Photoperiodic Flower Induction in Rice Plants as Influenced by Light Intensity and Quality

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Photoperiodically sensitive cultivars of rice require appropriate number of daily cycles consisting of light period and a sufficient duration of dark period to initiate flowers. In several short-day plants, however, the flowering is reduced when the day is extremely short or when the light period is given at a low irradiance. Rice plants need a considerably high-intensity light for their normal growth, and reduced sunshine often causes a retardation of their heading. It is now necessary to consider what role is played by the high-intensity light period for the photoperiodic flower induction in rice plants.

Rice cultivars which are very responsive to photoperiod are able to measure the duration of the critical daylength with a high degree of accuracy and some of them may be profoundly affected by even a relatively small change in daylength. Therefore, a precise estimation of the effective daylength in natural conditions is necessary. Under natural conditions the transition to and from darkness is not abrupt but occurs through a gradual change in light intensity, and its quality at dusk and dawn also changes.[7,8] The mechanisms by which rice plants discriminate between day and night and begin to measure the duration of night are not only of high interest in themselves but also of practical significance for rice growers.

The present paper was designed to provide some information about light requirement during photoperiod for floral induction as well as the effects of low-intensity light and its quality at the end of day on the initiation of measurement of dark period. The rice cultivar used here was Norin 18, which has the highest sensitivity to photoperiod in Japan and the floral stage system was used as the measure of flowering response.[1]

Requirement for light during photoperiod[2]

A photoperiod of 9 to 12 hr is most effective for floral induction in the rice cultivar used in the present study, and complete failure of flowering occurs under photoperiods of 2 hr or less as well as 15 hr or more. In order to study the effect of light intensity during short photoperiod, which is combined with a sufficient length of night for flower induction, plants raised in a vegetative state under continuous illumination were subjected to a 9-hr daily photoperiod during which light intensity from sunlight was reduced.

The reduction of light intensity during photoperiod resulted in an inhibition of flowering, showing a decrease in floral response with lowering light intensity. This inhibitory effect, however, was more pronounced when the number of short-day cycles was suboptimal. On the contrary, the more inductive cycles were given, the less the flowering was inhibited. When a sufficient number of inductive cycles was given, as little as 7% of full solar radiation was proved to be fully effective for flowering (Fig. 1).

To determine when high-intensity light during photoperiod is most required for flowering, plants were subjected to 7% of sunlight during a 9-hr daily photoperiod and 3 hr of full sunlight was given at the beginning, middle or the end of photoperiod, respectively. Although the flowering response

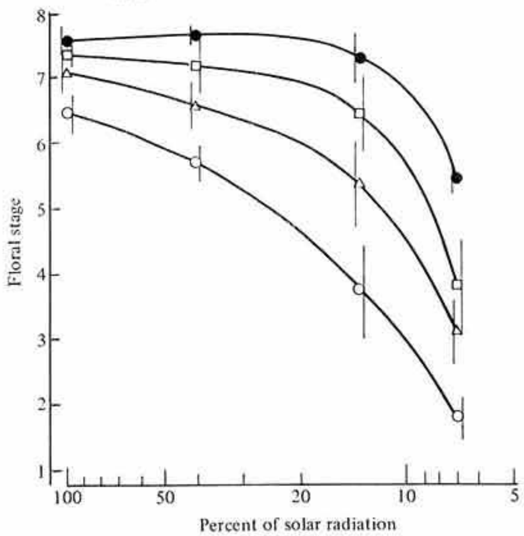

Fig. 1. Effect of reduction in light intensity during photoperiod on flowering response
Solar radiation during 9-hr day was reduced to 7, 14 and 41% of full light and 7 (○), 14 (△), 21 (□) and 28 (●) photoperiodic cycles were applied. Vertical bars show SD around the mean.

under diminished sunshine was depressed to almost one half that of plants kept in full sunlight, the inhibition of flowering caused by reduced light intensity was most effectively overcome by an exposure to 3-hr of full sunlight which immediately preceded the inductive dark period. Full sunlight of 3-hr given at the beginning or the middle of light period was not so effective as that given at the end of the light period (Table 1).

Table 1. Effects on flowering of exposure treatments to 3-hr full sunlight applied at different times during 9 hr of daily low-intensity light period

Treatment	Floral stage
Full sunlight throughout a day	7.0 (0.17)
7% of full light throughout a day	3.7 (1.02)
Exposed to full light at the beginning of day	5.6 (0.64)
Exposed to full light in middle of day	5.2 (0.73)
Exposed to full light at the end of day	6.9 (0.33)

Standard deviations around the mean are shown in parenthesis.

