THE EFFECTS OF DAY LENGTH AND LIGHT INTENSITY ON THE GROWTH OF BARLEY

VI.* INTERACTIONS BETWEEN THE EFFECTS OF TEMPERATURE, PHOTOPERIOD, AND THE SPECTRAL COMPOSITION OF THE LIGHT SOURCE

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Summary

The acceleration of flowering in barley due to the inclusion of incandescent illumination in the light source has been shown to be due to the far-red content of the light. A linear relationship between floral development and intensity of far-red light in a 16-hr photoperiod has been established with the cultivar CI 5611. Barley appears to be relatively unresponsive to blue light, however.

The photoperiodic control of flowering was profoundly influenced by temperature. In comparison with lower temperatures, flower formation at 30°C was considerably delayed in short photoperiods and in the absence of incandescent light from the light source. Three varieties, Prior, Piroline, and CI 5611, were converted from quantitative long-day plants at 20°C into obligate long-day plants at 30°C with a critical day length in excess of 12 hr. Flowering in plants growing in a 12-hr, 30°C environment could be induced by a single 24-hr light period, but only after the plants had grown for 50–75 days in the non-inductive environment.

Flower formation at 30°C was frequently abnormal with various degrees of reversion to vegetative development being commonly observed.

I. INTRODUCTION

It is now generally recognized that flowering in long-day plants, including the cereals, is enhanced by far-red light (Friend, Fisher, and Helson 1963; Friend 1964*a*; Paleg and Aspinall 1964; Vince, Blake, and Spencer 1964; Evans, Borthwick, and Hendricks 1965; Lane, Cathey, and Evans 1965; Vince 1965; Schneider, Borthwick, and Hendricks 1967) either in the main light period or a low-intensity extension. It has also been established that this is an effect on initiation and not solely on floral development or stem elongation as was earlier suggested (Downs, Piringer, and Wiebe 1959). Although the effect itself is now generally accepted, the mechanism which accounts for this response to far-red light is far from being understood. Various responses involving phytochrome have been canvassed as an explanation (Evans, Borthwick, and Hendricks 1965) as has the existence of a "high-energy" response system (Friend 1964*a*). These two suggestions may not be incompatible (Hartmann 1966) but it is clear that the response is mediated neither by a "simple" phytochrome system (Hendricks and Borthwick 1963) nor by the original high-energy response system described by Mohr (1962).

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Barley demonstrates accelerated floral initiation in response to far-red light (Lane, Cathey, and Evans 1965), although the earlier experiments (Paleg and Aspinall 1964) did not utilize pure sources of far-red light. It has been suggested that this promotion by far-red light is more pronounced at long photoperiods than at short (Aspinall 1965) but in wheat (Friend 1964*a*) there was greater promotion in short photoperiods. In these studies little attention was paid to the effect of temperature, although Friend (1964*b*) found the far-red response to be maximal at 30°C. Under continuous fluorescent and incandescent illumination, however, floral initiation of wheat was earlier with each increase in temperature from 10 to 30°C (Friend, Fisher, and Helson 1963). Similar data are not available for barley, although the results of Guitard (1960) suggest that there is little effect of temperature within the range 13–24°C.

Metabolic destruction of phytochrome P_{FR} (Pratt and Briggs 1966) and, presumably, dark reversion and synthesis of phytochrome, are temperature-dependent processes. In as far as these reactions affect flowering, a change in temperature would be expected to affect the photoperiodic response. Little is known of the influence of temperature on the flowering of long-day plants, however, and consequently the responses of the barley plant to different combinations of light and temperature were explored.

II. Experimental Methods

Four barley cultivars, Prior, Piroline, CI 3576, and CI 5611 were grown in the majority of the experiments. These cultivars cover a range of photoperiodic-response types ranging from a pronounced long-day response (Prior) to almost a day-neutral response (CI 3576) (Aspinall 1965). In addition, in two experiments the six-row variety Olli was used. This variety has a moderately pronounced long-day response (Guitard 1960).

Plants were grown in John Innes compost mixture at the rate of six per pot (8 in. diam.). Single plants were removed from each pot at various intervals, taking care not to disturb the remaining seedlings. Occasional comparisons with plants grown singly in similar pots indicated that this technique had negligible effects on the rate of apical development, at least up to double-ridge formation (Aspinall 1965). In the majority of experiments, the major aim was to determine the date of double-ridge formation with accuracy. As this was unpredictable in many of the environments tested, five plants were dissected every 3–10 days, depending on the rate of development, until the apex reached the late vegetative stage when double-ridge formation was imminent. Ten plants were then dissected daily until double-ridge formation had taken place. In most environments double-ridge formation took place in at least 90% of the plants within 1–2 days. In short photoperiods, where double-ridge formation was spread over a number of days, and with CI 3576, which was more heterogeneous than the other varieties, the day on which 50% of the plants had formed double ridges was determined.

