TIMING OF EVOCATION AND DEVELOPMENT OF FLOWERS IN

PHARBITIS NIL

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Summary

When P. nil seedlings were exposed to a single inductive dark period, the
main shoot apex and the lowest axillary bud which had not differentiated more
than one leaf primordium underwent floral evocation within about 12 hr of the
end of the dark period. The higher axillary buds appeared to be evoked in acropetal
sequence over the following 2 days at 28°C, or 4 days at 21°C.

The higher the temperature following an inductive dark period the lower
was the flowering response and the longer the critical dark period length. High
temperatures, even with short days, could cause axillary buds which had differenti­
tated sepal and anther primordia to revert to the vegetative condition. However,
exposure to additional inductive dark periods could prevent the reversion at high
temperatures.

Application of 5-fluorouracil (5-FU) could also inhibit floral differentiation.
The axillary buds escaped from inhibition of their floral differentiation, by 5-FU
or by exposure to high temperatures, progressively later the higher their position.
However, differentiation of the terminal flower could be prevented by exposure to
5-FU or high temperatures long after floral evocation of the shoot apex had taken
place.

No increase in the rate of leaf initiation was evident following photoperiodic
induction, but a sharp rise in the rate of axillary bud initiation occurred after 24 hr
at 28°C, and after 48 hr at 21°C.

It is concluded that the short-day stimulus to floral evocation may be thermo-
labile, and that it must continue to act after floral evocation has occurred if dif­
ferentiation of flowers, especially at the main shoot apex, is to ensue.

I. INTRODUCTION

Exposure of seedlings of Pharbitis nil Chois., Japanese morning glory, to a
single dark period of sufficient length leads to the conversion of the shoot apex to
a terminal flower and to the production of about seven axillary flower buds (Takimoto
1969). The nature of the processes occurring in the cotyledons of P. nil during an
inductive dark period, particularly the changes in phytochrome status, have been
examined by Evans and King (1969). As a result of induction the cotyledons generate
a floral stimulus which, by extrapolation from the time and velocity of its trans­
location, probably reaches the shoot apex 16–18 hr after the beginning of the dark
period (Wada 1966; Takeba and Takimoto 1966; King, Evans, and Wardlaw 1968).

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The early events at the shoot apex following the arrival of the stimulus and leading to the committal of the shoot apex or axillary buds to form flowers rather than leaves are referred to as evocation (Evans 1969). Floral differentiation usually ensues but, as will be seen, it may fail to progress at high temperatures unless the plants are exposed to additional photoperiodic induction.

In view of Nakayama’s (1958) suggestion that the floral stimulus in *P. nil* is thermolabile, such vegetative reversion implies that the floral stimulus is not only responsible for evocation but also for continued floral differentiation. It could also imply that the stimulus acts directly on existing buds, causing progressive changes in the pattern of their activities. If so, axillary shoot meristems would be evoked to form flowers only after they have reached a certain size but before they are committed to the vegetative pattern of differentiation.

The objective of the experiments described below was to obtain at least indirect evidence on the timing and nature of action of the short-day stimulus to flowering in *P. nil*.

II. Experimental Methods

(a) Seed Germination and Growing Conditions

Seeds of *P. nil*, strain Violet, from plants grown from seed supplied by Dr. A. Takimoto, were treated with concentrated H$_2$SO$_4$ for 30 min (4.30 p.m., day I), washed overnight at 24°C in a temperature-controlled water-bath, and sown (9 a.m., day II) in holes 2 cm deep in a mixture of equal parts of perlite and vermiculite. Eight seeds were sown in each pot (12 cm diameter), but only the most uniform five or six seedlings were retained for treatment. There were four pots in each experimental group.

The plants were held under continuous light from fluorescent and incandescent lamps, at an intensity of 1000 f.c., from sowing. For the first 2 days the temperature was 30°C, and for the next 2 days 25°C. In most experiments, the plants which were to be photoperiodically induced were moved to a dark room at 25°C for 15 hr, beginning at 7 a.m. on day VI, after which they were returned to continuous light and a temperature of 21°C until dissection.

In exploratory experiments, the age at which the seedlings were exposed to the dark period was varied, as were the intensity and spectral composition of the light, and the day length, both before and after the dark period. In still others the length and temperature of the dark period and the temperature following the dark period were also varied.