Low-intensity light immediately before the dark period of suboptimal duration

1) Effect of low-intensity light[3]

The abrupt change from high-intensity light to complete darkness is unnatural and we thought the following experiments might be necessary and valuable to determine the effective daylength. Plants were exposed to natural daylight reduced to 5 and 12% of full light for various hours preceding the time of astronomical sunset and immediately thereafter transferred to a 10-hr darkness which is some minutes longer than the critical dark period. Four hr of reduced solar radiation preceding a 10-hr dark period inhibited flowering to a slight extent, but 3-hr or less exposure to reduced sunlight caused an increase in flowering response, as compared with that

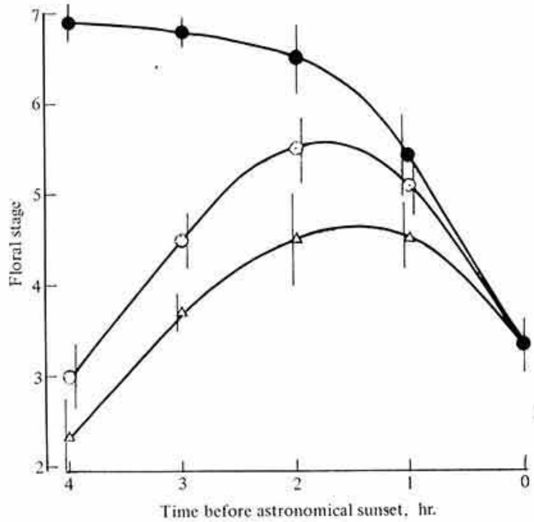

Fig. 2. Effect of reduction in solar radiation before the time of astronomical sunset on flowering response
Plants were subjected to 0 (dark, ●), 5 (○) and 12% (△) of full sunlight for various hr preceding the time of sunset and subsequently given 10-hr dark period. Vertical bars show SD.

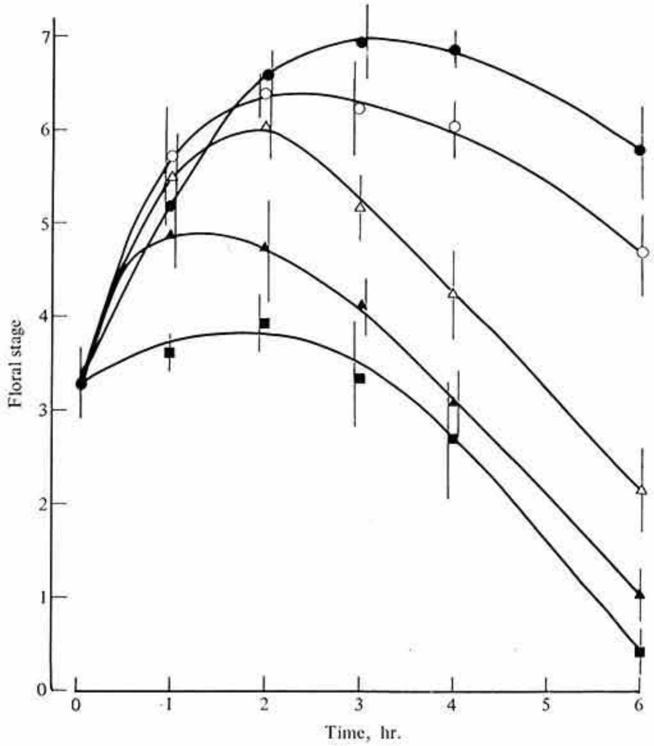

Fig. 3. Effects of fluorescent white light of different intensities preceding 10-hr dark period on flowering response

Plants were subjected to 0 (dark, ●), 1 (○), 5 (△), 10 (▲) and 20 ft-c (■) of fluorescent light for various hr and thereafter transferred to a 10-hr dark period. Vertical bars show SD.

of the plants subjected to a 10-hr dark period preceded by full light. As low as 5% of sunlight given for 1 hr prior to the time of sunset had almost the same effect as a complete darkness (Fig. 2).