The experiments were carried out in controlled-environment cabinets. In the initial experiments, treatments (day length or temperature) were given sequentially in the same controlled-environment cabinet. This cabinet was divided centrally by an opaque screen and the plants on one side received white fluorescent light alone (Phillips TLF 80/33) and on the other fluorescent light supplemented with incandescent light (Osram, 24-in., 75 W). These light sources were adjusted to provide a total light energy of 3800 μW cm^{-2} (1500 f.c.) of fluorescent light and 6600 μW cm^{-2} (50 f.c.) of incandescent light at plant height, as measured with a thermopile. These produced approximately 5 and 12 μW cm^{-2}mμ^{-1} respectively of light energy in the region 700–800 mμ when measured with a photometer fitted with a narrow-band interference filter (Robertson and Holmes 1963). Occasional checks were made to confirm that identical treatments would give similar results when interpolated at different times in the sequence of experimental treatments.

In the experiments designed to investigate the nature of the spectral sensitivity of the response, Sylvania Gro-Lux fluorescent tubes, with a low far-red component, were used as a basic light source. These were filtered through red cinemoid (Strand Electric Co.) to provide a red source, or blue cinemoid to provide a blue source. Far-red light was provided by General Electric BCJ incandescent lamps. The light energy provided by these sources in the relevant spectral bands is given in Table 1.

A purer source of far-red illumination was provided in some experiments by the use of incandescent light filtered through a Westlake FRF-700 filter (Evans, Borthwick, and Hendricks 1965).

TABLE 1

LIGHT ENERGY IN THE BLUE (450 mμ), RED (640 mμ), AND FAR-RED (740 mμ) REGIONS OF THE SPECTRUM INCIDENT ON PLANTS ILLUMINATED WITH VARIOUS LIGHT SOURCES

Light Source	Light Energy (μW cm^{-2}mμ^{-1}) at Wavelength (mμ):		
	450	640	740
Gro-Lux with red cinemoid	0·03	3·90	0·20
Gro-Lux with blue cinemoid	4·01	0·01	0·04
BCJ lamps	0·15	0·80	13·90
Gro-Lux lamps	4·00	5·21	0·19

III. EXPERIMENTAL RESULTS

(a) *Wavelength Dependence of the Response*

In an attempt to confirm that the promotion of flowering due to the inclusion of incandescent light in the light source was due to the far-red component and not to any enrichment in the red region of the spectrum (Aspinall 1965), plants of four cultivars were grown at different distances from a far-red source (incandescent light filtered through Westlake filter) in a large growth room otherwise evenly illuminated with fluorescent light (3800 μW cm^{-2}). A photoperiod of 16 hr and a constant temperature of 30°C were maintained throughout the experimental period. Plants of the cultivar CI 3576 showed no response to far-red light intensity, although they had reached an advanced stage of floral development (initiation of lemmas), a result consistent with the small response of this cultivar to the inclusion of incandescent light in the light source (Aspinall 1965). The cultivar Piroline was harvested too early to demonstrate a marked response but both Prior and CI 5611 showed pronounced acceleration of flower formation with increasing intensity of far-red light (Fig. 1). Of these two cultivars, CI 5611 appeared to require a higher intensity of far-red light for floral promotion. The experiment was not designed to distinguish between an absolute requirement for far-red light and promotion by a particular balance of red and far-red. There was no evidence, however, of an optimum intensity of far-red illumination.

This experiment confirmed that the enhanced rate of development noted when fluorescent light was supplemented with incandescent was due to the far-red component. In Mohr's (1962) description of a high-energy response, blue light was also

promotive. This did not appear to be the case in the present system as fluorescent light has a high blue component and yet is relatively poorly promotive. Two attempts were made to check the response to blue irradiation, however, using the cultivar

