Plant Physiol. (1979) 64, 1015–1021
0032-0889/79/64/1015/07/$00.50/0

Kinetics and Time Dependence of the Effect of Far Red Light on the Photoperiodic Induction of Flowering in Wintex Barley[1]

Received for publication February 28, 1979 and in revised form July 30, 1979

GERALD F. DEITZER, REBECCA HAYES, AND MERTEN JABBEN[2]
Smithsonian Institution, Radiation Biology Laboratory, 12441 Parklawn Drive, Rockville, Maryland 20852

ABSTRACT

Flowering in the long day plant *Hordeum vulgare* L. var. Wintex barley was enhanced by the addition of far red light to the main light portion of the photoperiod. Far red energy was provided to produce quantum flux ratios (660/730 nm) and phytochrome photoequilibria (Pfr/total phytochrome) equivalent to those reported both beneath a leaf canopy and outside a canopy at twilight. The photoperiodic requirement for long days can be completely eliminated by the addition of far red light. However, both the effect of extending the photoperiod without far red and the addition of far red to 12-hour photoperiods were suboptimal. Maximal stimulation was achieved only when far red was added to continuous light. The duration of the period of maximal apex elongation rate, as well as the reduction of the time required for floral initiation, were saturated by three inductive cycles. When far red energy was provided intermittently during 3 days of continuous light, the ability to respond varied in a circadian manner. This enhancement of flowering by far red appears to be mediated by the "high irradiance response" of phytochrome.

Wintex barley is a facultative long day plant (1) that is quantitatively stimulated to flower by increasing daylengths. Action spectra for the promotion of flowering in long day plants by R[3] light (4) and its reversal by FR light (24) given as brief interruptions of the dark period, clearly established that phytochrome can interact with an internal timing mechanism to regulate the perception of daylength in these plants. The similarity of action spectra for the promotion of flowering in long day plants (4, 24) and the inhibition of flowering in short day plants (25) led to the concept of phytochrome as the primary photoreceptor mediating photoperiodic responses in plants (14).

Subsequent experiments with daylength extensions, rather than dark interruptions, found that a mixture of R and FR was more effective for promotion than R alone (7, 21, 31). The action spectrum for this response (27) shows a single peak in the R-FR region between 710 and 720 nm and some action in the blue at high irradiances. Such responses have been termed "high irradiance responses" (HIR) (28), to distinguish them from the low energy R/FR reversible responses, and are assumed to be a complex function of the photostationary state between Pr and Pfr (13).

Although Hartmann (13) has interpreted the HIR responses solely in terms of phytochrome in etiolated systems, effects of such high irradiances on photosynthesis in light-grown plants complicate this interpretation in flowering experiments (9, 10, 26). Removal of CO_2 during an inductive period leads to decreased flowering (26). This inhibition can be reversed by simultaneous application of an exogenous carbohydrate source (22, 26). That this is not the result of simple maintenance of growth has been suggested by Bodson *et al.* (2) who reported alternate promotion and inhibition of flowering by CO_2 and high light intensity dependent upon whether the treatments were given during the first or second portion of an inductive long day. Thus, experiments dealing with high irradiances for extended periods must deal with the complication of photosynthesis in any tissue that contains functional chloroplasts.

If the promotion of flowering in long day plants is mediated by the HIR of phytochrome the question of how natural daylight interacts to control the response remains a problem. The spectral composition of daylight maintains a fairly constant high R/FR ratio of about 1.2 throughout the majority of the day (12, 17) that would be expected to produce phytochrome photoequilibria of about 60% Pfr (30). Shifts toward lower ratios have been reported to occur both at twilight (12, 17, 29) and below a canopy of leaves (18).

Wagner (32) has suggested that the twilight spectral shifts act through an external coincidence with an endogenous circadian rhythm to control photoperiodism. The importance of such twilight changes has been questioned (23) based on the highly variable nature and relatively small change in these ratios that reach levels of only about 0.4 outside the canopy (17). The work reported here was performed in an attempt to determine the effect of small changes in R/FR ratio on the photoperiodic enhancement of flowering in Wintex barley. Experiments were performed under conditions with equivalent total PAR and minimal distortion to the spectral distribution of the light between 400 and 700 nm as a consequence of the addition of FR to lower the R/FR ratio.