Further experiments were performed to examine the effect of reduced light preceding a dark period by giving daylight fluorescent light at constant intensities. Floral response of the plants subjected to low-intensity light preceding a 10-hr darkness increased as the duration of low-intensity light period was increased up to some 2 hr, and the lower light intensities were applied, the more the flowering was promoted. Fluorescent light of 1 and 5 ft-c, when applied for 1 or 2 hr, led to flowering as well as darkness does, indicating that the flower-inducing processes of the dark period begin to proceed under low-intensity light (Fig. 3). The effects of low-intensity light given at the end of day were investigated in relation to the length of the following dark period. Plants illuminated with 3-hr daylight fluorescent light of 8 ft-c were subjected to dark periods of different durations. A 9-hr dark period could not bring about flowering, but some flowers were formed when 3 hr of low-intensity light preceded it. When 8 ft-c of fluorescent light was given for 3 hr prior to 12-hr or longer dark periods, floral responses were not promoted but rather inhibited. Thus, the effect of low-intensity light given before dark period varied with the length of the following dark period (Fig. 4).

2) Spectral dependence of low-intensity light[3]

To study the spectral dependence of the

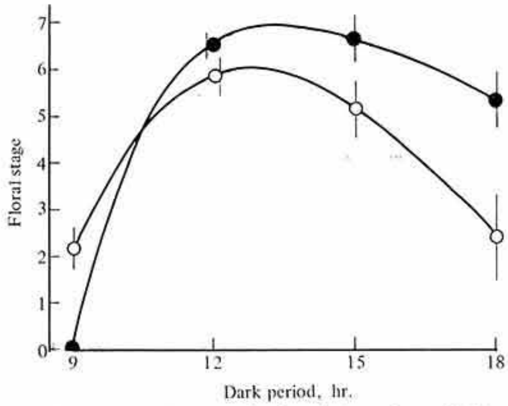

Fig. 4. Effect of low-intensity light preceding dark periods of various durations on flowering response

Plants were darkened for various hr, with (○) or without (●) 3-hr pre-illumination with fluorescent light of 8 ft-c. Vertical bars show SD.

effect of low-intensity light immediately before the dark period, some colored lights, including far-red (FR) light, adjusted at an intensity 2 W·m^{-2} were applied. Plants were irradiated with those lights for 2 hr preceding a 10-hr dark period. All colored lights used, excluding red (R) light, were effective in promoting flowering, though the response level was considerably lower, because of an insufficient repetition of photoperiodic cycles. It is noticeable that FR light has a marked flower-promoting effect in comparison with any other colored lights and its flowering level exceeds that of the control plants subjected to a 12-hr dark period (Table 2).

Promoting effect of FR light given at the end of photoperiod

1) FR action affected by the duration of the following dark period[4]

The effect of daily FR irradiation at the end of photoperiods was studied in detail. Plants were exposed to FR light (700–900 nm) of 35 W·m^{-2} for 2 hr immediately followed by 10- to 18-hr dark periods. Floral response of control plants varied with the length of dark period, i.e., higher responses were obtained with the increase in length of dark period up to 14 hr, but further lengthening the dark period caused a reduction of floral response. However, 2-hr exposure to FR light just before a 10-hr darkness which is a suboptimal length enhanced flowering strikingly. Although the FR irradiation prior to 12-hr dark period had little or no effect, the flowering was suppressed when the dark period exceeded 14 hr and this inhibitory action was intensified with increasing duration of the dark period. The effects of FR light as well as low-intensity light varied depending on the length of the following dark period. In other words, FR irradiation at the end of day was promotive in floral induction, if dark periods were of suboptimal length, while always inhibitory under supraoptimal conditions (Fig. 5).

Table 2. Effects of irradiation with 2-hr colored light preceding a 10-hr dark period on flowering response

Color of light	Floral stage
Blue	3.2 (0.81)
Green	4.2 (0.74)
Red	0.1 (0.22)
Far-red	7.1 (0.32)
Control	
10-hr dark	0.2 (0.38)
12-hr dark	6.2 (0.45)

Emission maxima of colored lamp used were 463 for blue, 541 for green and 653 mm for red, respectively. Radiant energy of all lights was adjusted at an intensity of 2 W·m^{-2} at plant level. SD is shown in parenthesis.