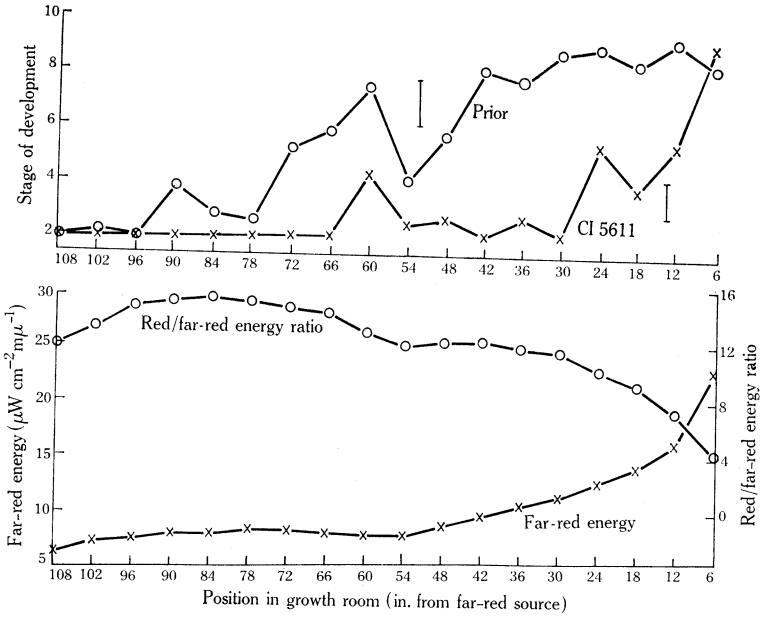


Fig. 1.—Flowering response of barley (cv. Prior and CI 5611) to intensity of far-red light (incandescent filtered through a Westlake FRF-700 filter) in the light source. Plants grown for 30 (Prior) or 42 days (CI 5611) in a 16-hr photoperiod at 30°C with fluorescent light (1500 f.c.) plus a varying intensity of far-red light. Bars indicate least significant differences ($P=0\cdot05$). Stage of development scored as follows: *1*, vegetative; *2* elongated vegetative apex; *3*, double-ridge formation; *8*, stamen initiation; *9*, awns initiated (Aspinall and Paleg 1963).

Olli as the test plant. Following growth for 3 days in continuous white light at 30°C, plants were grown in continuous white fluorescent (Gro-Lux), red, blue, or a mixture of red and blue light for some 9 days. The results are given in the following tabulation:

Light regime	White	Red	Blue	Red + Blue
Stage of development*	7·2	5·7	3·7	6·4

* Scored as for Figure 1. Least significant difference ($P = 0\cdot05$) is 0·7.

The apical development of the white light-grown plants was most advanced and that of the blue light-grown plants least. Adding blue light to the red light regime advanced development only slightly.

The above experiment could be interpreted in terms of a photosynthetic response to the light rather than a true photomorphogenetic response. Further evidence on this point was obtained by growing plants (cv. Olli) for a short period

in various photoperiods of light of different spectral composition (Fig. 2). In this experiment, far-red produced a pronounced photoperiodic response, whereas both red and blue light produced only a very slight response. It is unlikely that this difference in photoperiodic response could be attributed to a photosynthetic mechanism alone as plants in all light regimes had reached the same stage of development in the shortest photoperiod. Whilst these experiments do not disprove the possible existence of a response in the blue region of the spectrum, they do suggest that it is considerably less important than the far-red response.

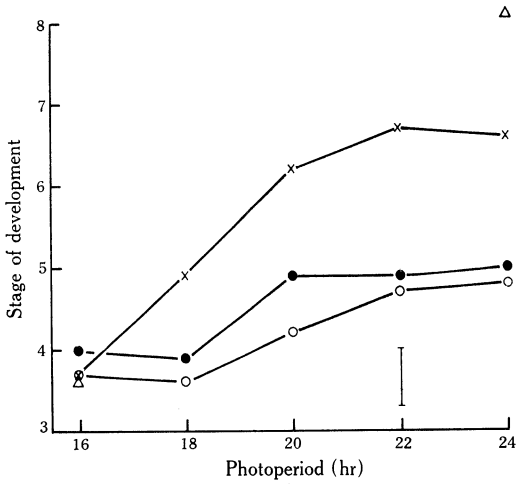


Fig. 2.—Flowering response of barley (cv. Olli) to different photoperiods of far-red, red, and blue light. Plants grown for 3 days in continuous white light, 5 days in the various light environments, and a final 5 days in continuous white light. Temperature 30°C throughout. ×Far-red; ● blue; ○ red; △ white light. Bar indicates least significant difference ($P=0{\cdot}05$).

The results discussed so far could be due to either continuous promotion by far-red during light exposure, or to the balance between the two forms of phytochrome at the beginning of the dark period. Several attempts were made, again with Olli, to affect the flowering response by exposure of plants to relatively brief (10 or 20 min) periods of red or far-red light at the termination of a 14-hr photoperiod (Table 2).

In general, the terminal light exposure had little or no effect on flowering. In those cases where statistically significant effects were observed, terminal red exposure reduced the flowering response after a main light period consisting of fluorescent and incandescent light, and terminal far-red exposure promoted flowering when following a main light period of fluorescent light alone. Exposure for 20 min was no more effective than that for 10 min, and these effects of the terminal light period were much less in magnitude than the response to the inclusion of incandescent light in the main light period. This experiment suggests that the state of phytochrome upon entering the dark period may have some influence on flowering, but little in comparison to the light regime during the main period of light exposure.

(*b*) *Temperature and the Flowering Response*

In the initial experiment, the effects of temperatures ranging from 10 to 30°C on the floral initiation of four cultivars (Prior, Piroline, CI 3576, and CI 5611) growing in continuous light were investigated. In all four varieties the optimum temperature for initiation was around 20°C, although in all but CI 5611 there was little difference

TABLE 2

EFFECTS OF A TERMINAL EXPOSURE TO RED OR FAR-RED LIGHT ON THE FLOWERING OF BARLEY

Stage of development was scored at the completion of each experiment, numbers being assigned as in Figure 1. In any one row, numbers bearing the same superscript are not statistically significantly different ($P = 0 \cdot 05$). Far-red/red energy ratios for the various light treatments are given in parentheses