In treatments with 5-fluorouracil (5-FU) or gibberellic acid (GA$_3$), 10μl of an aqueous solution of 2·5 × 10$^{-8}$M 5-FU, or 1 × 10$^{-9}$M GA$_3$, with 0·1% Tween-20, were applied to each plumule using a microsyringe.

(b) Measurement of Development and Flowering Response

To measure flowering response plants were dissected about 2 weeks after exposure to the inductive dark period, and the number and position of the flower buds on each plant were recorded. Buds were designated as flower buds only when bract, sepal, and anther primordia were visible with a dissecting microscope.

In order to follow development of the various buds, groups of 16 plants were harvested each day from four treatments; those exposed to a dark period on day VI followed by continuous light at either 21 or 28°C, and those in continuous light throughout (i.e. vegetative controls) at either 21 or 28°C after day VI. Development of the primary shoot and of the various axillary buds was examined under a dissecting microscope at ×50 magnification, and scored by the system developed for *Pharbitis* by Wada (1967), in which each vegetative plastochron is divided into three stages. In Wada’s system the initiation of each floral primordium is similarly divided
into three stages for scoring purposes, each fully differentiated flower bud of 2 bracts, 5 sepals, 5 petals, 5 stamens, and 3 carpels thus having a total score of 60. This arbitrary procedure results in a rapid increase in score at flower differentiation, but has the advantage of providing a sensitive and unambiguous scoring system for the earliest stages of floral differentiation when identification of the various floral primordia is difficult. It is also suitable for indicating reversion to the vegetative condition, and we used it for these reasons, since the arbitrary form of the score curves obtained was not a serious disadvantage.

III. Results

(a) Effect of Growing Conditions, Dark Period Temperature, and Seedling Age

Light and temperature conditions at all stages of an experiment, from before exposure to darkness to several days after, have a marked influence on the flowering response obtained with *Pharbitis* seedlings. For dark periods between 12 and 16 hr in duration, a temperature of 25°C was optimal, but temperatures between 23 and 27°C were almost equally effective. The flowering response was greatly reduced when the temperature of the dark period was only 21°C. The effect of temperature after the dark period is considered later.

The flowering response to a given dark period was greater when this was preceded by continuous light rather than 16-hr photoperiods, by fluorescent rather than incandescent light, and by light of high (1000 f.c.) rather than low (200 f.c.) intensity.

The effect of seedling age at time of exposure to darkness is indicated in Figure 1. Seedlings remained highly responsive to photoperiodic induction for only about 3 days. In other experiments with shorter dark periods and a higher temperature (25°C) afterwards, flowering was even more sensitive to seedling age, maximum flowering being obtained only with seedlings given a dark period on day VI.

Day IV seedlings, in which the hypocotyls were still elongating, were insensitive to induction, which agrees with the observation of Marushige and Marushige (1963), that attainment of photoperiodic sensitivity is associated with cessation of hypocotyl growth. The decline in photoperiodic sensitivity in older seedlings was particularly striking for terminal flower formation, which is also difficult to obtain in adult plants. Plumule growth became more rapid at about the time when photoperiodic sensitivity was lost, and may have been associated with the change in the relative responsiveness of the terminal and axillary shoot apices.

Figure 1(b) shows that, at 25°C, leaves were initiated on the main stem at a rate of 1·3 per day, whereas axillary buds appeared at a rate of 1·0 per day. The close relation between the nodal position of the first flower and the number of axillary buds indicates that the uppermost axillary bud visible at the end of the dark period is the lowest to form a flower. Considering the results with plants of all ages, from several experiments, it was found that axillary buds which had reached a score of 3 by the end of the dark period, i.e. were about to form a second primordium, were too advanced for floral evocation, whereas buds with a score of 2 or less could subsequently form flowers. With further development, the spiral leaf arrangement is established, whereas floral buds begin by differentiating two apparently opposite and approximately equal bract primordia.
(b) Development of the Primary Shoot

Changes in the scores for the primary shoots of both induced and vegetative plants, held at either 21 or 28°C after the dark period, are shown in Figure 2.