MATERIALS AND METHODS

Growth Conditions. *Hordeum vulgare* var. Wintex barley seed is not commercially available and was supplied by Dr. D. A. Reid at the USDA/ARS, Tucson, Arizona, from a stock harvested in July 1976. Preliminary experiments established that the minimum age required for optimal induction of flowering was 7 days from the start of imbibition. Groups of 25 seeds were sown on Vermiculite in plastic freezer boxes and allowed to imbibe on deionized H_2O for 4 days in the dark at 20 ± 0.5 C. At the end of this time all seedlings had coleoptiles above the level of the Vermiculite. They were then transferred for an additional 4 days to full strength Hoagland No. 1 solution (with a chelated iron source) in growth chambers with 12-h daylight fluorescent photoperiods at a constant temperature of 20 ± 0.5 C and RH of 70 ± 5%.

Light Treatments. At the end of the 8-day pretreatment plants were given various treatments with either daylight fluorescent alone or daylight fluorescent supplemented with FR light. Day-

[1] This work was carried out under partial support of the Department of Energy under Contract EY-76-S-05-4241 and was partially supported by the Deutsche Forschungsgemeinshaft.

[2] Present address: Institut für Biologie II, Universität Freiburg, Schänzlestrasse 1, D-7800 Freiburg, Federal Republic of Germany.

[3] Abbreviations: R: red; FR: far red; HIR: high irradiance response.

light fluorescent sources (Sylvania F48T12/D/VHO) were used at an irradiance (400–700 nm) of 432 ± 30 μmol $m^{-2}s^{-1}$ (94.0 ± 6.5 w m^{-2}) during all 12-h photoperiods and 222 ± 8 μmol $m^{-2}s^{-1}$ (48.3 ± 1.7 w m^{-2}) for all 24-h photoperiods (measured with a Lambda quantum sensor, radiometrically calibrated for daylight fluorescent light, and averaged from readings taken at bed height for each position within the chambers before and after each experiment. Radiometric equivalents were based on the quantum flux at 550 nm, the mean wavelength of the spectral energy distribution from 400 to 700 nm of the daylight fluorescent emission in Fig. 1). The maximal FR energy (700–800 nm) with daylight fluorescent light alone was 2.7 w m^{-2} under 12-h photoperiods and 0.9 w m^{-2} with 24-h photoperiods (readings taken as a single measurement in the center of the chamber before and after each experiment using a scanning radiometer with 50 nm bandpass filters similar to the unit described by Goldberg and Klein [11]). The relative quantum flux ratio (660/730 nm) was about 5.6 (Table I) for both daylight fluorescent photoperiods (measured at ± 4.0 nm with a Schoeffel GM-100 spectral radiometer, calibrated against an NBS radiometric standard lamp).

Supplemental FR energy was provided by mixing daylight fluorescent lamps with single FR-emitting phosphor fluorescent lamps (Westinghouse F48T12/IR/VHO obtained from Controlled Environment Systems, Inc., Rockville, Md.) in a 1:1 ratio. Irradiances (400–700 nm) were 428 ± 28 μmol $m^{-2}s^{-1}$ and 213 ± 18 μmol $m^{-2}s^{-1}$ (93.1 ± 6.1 and 46.3 ± 3.9 w m^{-2}) for 12- and 24-h photoperiods, respectively. The FR energy during 12-h photoperiods was 22.3 w m^{-2} and 10.1 w m^{-2} for the 24-h photoperiods. The relative quantum flux ratio was about 0.45 (Table I).

Thus, all conditions had equivalent total energies (PAR) between 400 nm and 700 nm of 18.7 ± 0.2 mol m^{-2} day^{-1} (4.06 ± 0.04 MJ m^{-2} day^{-1}) irrespective of photoperiod and differed solely with respect to the amount of FR (700–800 nm) light (see spectral emission curves in Fig. 1). Net photosynthetic CO_2 uptake is below saturation at both irradiance levels (unpublished data).