Duration of Experiment (days)	Time of Extension (min)	Main Light Period (14 hr)*	Stage of Development after Extensions of: None (0·04)	Red Light (0·04)	Far-red Light (108·96)	Main Light Period (14 hr)*	Stage of Development after Extensions of: None (1·27)	Red Light (0·04)	Far-red Light (108·96)
19†	10	F (0·04)	$2 \cdot 4^{a}$	$2 \cdot 2^{a}$	$3 \cdot 0^{a}$	F+I (1·27)	$5 \cdot 6^{b}$	—	—
12‡	10	F (0·04)	$2 \cdot 9^{a}$	$2 \cdot 9^{a}$	$2 \cdot 5^{a}$	F+I (1·27)	$4 \cdot 1^{b}$	$4 \cdot 1^{b}$	$3 \cdot 8^{b}$
20‡	10	F (0·04)	$8 \cdot 1^{a}$	$8 \cdot 9^{b}$	$9 \cdot 1^{b}$	F+I (1·27)	$9 \cdot 6^{c}$	$9 \cdot 1^{b}$	$9 \cdot 6^{c}$
21†	10	F (0·04)	—	$2 \cdot 6^{a}$	$3 \cdot 1^{a}$	F+I (1·27)	$5 \cdot 1^{bc}$	$4 \cdot 4^{c}$	$5 \cdot 8^{b}$
21†	20	F (0·04)	—	—	—	F+I (1·27)	—	$5 \cdot 1^{bc}$	$5 \cdot 7^{b}$
35†	10	F (0·04)	—	$2 \cdot 7^{a}$	$4 \cdot 4^{b}$	F+I (1·27)	$8 \cdot 2^{c}$	$7 \cdot 2^{d}$	$8 \cdot 7^{c}$
35†	20	F (0·04)	—	—	—	F+I (1·27)	—	$8 \cdot 0^{cd}$	$8 \cdot 6^{c}$

* F, fluorescent; F+I, fluorescent+incandescent.

† Grown in stated environments from sowing.

‡ Grown for 5 days in continuous fluorescent light at 30°C then transferred to stated environments.

within the range 15–25°C as long as incandescent light was included in the light source (Fig. 3). The inclusion of incandescent light in the source had only marginal effects on the time of initiation at 20°C or below. In Prior and Piroline there was an increase in the time to double-ridge formation in the absence of incandescent light at temperatures above 20°C. This temperature-induced delay in development was not as evident when incandescent light was present. In Piroline, the delay due to the omission of incandescent light from the source increased from 2 days at 20°C to 23 days at 30°C. CI 3576 and CI 5611 demonstrated little trace of this interaction of the effects of temperature and light spectrum. In CI 3576 the maximum effect of the spectral composition of the light source was a 3-day difference in initiation and in CI 5611 it was a 2-day difference.

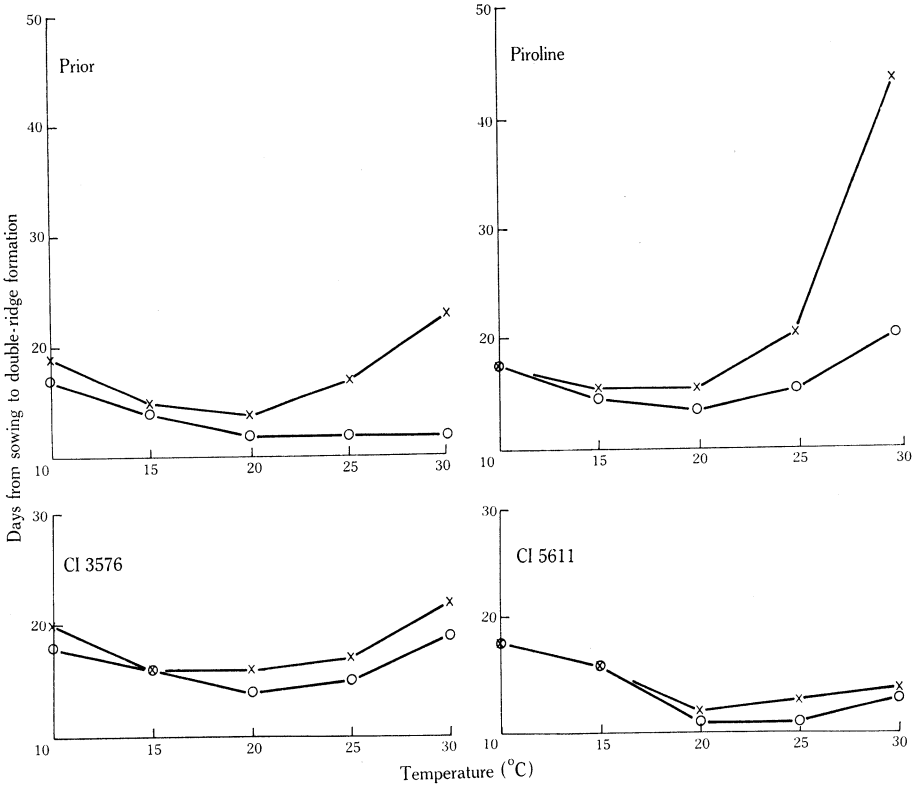


Fig. 3.—Effect of temperature on the time from germination to floral initiation in continuous light. × Fluorescent light alone (light energy in 700–800 mμ region, 5 μW $cm^{-2}m\mu^{-1}$). ○ Fluorescent plus incandescent light (light energy in 700–800 mμ region, 17 μW $cm^{-2}m\mu^{-1}$).