Vegetative plants initiated leaves at the rate of 1.1 per day at 21°C, and 1.8 per day at 28°C (cf. 1.3 per day at 25°C from Fig. 1). At 21°C the score for photo-

periodically induced plants began to exceed that for vegetative plants after 72 hr from the end of the dark period, because of the appearance of floral primordia at the shoot apex, not because of any increase in the rate of leaf initiation. However, floral evocation was probably completed within 12 hr of the end of the dark period, as the following analysis shows. Plants forming a terminal flower following exposure to a dark period on day VI had an average score of 27.5 for the leaf and bract primordia below the terminal flower. Like the axillary flowers, the terminal flower has two floral bracts, as indicated by Takimoto (1967), of which one commonly bears an axillary flower bud. Thus, 6.0 units (= two bracts) should probably be subtracted from the
score of 27.5 to obtain the score when floral evocation of the shoot apex was completed. By interpolation in Figure 2(a), this would have been about 12 hr from the end of the dark period.

Plants forming a terminal flower at 28°C had the same average score (27.5) for the leaf and bract primordia below it, and from Figure 2(b) we can deduce that floral evocation of the shoot apex was probably completed 9–10 hr after the dark period. Floral primordia were first evident 72 hr after the dark period.

![Graph](image)

**Fig. 2.—Development of the primary shoots of seedlings exposed either to 15 hr of darkness (●, ○) or to continuous light (×) at 25°C, followed by continuous light at (a) 21°C or (b) 28°C. The horizontal line indicates the total score (21.5) for the leaves initiated before the terminal flower, including two bracts, was differentiated. The two curves for the induced plants at 28°C represent those which formed a terminal flower (●) and those which did not (○). The letters S, P, A, and C refer to the appearance of sepal, petal, anther, and carpel primordia respectively.**

Only about half of the plants held at 28°C after the dark period eventually formed a terminal flower, many of the remainder forming only two axillary flowers. The two groups, those with and those without terminal flowers, could be distinguished only 96 or more hours after the dark period [Fig. 2(b)], the primary shoot score of those not forming terminal flowers falling back to, and then below, the score for the vegetative controls.

(c) **Axillary Bud Development**

The scores for each axillary bud on plants at 21°C and not exposed to an inductive dark period increased approximately linearly with time, but at a lower rate the higher the nodal position of the bud [Fig. 3(b)]. Development at 28°C was similar, but faster.

Development of the first two axillary buds on photoperiodically induced plants at 21°C was the same as that on vegetative plants, and showed no acceleration of the kind found by Wada (1967). On the third axillary bud, however, floral bract primordia were apparent 48 hr after the end of the dark period, and the bud score rose rapidly as the other floral organs were differentiated. The higher axillary buds followed a similar course of development, but at progressively later times.
Progress of the development score for the terminal flower, including two bracts, is included in Figure 3(a), and coincides closely with that for the third axillary bud, which suggests that floral evocation of the shoot apex and of the third axillary bud may have been completed at the same time, about 12 hr after the dark period.

It was concluded above that axillary buds, if they are to form flowers, must undergo floral evocation before they have developed beyond a score of 2. The third axillary bud reached a score of 2 about 12 hr after the end of the dark period, again suggesting that its floral evocation occurred at about the same time as that of the shoot apex.

![Graph](image)

**Fig. 3.—**Development of the various axillary buds on induced (a) and vegetative (b) plants at 21°C. The numbers on the curves refer to the nodal position of each bud. The broken line in (a) indicates the development score for the terminal flower (T), including two bracts.

The latest times at which evocation of the various axillary buds could occur, as defined by their reaching a score of 2, are given in Figure 5, for development at 21 and at 28°C.

At 28°C development of the floral buds at the various axillary positions on plants forming a terminal flower (Fig. 4, broken curves) followed a course like that at 21°C, but at a faster rate. The detailed data for these plants are not presented in Figure 4. The solid curves and the symbols depict development of the buds on those plants, about half the total number, which failed to form a terminal flower. On these, the third and fourth axillary flower buds developed at the same rate as those on plants forming terminal flowers. The fifth and sixth axillary flower buds also developed
normally for the first 120 hr after the dark period. By that time they had reached scores of 20–30, having differentiated bract, sepal and anther primordia. At later times of dissection, however, the bud apices had reverted to vegetative organization and eventually lost all trace of their floral primordia. The seventh axillary bud, and those above it, showed signs of floral evocation in that they began to develop before their counterparts on the vegetative controls were evident, but no floral primordia were formed, and their scores increased at rates comparable with those on the vegetative controls.
The rise in the rate of axillary bud initiation following photoperiodic induction is shown in Figure 6. At 21°C [Fig. 6(a)] buds were initiated at a rate of 1 every 31 hr in vegetative plants and in induced plants up to 48 hr from the end of the dark period, but the rate then rose rapidly in induced plants. At 28°C [Fig. 6(b)] there was a comparable rise after 24 hr from the end of the dark period. This rise was apparent both in the plants forming terminal flowers and in those not forming them. In the latter case, however, the rate of bud initiation then fell, after 72 hr, to less than the rate in vegetative plants.