2) Shortening the critical dark period[4,5]

A 9-hr dark period, which is some minutes shorter than the critical length and rarely leads to flowering, enabled some plants to flower with exposing to FR light for some hr preceding the dark period. That is, flowering responses of plants exposed to FR light prior to 9-hr dark period increased with increasing duration of FR irradiation up to 2 hr, exceeding flowering responses caused by

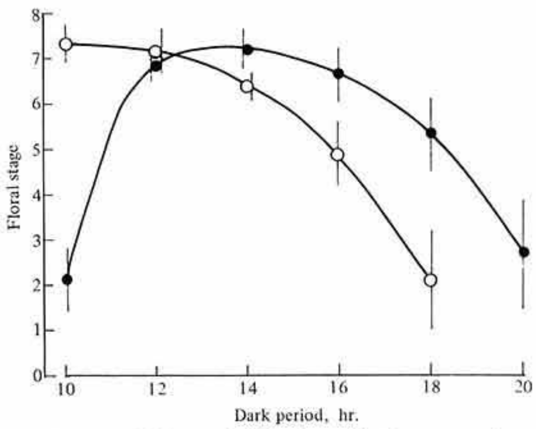

Fig. 5. Effect of FR irradiation preceding dark periods of various durations on flowering response
Plants were darkened for various hr, with (○) or without (●) pre-irradiation with 2-hr FR light. Vertical bars show SD.

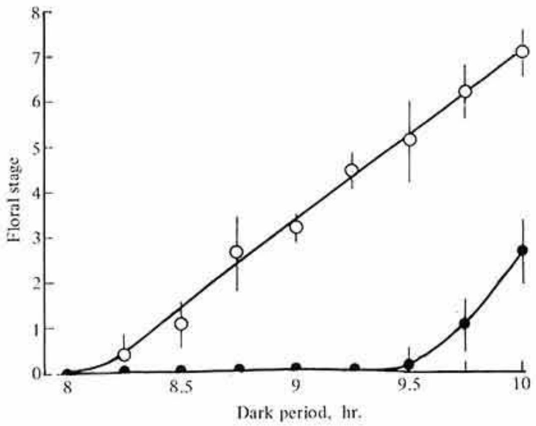

Fig. 7. Effect of FR irradiation preceding dark periods of subcritical length on flowering response
Plants were darkened for various hr, with (○) or without (●) pre-irradiation with 15 min FR light. Vertical bars show SD.

the extension of dark period (Fig. 6). The flower-promoting effect of FR light became more evident with a brief exposure prior to the dark period of subcritical length. Only a few floral buds could be produced by exposing to 9.5-hr dark period and the plants subjected to shorter nights less than 9.25 hr completely failed to flower. Even an 8.25-hr dark period, however, was capable of inducing flowering if 15 min of FR light was applied at the end of day, and hence the dark period required for floral initiation was shortened by some 1.25 hr in this case (Fig. 7).

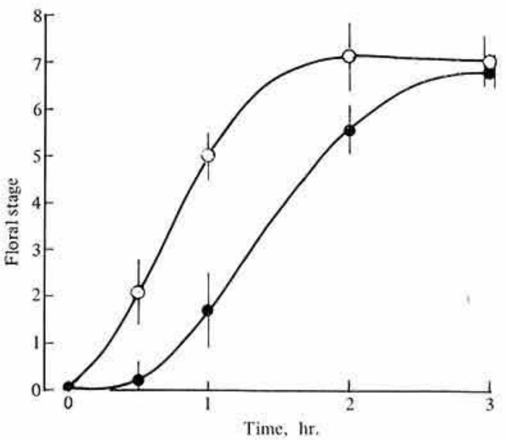

Fig. 6. Effects of time of exposure to FR light preceding 9-hr dark period on flowering response
Plants were subjected to various hr of FR light (○) or darkness (●) preceding 9-hr dark period. Vertical bars show SD.

3) Reduction in number of inductive cycles required for flowering[5)]

There is another evidence that the promotion of flowering with FR irradiation at the end of day may also bring about a reduction in the minimum number of cycles required for flower induction. In rice plants, even in adult ones, several inductive cycles are required for their flowering, and under suboptimal conditions generally so many repetition of photoperiodic cycles are necessary to induce flowering. Plants subjected to 10-hr darkness without giving FR radiation needed a minimum of 10 cycles for induction, while only 3 cycles were fully effective to induce flowers when exposed to 1-hr FR radiation before being subjected to 10-hr dark period (Fig. 8).

