, flowering response was suppressed strikingly whether the following dark period was 12 or 16 hours. The same effect had been found for far-red light of 60 kiloerg/cm.²/sec. for 8 hours. Further increase in length of the low-intensity incandescent light had little effect on floral inhibition.

5) Effect of daylight fluorescent light of low intensity preceding the inductive dark period.

As low-intensity light of the incandescent lamp and the far-red light of high intensity showed a similar effect upon flowering responses when given prior to the inductive dark period, low intensity light of a daylight fluorescent lamp comprising little far-red light was investigated in this experiment for its effect on flower initiation when given to the plant preceding the 16- and 12-hour dark periods.

Plants were exposed to the daylight fluorescent light of 10 lux for 0, 2, 4, 8, 16 and 24 hours, and subsequently given 16- or 12-hours of darkness. Flowering responses are shown in Table 8. The fluorescent light preceding 16-hour dark

Table 8. Effect of low-intensity light of daylight fluorescent lamp (10 lux) (FL) preceding 16- and 12-hour dark periods on flower initiation of *Pharbitis* seedlings. (Treated on May 5, and dissected on May 21, 1958)

Treatment	No. of plants dissected	% of plants with flower buds	No. of flower buds per plant	% of plants with terminal flower bud
16hd	37	100	4.1	100
2hFL→16hd	37	100	4.3	100
4hFL→ "	38	100	4.2	100
8hFL→ "	38	100	3.8	63.2
12hFL→ "	39	100	4.0	64.1
16hFL→ "	40	100	3.1	37.5
24hFL→ "	38	100	4.3	92.1
12hd	38	79.0	1.4	0
2hFL→12hd	37	100	4.2	51.3
4hFL→ "	38	100	4.3	100
8hFL→ "	38	100	3.4	44.8
12hFL→ "	39	76.9	1.3	0
16hFL→ "	36	94.5	1.8	13.9
24hFL→ "	39	89.8	1.6	0

period inhibited the flowering to some extent if the duration of the irradiation was increased up to 8 hours or more, but the inhibitory effect was far less than that of far-red light. In this case, too, further increase in the length of irradiation beyond 8 hours has little effect, the inhibitory level remaining about the same (cf. Table 7). Several other experiments showed similar results.

Daylight fluorescent light of low intensity promoted flower initiation more strikingly than the incandescent light when followed by the 12-hour dark period, and even if the duration of irradiation was increased up to 8 hours, flower initiation was promoted.

Discussion

In the foregoing experiments far-red light preceding a 16-hour dark period inhibited flower initiation, but that of less than 4 hours given prior to 12-hour dark period promoted flowering. Nakayama reported recently a flower inhibitory effect of far-red light given prior to a 16-hour dark period in *Pharbitis* seedlings³⁾. This is also the case in our experiments reported here, in which the duration and the intensity of far-red irradiation differs from that in Nakayama's experiment considerably. In his experiment, 2 minutes of far-red irradiation of high intensity resulted in the complete suppression of flowering. The material of his experiment seems to be not so sensitive to the dark period as ours. His experimental treatments were repeated 3 times, whereas in our experiments only one treatment was given. The differences between the present results and Nakayama's may be due to the difference of photoperiodic sensitivity of the material used.

Borthwick *et al.* reported with *Xanthium* the flower-promoting effect of far-red light given prior to the dark period, resulting in a reduction of critical dark length³⁾. This may correspond to the flower-promoting effect of the far-red light preceding the 12-hour dark period in *Pharbitis* seedlings, but the flower-promoting effect reported by Borthwick *et al.* appears more striking than that represented here.

Why does far-red light of 4 hours or less preceding a 16-hour dark period prevent flowering, and the same light preceding a 12-hour dark period promote flowering? The results may be elucidated plausibly by the following assumptions.

1) The first partial process taking place in the inductive dark period can proceed under far-red light as well as under darkness or low-intensity fluorescent light⁴⁾.

2) Far-red light preceding the inductive dark period brings about changes or conditions which make the following dark period ineffective. This inhibitory action is not effective in the first 4 hours but becomes so after some 8 hours.

Thus far-red light given prior to the dark period has dual effects: the first effect is promoting and the second inhibitory to the flowering responses.

Pharbitis seedlings are induced to flower only to a slight extent when subjected to a 12-hour dark period, but induced to a maximum with a 16-hour dark period, and the further lengthening of the dark period can increase flowering responses.