![Figure 6](image-url)

**Fig. 6.—** Effect of photoperiodic induction on the initiation of axillary buds at 21°C (a) and 28°C (b). × Data for plants not exposed to a 15-hr dark period. ○ Plants exposed to dark period and which formed a terminal flower. □ Plants exposed to dark period but which did not form a terminal flower.

(d) Effect of Temperature Following the Dark Period

Figure 7 shows the effect on flowering of the temperature at which plants were held in continuous light after being in darkness at 25°C for various times. At 31°C there was little flowering, even after a dark period of 17½ hr. Flowering response increased progressively as the temperature fell, particularly from 21 to 18°C, despite the severe limitation to growth at 18°C, at which all leaves except the cotyledons lacked chlorophyll. The critical dark period length also appeared to be shorter at the lower temperatures.

Several experiments were carried out in which, following exposure to darkness at 25°C for 15 hr, groups of plants were transferred from high to low temperatures or vice versa at various times and for various periods during development under continuous light. Some results from two of these experiments are shown in Figure 8 for reciprocal transfers at various times between 21 and 28°C, and between 18 and 32°C. Holding plants at 28°C for the first 24 hr after the dark period caused no
reduction in their flowering response, but thereafter the inhibitory effect of the high temperature increased. At 32°C, some reduction in flowering response occurred even when plants were transferred to a low temperature after 18 hr, but the most marked inhibition occurred in the following 24 hr. For plants held initially at 21°C, 72 hr were required before flowering had escaped from inhibition by high temperatures, while for those initially at 18°C more than 84 hr were required. Thus, the higher the temperature following the dark period the sooner plants entered a period when their flowering processes were inhibited by high temperatures, and the sooner they passed through it. As seen above (Fig. 4), the lowermost flowers were least affected by high temperatures, whereas the terminal and uppermost axillary flowers were the ones most affected.

Two experiments have been carried out to determine whether the inhibition of flowering under continuous light at high temperatures is due only to the high temperature, or to high temperature combined with long-day conditions. Following exposure to darkness at 25°C for 16 hr plants were placed in the following conditions,
either continuously or for various periods:

(1) 32°C, continuous light;
(2) 10 hr light, 32°C/14 hr darkness, 32°C;
(3) 10 hr light, 32°C/14 hr darkness, 25°C;
(4) 10 hr light, 32°C/14 hr light, 25°C.

A temperature of 32°C was chosen because Ikeda (1965) had shown that dark periods at 32°C have little inductive effect. The detailed results are not presented, but both experiments showed that the inhibitory effect was due to high temperature alone, since no flowering occurred at 32°C whether the plants were under continuous light (condition 1) or short days (condition 2) for the first 4 days after the inductive dark period. Plants held continuously in short days at 32°C did eventually flower, however, but only at a high nodal position (8.7 average). Thus, short days at 32°C must have been weakly inductive. In continuous light at high temperature the inhibition was evident even when only 10 hr each day were at 32°C since plants in condition 4 formed only 0.18 flowers per plant.

The high temperature inhibition due to 10 hr at 32°C each day could be overcome by exposing plants to additional inductive dark periods (condition 3). The more inductive dark periods given, the greater was the number of flowers. Flower numbers per plant in the two experiments were: no additional short days, 0.04 and 0; 1 additional short day, 0.96 and 0.28; 2 additional short days, 4.1 and 5.2; 3 additional short days, 6.3 and 6.5. The important feature of these results was that the additional inductive short days not only increased the proportion of plants with flowers at the higher nodes, but also the proportion with flowers at the third node. This was particularly so when at least 2 additional short days were given. Thus, the flower at the third axil, evoked soon after the first dark period as deduced above, was rescued from reversion to the vegetative condition by an additional short day 2 days later.