The influence of photoperiod and light source at one temperature was next investigated. Plants of the same four cultivars were grown at 23°C with and without incandescent light in photoperiods ranging from 8 to 24 hr. Of the four cultivars, Prior showed the greatest effect of incandescent light with a 5-day difference in the

time of floral initiation between the two light sources (Fig. 4). In this and the other cultivars, there was no evidence of any change in the response to incandescent light with photoperiod. CI 5611 demonstrated the greatest photoperiodic response and CI 3576 the least.

This experiment was repeated at 30°C and it was found that the increase in temperature profoundly influenced floral initiation (Fig. 5). In the 12-hr photoperiod no plants, except CI 3576, initiated flowers within the 95-day period that the plants were grown. The CI 3576 plants (under both light sources) initiated flowers after some 88 days, but the apices showed varying degrees of abnormal development. Several apices appeared to have reverted from a floral to a vegetative state (Fig. 6) with double-ridge primordia at the base of the apex and leaf primordia near the tip.

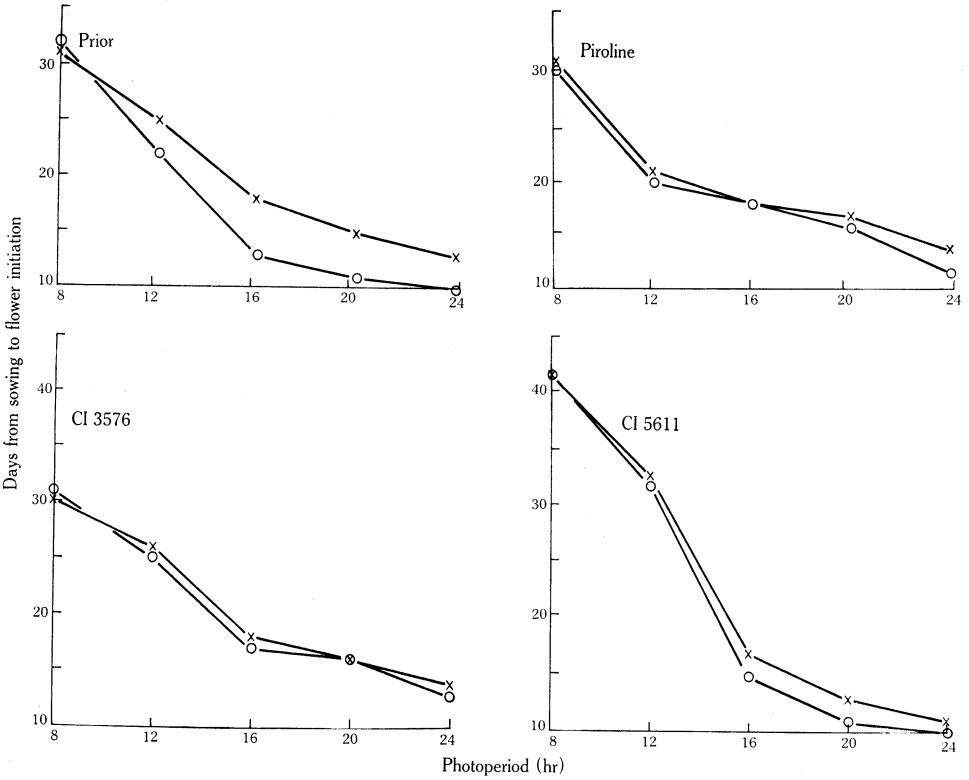


Fig. 4.—Effect of photoperiod on floral initiation at 23°C. × Fluorescent light alone. ○ Fluorescent plus incandescent light.

In the other photoperiods, again excepting CI 3576, promotion of floral initiation by incandescent light was relatively greater in the shorter photoperiods. With Prior and CI 5611 plants growing in a 16-hr photoperiod, flowering was delayed by some 25 days by the omission of incandescent light from the light source. Piroline plants did not initiate flowers in the 16-hr photoperiod when incandescent light was not included in the light source, and required 52 days when it was included.

The data from these three experiments suggest the operation of a profound temperature–photoperiod interaction in the control of flowering in barley. Even in the cultivar CI 3576, when there was little evidence of any response to incandescent light and the photoperiodic response was weak, initiation was greatly delayed by high temperature at the shortest photoperiod. In Prior and CI 5611 at 30°C there was a very marked photoperiodic response in the absence of incandescent light but a much lesser effect, in the 16- to 24-hr photoperiods, in its presence.