Phytochrome Measurements. Oat seedlings (*Avena sativa* L. var. Garry oat; Agway Seed Company, Syracuse, N.Y.) were grown either for 5 days in the dark at 22 C on one layer of Kimpack moistened with distilled H_2O or for 6 days under the various light sources described above at 22 C on one layer of Kimpack moistened with 0.2 mM of the herbicide 4-chloro-5-(methylamino)-2-(α,α,α-trifluro-*m*-tolyl)-3(2H)-pyridazinone (San 9789 or Norflurazon, for details see ref. 19). The etiolated seedlings were then exposed for 10 min to the various light sources and 20 coleoptiles (including leaf) were placed vertically in a metal cuvette (1.2 × 1.2 × 4 cm aluminum block with two 5-mm-wide glass windows and a horizontal path length of 8 mm). Twenty-five fully expanded leaves of light-grown (herbicide-treated) tissue were harvested in a similar manner. The cuvettes were kept on ice in the dark prior to measurement.

Phytochrome levels were determined *in vivo* using an Aminco model DW-2 spectrophotometer with the measuring beam wavelengths set at 660 and 730 nm with a 5 nm bandwidth. The actinic light was obtained from a 24-v side illumination accessory using 660 and 730 nm Baird-Atomic interference filters (10 nm half-bandwidth). The calculated values in Table I were based on the equation of Hartmann (13) using measured values for 660 and 730 nm and a value of 0.8 for the relative amount of Pfr in R.

Sampling. A single sample consists of one individual box with about 25 seedlings. Samples were removed at the onset of the light period of the day indicated and placed in the dark at 4 C during harvest. Roots were removed and fresh weight determined for the whole population. Ten plants were selected that were within the

Table I. *Measured and Calculated Values for the Quantum Flux Ratios (660/730 nm) and Phytochrome Photoequilibria (Pfr/Ptot) Established by the Various Lamp Sources Described in Fig. 1 for Both Dark- and Light-grown Garry Oat Seedlings*

Lamp Source	Quantum Flux Ratio	Pfr/Ptotal		
			Measured	
	660/730	Calculated[1]	Dark-grown[2]	Light-grown[3]
Daylight fluorescent	5.6	0.73	0.68	0.63
Daylight fluorescent + far red fluorescent	0.45	0.45	0.38	0.47
Far red fluorescent	0.02	0.04	0.04	0.05

[1] From equation of Hartmann (13).
[2] Grown in dark for 5 days and exposed to 10 min of light described.
[3] Grown for 6 days in light described (20).