(e) Effect of 5-Fluorouracil and Gibberellic Acid

5-FU was applied to the plumules at various times in three experiments. The time course of its inhibition of flowering differed somewhat in the two main experiments, probably reflecting differences between them in the intensity of photoperiodic induction. In the first experiment, the same as that in which the course of development was followed [Figs. 2(a) and 3], the control plants responded with 100% terminal flowering. Treatment of the plumules with 5-FU gave results very similar to those obtained by Zeevaart (1962) in that, while highly inhibitory to flowering when applied at the end of the dark period, it rapidly became less so, and caused no reduction in flower number or percentage terminal flowering when applied 48 hr after the dark period. These results imply that nucleic acid synthesis is an essential component of evocation.

In the other main experiment, only 52% of the control plants formed terminal flowers at 21°C, and 5-FU was inhibitory to flowering over a longer period. The results in Figure 9 show that flowering at the various axillary positions escaped from inhibition by 5-FU progressively later the higher their nodal position. However, the terminal flower, which was probably evoked at the same time as the axillary
flower at the third node, continued to be inhibited by 5-FU even when applied 60 hr after the dark period.

In other treatments groups of plants were held in darkness beyond the usual period of 15 hr, and 5-FU was applied when the plants were removed from darkness. Exposure to a longer dark period resulted in a higher proportion of plants with terminal flowers in the untreated controls, reflecting more effective induction, and 5-FU application had no inhibitory effect on terminal flowering after 51 hr of darkness, i.e. 36 hr after the end of the standard dark period. Like the difference in the time course of 5-FU inhibition between the two main experiments, this also suggests a faster escape from inhibition by 5-FU the more effective is photoperiodic induction. Nevertheless, 5-FU was progressively more inhibitory the higher the node of flowering.

GA$_3$ (1 x 10$^{-3}$M) applied to the plumule at various times after a dark period of 15 hr at 25°C had no effect on the flowering response at 21°C at any time of application between the beginning of the dark period and 72 hr after its end. This was so despite the fact that GA$_3$ applied at the end of the dark period increased plumule growth at 21°C to such an extent that it equalled that of untreated plants at 28°C for at least 7 days after the dark period.

IV. DISCUSSION

Analysis of the timing of floral development at 21 and 28°C suggested that floral evocation of the shoot apex and of the axillary bud at the third node, the lowest to form a flower in day VI seedlings, must have occurred within a few hours of the arrival of the photoperiodic stimulus soon after the end of the inductive dark period. The extensive changes in RNA and protein distribution evident in the central zone of the shoot apex 24 hr after the end of the dark period (Healey 1964) also suggest that it is florally evoked soon after the end of the dark period.

The experiments with seedlings of various ages indicated that axillary bud primordia could be florally evoked provided they had not reached a score of 3,
i.e. were about to differentiate a second leaf primordium, at the end of the dark period. We had not expected buds in such an advanced stage of vegetative differentiation to be convertible to flowers, particularly in view of Marushige's (1965) statement that axillary buds more advanced than a group of meristematic cells with large nuclei could not be transformed into floral buds. However, Wada's results (1967, fig. 3) agree closely with ours in that axillary buds with a score of 4 at the end of the dark period (i.e. with two leaf primordia) could not be evoked, whereas buds with a score of 2 could be.

By knowing the most advanced stage of development beyond which axillary buds cannot be transformed to floral buds, the latest times at which the various axillary buds could be evoked were estimated (Fig. 5). But to understand the nature of floral evocation it is equally important to know whether there is also a lower limit to axillary bud size below which evocation does not occur. The results in Figure 5 could be explained not only by evocation being progressively later the higher the position of the axillary bud, but also by all axillary sites being evoked at the one time, when the stimulus reaches the apex, the expression of evocation being possible only as the buds are initiated in acropetal sequence. In the latter case the uppermost axillary buds would be evoked up to 6 plastochrons before they became visible, which would make it unlikely that floral evocation could be due to direct action by the short-day stimulus on the geometrical pattern of activity in an existing shoot meristem. In two long-day plants, peas (Paton 1967) and Anagallis (Ballard and Grant Lipp 1964), there is evidence which suggests that axillary buds may be evoked well before they become recognizable even at a histological level.