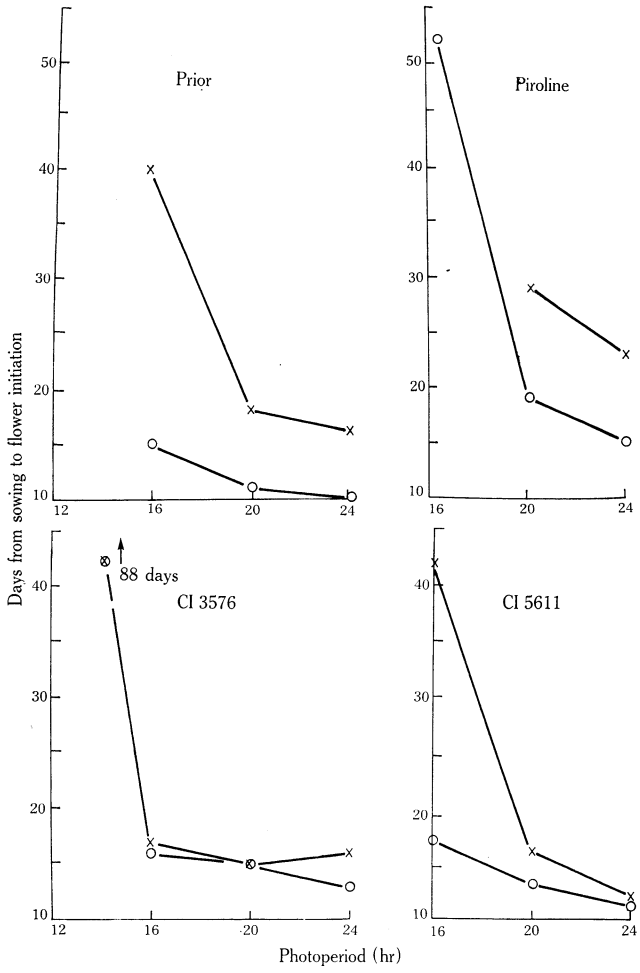


Fig. 5.—Effect of photoperiod on floral initiation at 30°C. Symbols as in Figure 4.

(c) *Photoperiodic Induction by Short-term Treatments*

In the experiments considered so far, plants were exposed to set photoperiodic and temperature regimes throughout development. Cereals in general have been found to require several inductive photoperiodic cycles to influence apical morpho-

genesis and, for this reason, have not been used as frequently in photoperiodic research as have plants florally inducible by a single cycle. The increase in the difference in rate of flower formation between plants grown in long and in short photoperiods at 30°C, as compared with 20°C, suggested that single-cycle induction may be effective at the higher temperature. This possibility was investigated in a series of experiments in which barley plants were grown for various periods in a 12-hr, 30°C regime, and were then subjected to a single 24-hr, 30°C cycle. No consistent effects of this treatment on floral initiation were obtained with less than a 50-day growth period prior to exposure to the inductive cycle. Even then, only some 50% of the plants formed flowers in Prior, which demonstrated the greatest response. Plants grown for 80 days in the 30°C, 12-hr environment before exposure to a single 24-hr cycle gave more uniform floral induction (Table 3). One feature of the response,

TABLE 3

RESPONSE OF BARLEY PLANTS TO A SINGLE 24-HR LIGHT PERIOD AT 30°C AFTER GROWTH FOR 80 DAYS IN A 12-HR, 30°C ENVIRONMENT

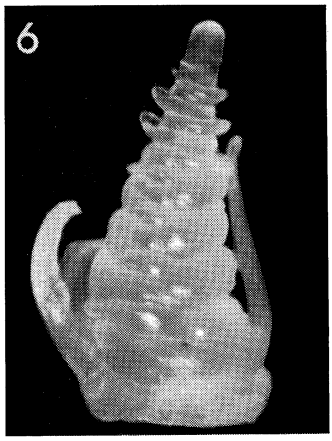
Plants were scored 15 days after the inductive cycle, numbers being assigned as in Figure 1

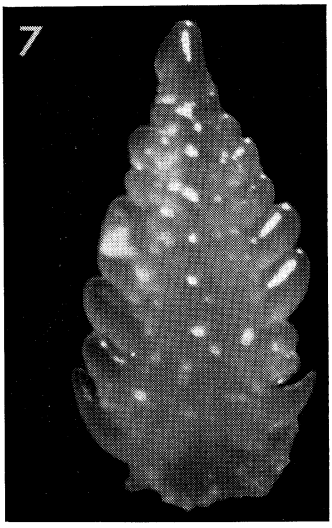
Cultivar	Stage of Development after:	
	No Inductive Cycle	One Inductive Cycle
Prior	2	8
Piroline	2	4
CI 3576	4	9
CI 5611	2	2