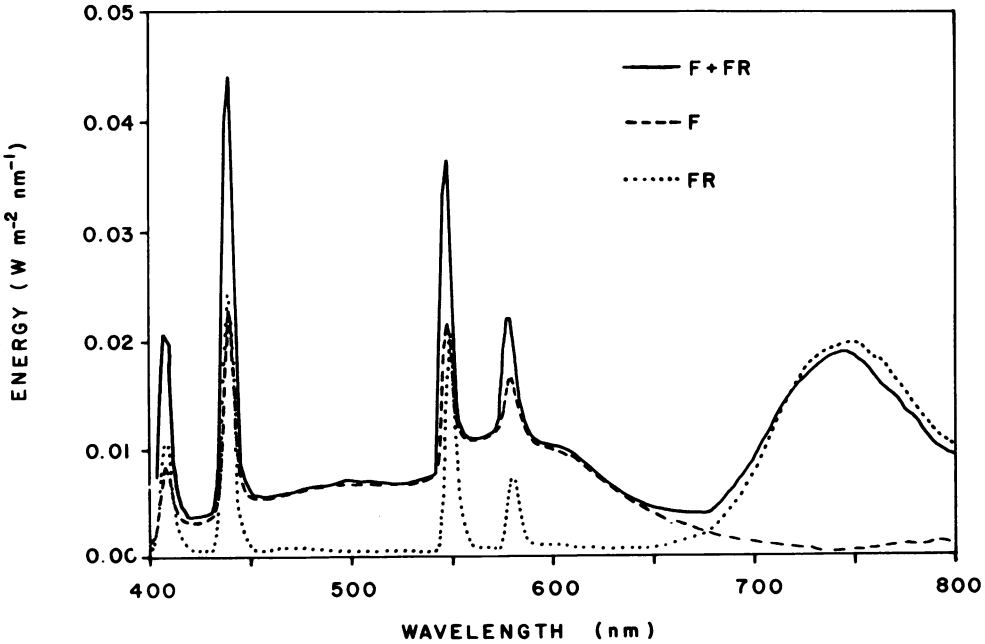

FIG. 1. Spectral emission curves for the daylight fluorescent (– – –), the FR phosphor fluorescent (·····), and both combined (——). Curves were measured with a Schoeffel GM-100 spectral radiometer calibrated against an NBS standard tungsten source.

standard deviation of the mean fresh weight. Preliminary experiments established that the fresh weight of plants was normally distributed and the variation in fresh weight was correlated with the time of germination. Attempts to synchronize germination were unsuccessful, necessitating some selection criteria. The 10 plants so selected were stored in Petri dishes containing distilled H_2O at 4 C during dissection.

Apices were removed using a dissecting microscope, and scored as floral stage according to Bonnett (3). Stage 1 refers to an indeterminate vegetative apex and stage 2 to a fully determinate reproductive apex that produces no further leaf primordia. Stages 3 to 10 are distinct morphological steps in the development of the mature inflorescence. No attempt was made to choose stages for linearity of development with time. Intermediate stages reported are statistical and no attempt was made to define such stages. Apex length was measured at the same time with a calibrated reticle in the dissecting microscope. Finally, all plants used for dissection were dried for 24 h at 110 C in a drying oven and used for dry weight determinations.

RESULTS

Energy Sources. A fluorescent source of FR energy was used in place of the usual incandescent source. The spectral emission curves for daylight fluorescent lamps, with or without the FR phosphor sources, are shown in Figure 1. Since the only energy from the FR source between 400 and 650 nm occurs in the mercury lines, the distribution of the energy when combined with the daylight fluorescent is virtually identical to the daylight fluorescent alone over this region. There is a slight difference between 650 and 700 nm due to the emission of the FR phosphor. When combined at equal PAR, the spectrum resembles that of solar daylight with minimal distortion due to the addition of FR while avoiding the problem of radiative heat transfer to the leaves with no requirement for additional heat-absorbing filters.

Phytochrome photoequilibria measured in oat seedlings, either exposed to 10 min or grown for 6 days in continuous light with the spectral distribution reported in Figure 1, are shown in Table I. Both calculated and measured values are in good agreement with each other as well as with values reported by Smith and Holmes (30). Differences among all three methods for any given light source are not significant while those between different light sources are significant at the 95% confidence level.

Floral Kinetics. The effect of adding FR light to either 12- or 24-h fluorescent photoperiods is shown in Figure 2. Under 12-h fluorescent photoperiods, the transition to state 2 (initiation) takes place between days 17 and 21, but there is no further development until about day 26 (not shown). Both maximal extension of the photoperiod to 24 h, and addition of FR light to 12-h photoperiods, cause a significant decrease in the lag prior to initiation and are quantitatively very similar. When FR is added to continuous fluorescent light, there is a further enhancement in the time of initiation and in the rate of floral development. The 1-day lag between initiation and the onset of development is very repeatable.

Although care was exercised to equalize the energy available for photosynthesis, effects on growth measured as dry weight were nevertheless found (Table II). Both the addition of FR and the extension of the photoperiod caused an increase in dry weight accumulation. Therefore, a parameter was sought that would reflect changes in both growth and development. The increase in apex length was found to be continuous and directly correlated

Table II. *Dry Weight Accumulation during Growth under Continuous 12- or 24-h Photoperiods with or without Supplemental FR*

Total PAR is equal under all conditions and standard errors are less than 5%.