If the 12-hour dark period is preceded by 4 hours of far-red light, during which the first process of the dark period proceeds, the flowering response corresponds to that induced by 16-hour dark period; that is, in flower promotion. As the far-red light, on the other hand, prevents the subsequent dark process, the overall response is determined by the difference between the flower promoting and inhibiting effect

of the far-red light. In this case, the promoting effect exceeds the inhibitory one, and results in a flower promotion. When the 12-hour dark period is preceded by 8 hours of far-red light, the flower inhibitory effect exceeds the promoting one, and results in a flower inhibition.

If the 16-hour dark period is preceded by 4 or 8 hours of far-red light, even if the first process of the inductive dark period proceeds under this light, flowering may not be promoted, because the 16-hour dark period is sufficient to induce maximum flowering responses, and further extension of the dark period has no further effect. In these cases, only the flower inhibitory effect of the far-red light appears, and results in a flower inhibition.

The above hypothesis for the action of the far-red light preceding the dark period is also applicable to that of the incandescent light of low intensity, which includes abundant far-red light. As a whole, the incandescent light of low intensity has less flower inhibitory effect than the far-red light of high intensity, and has more flower promoting effect than the latter when followed by a 12-hour dark period.

When the low intensity light of a daylight fluorescent lamp, which includes little far-red light, precedes the 12-hour dark period, the above mentioned flower-inhibitory effect of the far-red light can be neglected; therefore, pronounced flower promotion is the result, even if the irradiating duration exceeds 8 hours.

If the daylight fluorescent light of low intensity was given for 8 hours or more preceding the 16-hour dark period, flowering was inhibited to some extent, as revealed in the percentage of plants with terminal flower in Table 8. Similar results were reported in the previous paper¹⁾, and it was supposed that this inhibitory effect of low intensity light of longer duration might be due to the lack of photosynthates.

It is interesting that the flower inhibitory effect of far-red light of high intensity, and of incandescent and daylight fluorescent light of low intensity increases abruptly when the irradiating duration is extended up to 8 hours, and further extension has little effect. Under these lights, the first process of the flower-inducing dark period is supposed to proceed, and some critical changes may take place after some 8 hours.

Summary

1) Far-red light given to *Pharbitis* seedlings preceding a 16-hour dark period inhibits flowering. This flower inhibitory effect is intensified with increasing duration of the far-red irradiation and becomes marked with 8-hour irradiation.

2) The flower inhibitory effect of the far-red light is obvious even if the intensity is decreased to 10 erg/cm.²/sec.

3) Far-red light of 2-4 hours preceding a 12-hour dark period promotes flowering, but the same light of 8 hours inhibits completely.

4) Red light preceding the inductive dark period has no influence upon flowering response whether a 16- or 12-hour dark period follows.

5) The flower inhibitory effect of far-red light preceding the inductive dark period can be reversed by red light applied just before the dark treatment.

6) Incandescent light of 10 lux promotes flowering remarkably when applied for 2-4 hours preceding the 12-hour dark period, but inhibits when given for 8 hours or more.

7) Daylight fluorescent light of 10 lux which includes little far-red light promotes flowering remarkably when preceding the 12-hour dark period.

A discussion was given of the possible role of far-red light and low intensity light preceding the inductive dark period in flowering responses.

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References

- 1) Takimoto, A. and Ikeda, K., Bot. Mag. Tokyo, 72: 137 (1959). 2) Nakayama, S., Ecological Rev., Sendai, 14: 325 (1958). 3) Borthwick, H. A., Hendricks, S. B. and Parker, M. W., Proc. Natl. Acad. Sci. U. S. A., 38: 929 (1952). 4) Takimoto, A., Ikeda, K. and Imamura, S., Bot. Mag., Tokyo, 71: 317 (1958).

摘 要

1) アサガオの子葉に 16 時間の暗期を与える前に、近赤外光 (FR) を与えると花芽形成が抑制される。しかし 12 時間の暗期前に FR を与えると、その照射時間が 4 時間以下の場合のみ花芽形成の促進がみられる。

2) 暗期前に与えた赤色光 (R) は花芽形成に対してほとんど影響を及ぼさない。

3) 暗期前に与えた FR の花芽形成抑制効果は暗期直前に R を与えることにより消却される。

4) 10 ルックスの FR を多く含む白熱電灯光 (IL) も FR と同じような効果を示すが、FR よりも花芽形成促進効果が強く、抑制効果が弱い。

5) 10 ルックスの FR をほとんど含まない昼光色蛍光灯光 (FL) を 12 時間暗期前に与えるといちじるしく花芽形成が促進される。同じ光を 16 時間暗期前に与えると、照射時間が長い場合のみ、わずかに花芽形成が抑制される。

6) 暗期前に与えた FR, IL および FL の作用に関し二、三の考察を行なった。