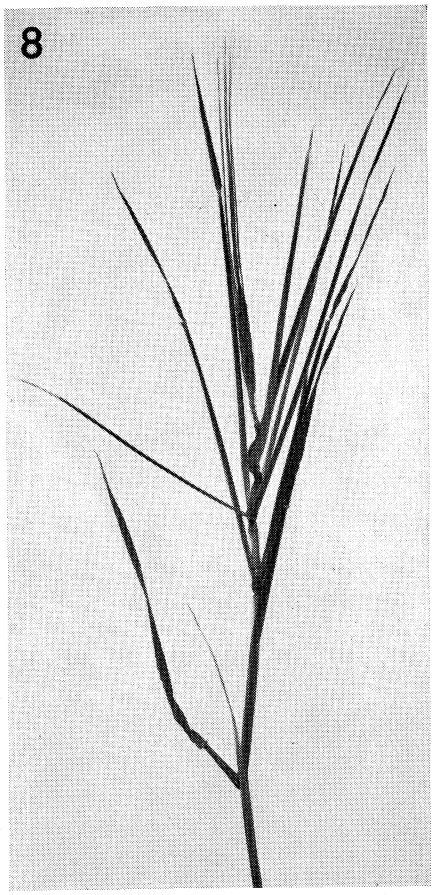
however, was the large number of abnormal apices produced. The abnormalities generally involved apparent reversion towards the vegetative state, as has been described for CI 3576 plants grown in a 12-hr, 30°C environment (Fig. 6), or showing abnormal elongation of the primordia (Fig. 7) as described by Koller, Highkin, and Caso (1960). Plants allowed to mature in a glasshouse subsequently produced groups of leaves separated by very short internodes immediately below the ear (Fig. 8).

The four cultivars considered in these experiments demonstrated a wide range of responsiveness to single-cycle induction and it is possible that experiments with a wider range of genotypes would lead to the discovery of a cultivar giving a more uniform response earlier in development. Nine further varieties exposed to single-cycle induction 21 days after sowing showed no floral induction however (Table 4), so a prolonged insensitive period may be general under these circumstances. The cultivar Volla appeared to be unusual in that it developed very rapidly at 30°C, even in the 12-hr photoperiod.

Consideration was also given to the effects of a temperature reduction for one or more 24-hr cycles on plants growing otherwise in a 12-hr, 30°C environment.







Figs. 6–8.—Abnormal development induced by high temperature. **6**, Apex of CI 3576 plant grown for 88 days at 30°C in a 12-hr photoperiod, showing extensive floral development in basal primordia with subsequent reversion to leaf development in upper primordia. **7**, Apex of Piroline plant grown for 80 days in a 12-hr, 30°C environment and then exposed to one 24-hr light period. Primordia on the apex show abnormal elongation. **8**, Piroline plant treated as above and then grown for a further 6 weeks in the glasshouse, showing numerous leaves separated by abnormally short internodes immediately below the ear.

Reducing the temperature to 20°C for from 1 to 6 days did not result in floral induction in Prior, Piroline, or CI 5611 although there was some stimulation of apical growth,

particularly in Piroline (Fig. 9). Similarly, reducing the temperature to 20 or even 10°C during a single 24-hr inductive cycle given 42 days after sowing did not result in floral initiation.

TABLE 4

RESPONSE OF 9 BARLEY CULTIVARS TO A SINGLE 24-HR LIGHT PERIOD AT 30°C AFTER 21 DAYS GROWTH IN A 12-HR, 30°C ENVIRONMENT

Plants were scored as in Figure 1

Cultivar	Stage of Development after:	
	No Inductive Cycle	One Inductive Cycle
Prior	1·3	1·4
Winter habit (sh)	2·0	2·0
Spring habit (Sh)	2·0	2·0
Noyep	1·0	1·0
Volla	6·0	5·3
CI 3576	1·0	1·0
Naked Blanco Mariout	1·0	1·0
Long Outer Glume	2·0	2·0
Bankuti Korai	2·7	2·8

IV. DISCUSSION

The existence of a high-energy far-red photoresponse controlling flower formation in barley is confirmed by the present experiments. In many respects the system resembles that described for the control of flowering in *Hyoscyamus niger* (Schneider, Borthwick, and Hendricks 1967) and has features in common with those suggested for several other long-day plants including wheat and barley (Friend 1964*a*; Lane, Cathey, and Evans 1965). As with these other systems, it is impossible at present to deduce the nature of the responsible pigment system from the available data. In comparison with the *H. niger* photoresponse, which has been best characterized, barley appears to respond but little to irradiation in the blue region of the spectrum (400–500 mμ). This was particularly evident in the lack of response to increasing photoperiods of blue light in comparison to the marked response to far-red irradiation (Fig. 2). The effect of the far-red region of the spectrum is pronounced and requires relatively high energies for significant responses. Although a complete action spectrum is not available, preliminary interference-filter experiments indicate a peak response at 710 mμ, which agrees well with the action spectrum for the high energy response of *H. niger* (Schneider, Borthwick, and Hendricks 1967).