Growth Conditions	Dry Weight Measured on Day			
	5	10	15	20
	g/plant			
12-h − FR	0.032	0.056	0.103	0.150
12-h + FR	0.029	0.058	0.122	0.282
24-h − FR	0.037	0.074	0.147	0.276
24-h + FR	0.041	0.096	0.186	0.343

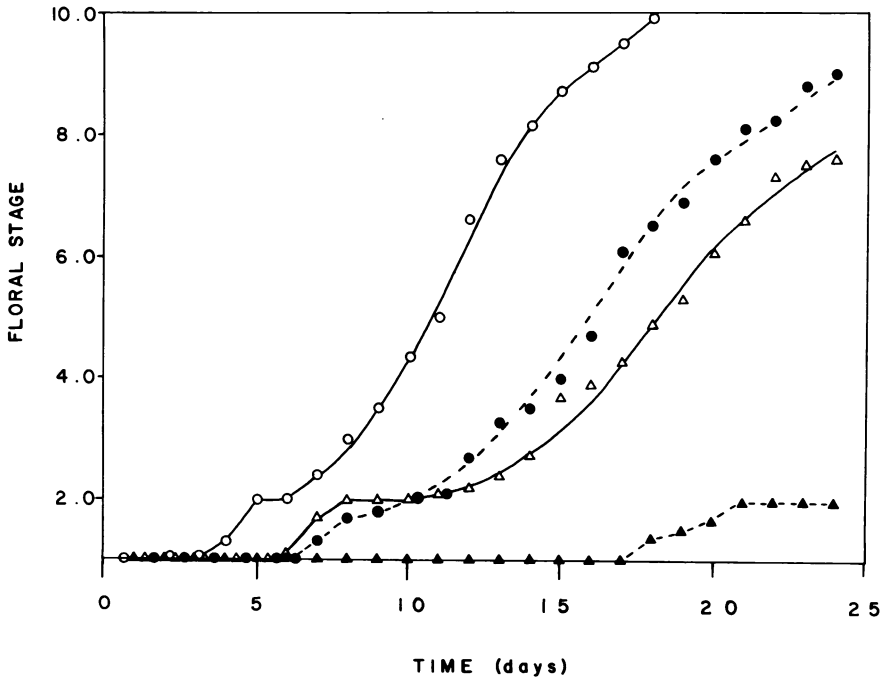

FIG. 2. Floral stage as a function of time under different light regimes. Floral stage 1 is vegetative, floral stage 2 is the first fully transformed floral apex, and stages 3 to 10 are clearly defined morphological steps (2) leading to the fully mature influorescence (stage 10). After 8 days pretreatment, plants were grown continuously under either 12-h daylight fluorescent (▲), 12-h daylight fluorescent supplemented with FR (△), or 24-h daylight fluorescent (●) and 24-h daylight fluorescent supplemented with FR (○) photoperiods. Each point is the average of five separate determinations of 10 plants each with standard errors less than 5%.