4) Enhancement of flowering by FR mixing light[6)]

Light from incandescent lamps is strongly

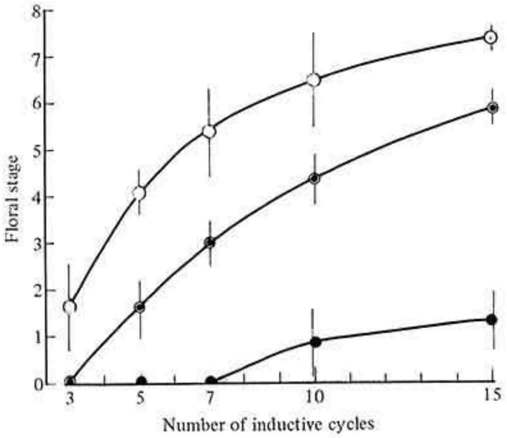

Fig. 8. Flowering of the plants irradiated with FR light in response to various number of photoperiodic cycles

Plants were subjected to 10-hr dark period, with (○) or without (●) pre-irradiation with 1-hr FR light. Symbol ◉ indicates 11-hr dark control. Vertical bars show SD.

contaminated with FR, while that from daylight fluorescent ones comprises little FR radiation. To compare both lights for their effectiveness in flower promotion, plants were exposed to each light of various intensities for 2 hr preceding a 9-hr dark period. The higher light intensities were given, the less flowering was promoted. The flowering of plants illuminated with incandescent light, however, was far more promoted than that with fluorescent light at the same intensity. Thus, the strong promotion of the former is presumably attributable to an abundant FR light included in it (Table 3). Further evidence of a role of FR light for flower promotion comes from the following results. Floral responses of plants exposed to 1- to 3-hr R light alone before being subjected to 10-hr dark period were hardly influenced, but increased to a considerable extent, when R light was mixed with FR simultaneously (Table 4).

Table 3. Comparison of effectiveness of incandescent and fluorescent light in promotion of flowering

Light intensity, $W \cdot m^{-2}$	Type of lamp	
	Incandescent	Daylight fluorescent
0.1	7.0 (0.51)	5.2 (0.88)
0.7	6.4 (0.63)	1.3 (0.92)
4.0	4.1 (0.71)	0.3 (0.60)
Control		
9-hr dark	0.0 (0.0)	
11-hr dark	6.9 (0.32)	

Plants were exposed to 2-hr light of different intensities preceding 9-hr dark period. SD is shown in parenthesis.

Table 4. Effects of time of exposure to red (R), far-red (FR) and mixed (R plus FR) light preceding a 10-hr dark period on flowering response

Exposure treatment	Exposure time, hr		
	1	2	3
R	2.2(0.95)	2.1(1.11)	1.9(1.03)
FR	5.9(0.88)	6.5(0.73)	6.8(0.64)
R+FR	3.8(0.60)	3.9(0.91)	3.7(0.65)
Darkness	4.4(0.75)	5.2(0.59)	5.9(0.43)
10-hr dark control	2.0(0.89)		

Light energy was 0.95 for red and 12.5 $W \cdot m^{-2}$ for far-red light, respectively. SD is shown in parenthesis.

Conclusions

The amount of flowering was reduced by keeping plants at low irradiance throughout a daily short photoperiod, even if a sufficient length of the dark period was applied. Extremely reduced daylight, however, could induce some flowering with increasing photoperiodic cycles, and a brief exposure to high-intensity light just before the inductive dark period was effective for flowering. These phenomena suggest that the requirement for light in floral induction of rice plants does not appear to be entirely concerned with photosynthesis.

On the contrary, a relatively short period of low-intensity light given at the end of day, which associated with a suboptimal length of night, promoted flowering, indicating that the flower-inducing process taking place in the first part of the dark period is relatively insensitive to light and allows to proceed under low-intensity light. The flower-promoting effect of low-intensity light was also dependent on light quality. FR light was the most promotive and very conspicuous in its effectiveness. FR irradiation at the end of day could bring about a shortening of the critical night length as well as the reduction in minimum number of inductive cycles required. The flower promotion caused by FR light far exceeded that caused by low-intensity of white light, suggesting that flower-promoting effects of both lights might be based on the different mechanisms.

These facts must be taken into consideration when we determine the starting point at which flower-inducing dark reaction begins to proceed.[7] However, we have not yet sufficient data on light conditions to give an accurate estimation of a photoperiodically effective daylength under natural conditions. In consideration of a gradually changing intensity and quality of natural light during dusk,[8] further detailed studies are needed.

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