The participation of a photo-reversible, phytochrome-mediated step in the control of flowering in barley is not confirmed by these data, although there is adequate evidence both for the presence of phytochrome in barley (Siegelman and Butler 1965) and for its role in the control of flowering by night interruption with brief periods of illumination (Borthwick, Hendricks, and Parker 1948). In the series of experiments designed to investigate the hypothesis that the high-energy far-red promotion of flowering was photoreversible, the responses obtained were only marginal in comparison with the flowering induced by long exposure to far-red

illumination (Table 2). The data suggested a slight promotion of flowering by low phytochrome P_{FR} levels in the plant at the beginning of the dark period, a finding in agreement with the conclusion of Lane, Cathey, and Evans (1965). This, of course, does not conflict with the possibility that phytochrome may be the photomorphogenetic pigment controlling all aspects of the flowering response in barley by means which are so far not understood (Lane, Cathey, and Evans 1965).

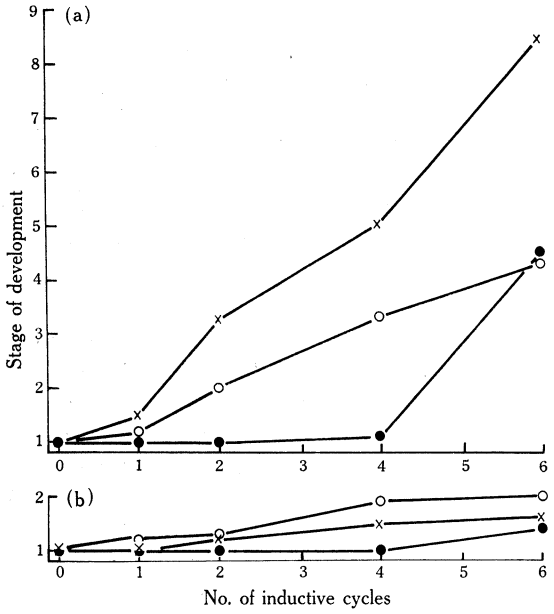


Fig. 9.—Promotion of apical development by exposing plants growing in a 12-hr, 30°C environment to inductive cycles at 20°C, with 24-hr (*a*) and 12-hr (*b*) photoperiods. Stage of development scored as for Figure 1. × Prior ○ Piroline. ● CI 5611.

It is clear that, whatever pigment system is responsible for the control of flowering in barley, control is subject to considerable modification by the ambient temperature. Temperatures over the range 10–20°C have no differential effects on flowering, the delays in flower formation at low temperatures being explicable purely in terms of general metabolic rates. At higher temperatures, however, there was a marked interaction between the effects of temperature and both the photoperiod and the spectrum of the light source. In all four varieties, the higher temperatures (particularly 30°C) delayed flowering more in short than in long photoperiods and, with the exception of CI 3576, more in low intensities of far-red light than in high. CI 3576 was exceptional in showing very little response to far-red light under any circumstance although flowering was delayed considerably by a short photoperiod–high temperature combination.

The attempts to induce flowering in several barley varieties by a single inductive cycle at high temperature were unsuccessful except after relatively prolonged growth in short-day conditions. The minimal period of 70 days required before complete induction occurs compares with 42 days in *Lolium temulentum* (Evans 1960). Floral development after induction at 75 days was very rapid in Prior. This may suggest a slow change in state or the accumulation of a substrate under short-day, high-temperature conditions, enabling rapid morphogenesis to occur once the plants were

florally induced. The situation was evidently different in CI 5611 as single-cycle induction was completely ineffective in this variety even after prolonged growth in a short photoperiod.

In the Gramineae, flowering involves the precocious initiation of the growth of axillary branches on the apex, followed by the conversion of these axillary branches into floral structures. Using the initiation of axillary branches (double ridges) as a criterion of flower induction assumes that further growth of these axillary branches to floral structures follows. This is a reasonable assumption in normal circumstances, but some exceptions have been found. The relative rate of differentiation at each node on the apex varies considerably (Nicholls and May 1963), and the rate is particularly low at the base of the apex. In conditions under which differentiation is slow (e.g. short photoperiods) a precocious axillary branch may commence to develop on the apex, particularly in a basal position, but will not continue to do so, resulting in the ultimate presence of a leaf at that node (Gott, Gregory, and Purvis 1955). When floral differentiation is rapid this does not occur and all nodes scored as bearing double ridges ultimately form flowers.

Once a double ridge has formed and further development occurs, progress of that branch to form floral structures is not invariable. In the best-documented exception, treating unvernalized winter grasses with gibberellic acid induces precocious vegetative branch formation on the apex (Koller, Highkin, and Caso 1960). The present abnormalities suggest a similar situation occurring in a short photoperiod at high temperature. Furthermore, once a few primordia on the apex have formed double ridges, all further primordia produced will also normally form floral primordia. Again, this does not appear to be inevitable as leaf initials formed at sites above double-ridge primordia on some apices grown at 30°C.

These abnormalities of the development of the apex appear to occur under environmental conditions which are marginal for flower induction. Nevertheless, they do suggest that flower formation in the Gramineae may be complex. As the initiation of growth in the axillary positions on the apex does not necessarily indicate the commencement of floral development, it is not likely that induction is a single-step process. Rather, it appears that at least a two-phase system is more feasible, with cell division at the axillary branch site being first activated, followed by direction of the development of these dividing cells towards floral morphogenesis.

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