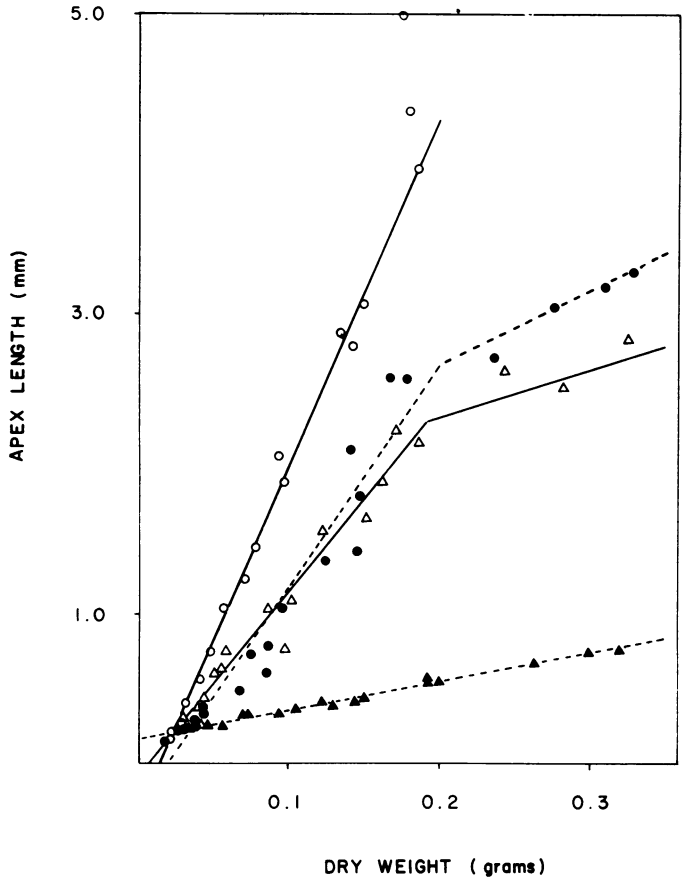

FIG. 3. Correlation of increase in apex length with increase in dry weight when grown under 12-h daylight fluorescent (▲), 12-h daylight fluorescent supplemented with FR (△), 24-h daylight fluorescent (●) or 24-h daylight fluorescent supplemented with FR (○) photoperiods.

with the increase in dry weight (Fig. 3). The effect of adding FR light to the 12-h photoperiods or extending the photoperiod to 24 h is to increase the rate of apex elongation (slope of the linear regression) by a factor of about 6 to 7 in both cases. The combination of adding FR and extending the photoperiod is roughly additive, increasing the rate by a factor of about 12. The control increases linearly throughout the experiment. However, both those with added FR and those with an extended photoperiod increase rapidly for only about 18 days. The rate then reverts to that of the control. When both conditions are combined the increase is also biphasic but, at about day 18 when stage 10 is reached, the rate of increase becomes even more rapid. The correlation coefficients for the initial phase are all greater than 0.95 and greater than 0.90 for the second phase.

Number of Inductive Cycles. Since optimal induction was obtained only when the photoperiod was extended with light containing FR, various numbers of 24-h photoperiods containing FR were given and the kinetics followed after return to 12-h photoperiods without FR (Fig. 4). A single inductive period enhances initiation by about 12 days, but does not yield further development for at least 26 days. A second inductive period enhances initiation by an additional 2 days and results in further floral development after a lag of only 3 days. Both the enhancement of initiation and the time of onset of continued development are saturated by three inductive cycles. However, when returned to 12-h photoperiods without added FR, the rate of floral development immediately decreases by a factor of 2 when compared to continuous light containing FR.

If apex length is again considered as a function of dry weight (Fig. 5), it is clear that each inductive period stimulates the elongation of the apex to the same extent as continuous induction. However, apex growth then reverts to the control rate at a time dependent on the number of inductive cycles. As with floral stage, the duration of this initial rate is saturated with three inductive cycles. Additional inductive cycles cause the apex to cease elongation at the initial rate at the same time, but the rate of elongation under noninductive conditions now increases above that of the control. This rate is saturated only under continuous inductive conditions.

Intermittent FR. Since 3 days of continuous light with added FR is saturating for the enhancement of initiation, the effect of adding FR at varous times to 72 h of continuous fluorescent light alone was tested. After the standard 8-day pretereatment, all plants were placed in continuous light with or without supplemental FR at equal PAR as in previous experiments. At 3-h intervals, groups of plants were moved from fluorescent alone to a cabinet with supplemental FR for 6 h and then returned for the remainder of the 72-h period. At the end of this 3-day period all plants were returned to 12-h fluorescent photoperiods for an additional 10 days and then evaluated for floral stage, apex length, and dry weight. The results (Fig. 6) represent the means from two independent experiments with a total of four to five replicate determinations of 10 plants each for every point. Standard errors are indicated by error bars.

Supplemental FR (F + FR) given continuously for 72 h results in an increase in both floral stage and apex length by a factor of 2 but has no significant effect on dry weight when compared to continuous fluorescent alone (F). Addition of FR for 6 h stimulates both floral parameters to a maximum of about 50% of that attained by 72 h with FR, and the response shows a very marked time dependence with maxima and minima recurring with circadian frequency. This rhythm of effectiveness of FR damps after two cycles and is just barely above the fluorescent control in the third cycle. There is no evidence of any oscillatory behavior in dry weight and the apparent slight decrease over the 72-h period is not significant.