In Pharbitis, however, the fact that the axillary buds escape from inhibition of their floral development by 5-FU or high temperatures progressively later the higher their position suggests that they may be evoked in acropetal sequence. This conclusion is strongly supported by the finding of Wada (1968) that the buds not only escape in acropetal sequence from inhibition of their flowering by \( \gamma \)-ray irradiation, but also become sensitive to it in the same order. It is also supported by the observation that adventitious buds replacing excised axillary buds will respond maximally to the short-day stimulus only when excision takes place at least three days earlier (King, Evans, and Wardlaw 1968). Thus, the concept of floral evocation as due to the direct action of the short-day stimulus on the activity of existing meristems in Pharbitis is not excluded. We now consider other evidence bearing on this concept.

The sudden rise in the rate of initiation of axillary buds on induced plants (Fig. 6) could result in the upper buds developing under a different pattern of correlative influence from neighbouring primordia compared with the lower buds, which in itself might cause evocation. However, the rise in bud initiation rate did not take place until more than 24 hr at 28°C, or 48 hr at 21°C, after the dark period, by which time the shoot apex and the lowest axillary flowers were already evoked. This timing is similar to that in Lolium temulentum in which evocation of both the lower axillary bud sites and the shoot apex occurs at the end of the inductive long day (Knox and Evans 1968), whereas the rise in the rate of bud initiation does not occur until 2 days later (Knox and Evans 1966). Thus, floral evocation of a bud is apparently not dependent on a changed geometry of influence from neighbouring primordia.
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The shoot apex of plants exposed to darkness for 15 hr and then placed under continuous light at 28°C apparently undergoes floral evocation within 10 hr, and plants returned to a lower temperature (21°C) within a day show full flower differentiation. The higher the temperature at which they are held after the dark period the less their flowering response (Fig. 7), and the sooner it is reduced by high temperatures (Fig. 8). Such reversion could be due to:

1. greater production of an inhibitor of flowering under long days at high temperatures;
2. faster vegetative growth, causing diversion of the substrates required for differentiation away from the florally evoked meristems;
3. thermodolability of the floral stimulus, and a requirement for its continued action even after floral evocation.

In relation to (1) Imamura (1961) has presented evidence for the action of a long-day inhibitor of flowering in seedlings of Pharbitis, and Cleland and Briggs (1967) have ascribed the abortion of flower primordia in Lemna gibba to photoperiodic inhibition. Flowering in Kalanchoë was also reduced the higher the temperature in which plants were held in long days after short-day induction (Rünger 1958). However, since high temperatures were equally inhibitory in our experiments under continuous light or short days, reversion to the vegetative condition is unlikely to have been due to long-day inhibition.

As for (2), the fact that GA3 had no effect on flowering at 21°C, although it increased plumule growth to the level of that at 28°C, suggests that increased competition from stem growth was not the cause of reversion.

Since the high temperatures did not act immediately after the dark period (Fig. 8), yet appeared to extend the length of the critical dark period (Fig. 7), it seems most likely that they reduced the flowering response by increasing the lability of the short-day stimulus. At high temperatures, additional inductive short days not only increased the flowering response, but also rescued from reversion some of the axillary buds already evoked by the first inductive dark period. Thus, the short-day stimulus must be required for the continuation of floral differentiation, even after evocation is completed. In Pharbitis this requirement apparently continues until a late stage of floral differentiation. For example, the axillary buds at the fifth and sixth nodes of plants at 28°C had well-developed sepal and petal primordia present 120 hr after the dark period (Fig. 4), yet failed to differentiate further and reverted to the vegetative condition with no sign of floral primordia, during the next 2 days at 28°C. Even more striking reversion has recently been reported in another short-day plant, Impatiens balsamina (Krishnamoorthy and Nanda 1968). Depending on the stage of differentiation of the uppermost floral bud when the plants were returned to long days, even after as many as 90 short days, one or more inner whorls of the flower were replaced by a vegetative apex. Even the tip of the placenta could resume vegetative growth.

Such a continuation of the requirement for the short-day stimulus beyond evocation and up to the final stages of floral differentiation is strong evidence that the stimulus acts not simply by initiating the sequence of gene action controlling floral differentiation, but directly on the pattern of activity in the differentiating meristems.
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VI. References