DISCUSSION

Inasmuch as both the addition of FR energy and an extension of the photoperiod lead to an increase in dry weight accumulation (Table II) the assumption that the complications of photosynthesis can be avoided by comparing conditions under equal PAR is not always valid. The reason for this may reside in the nonreciprocity of photosynthesis when periods as long as 12 and 24 h are compared (*i.e.* there is a greater increase in dry weight with 24-h photoperiods compared to 12-h photoperiods even though the total PAR is the same in both), and the effect of FR energy on the efficiency of photosynthesis. It is possible that the FR effect results from the slight difference in the spectral emission between 650 and 700 nm.

Whatever the cause, differences in net photosynthesis can be normalized by basing the results on a parameter of flowering that is correlated directly with the change in dry weight. For this reason, the kinetic behavior of both floral stage and apex length development was followed. Floral stage is not correlated with the increase in dry weight. This is most clearly seen by the variable lag period at stage 2 (Fig. 4) when the number of inductive cycles is varied. No such lag is seen in dry weight accumulation, which is a continuous log-linear function of time. The increase in the elongation of the apex is also a continuous function and is correlated directly with the increase in dry weight ($r > 0.95$).

Null responses in both short (8, 20) and long day plants (6) have led to the concept of two phytochrome-controlled events involved in photoperiodic induction. Holland (15, 16) has also demonstrated a requirement for a low Pfr reaction followed by a high Pfr reaction in the long day plant *Lolium*. Thus, there seems to be a change during the course of the day in the optimal photoequilibrium requirement, which has the opposite phase in short and long day plants. Results presented here also show a time-dependent change in response to a decrease in the R/FR ratio or low Pfr

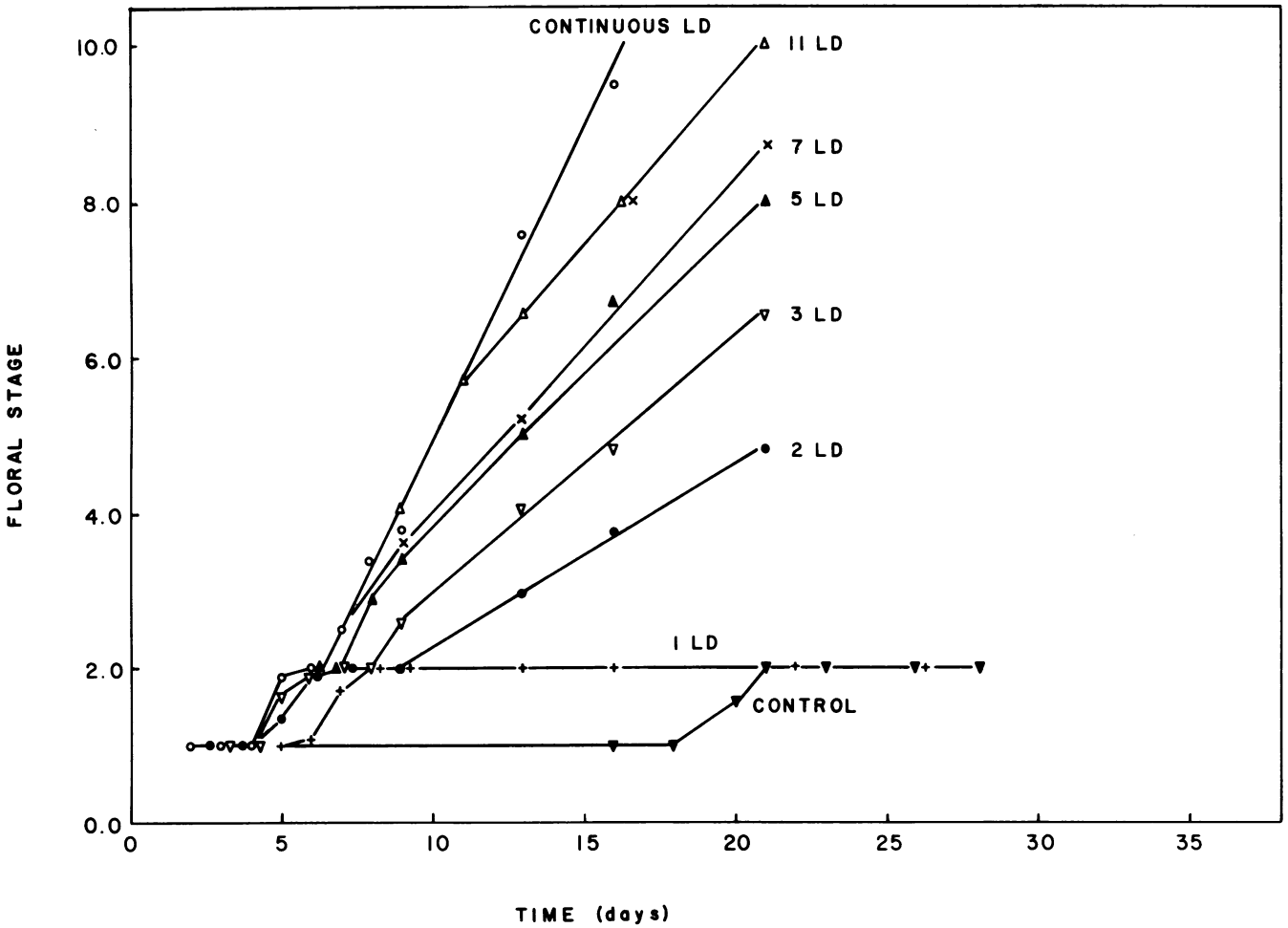

FIG. 4. Floral stage as a function of time following treatment with varying numbers of 24-h long day photoperiods supplemented with FR light prior to return to 12-h short day photoperiods without supplemental FR light. Control, continuous 12-h short-days (▼), 1 long day (+), 2 long days (●), 3 long days (▽), 5 long days (▲), 7 long days (×), 11 long days (△), and continuous 24-h long days (○).

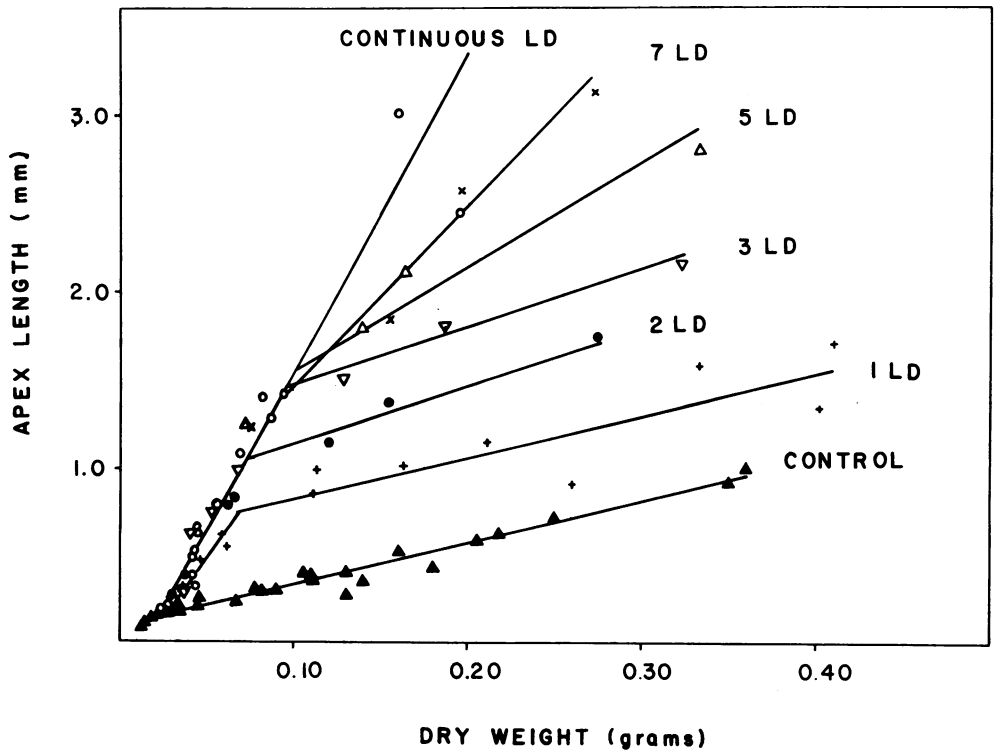

FIG. 5. Correlation of apex length with dry weight following treatment with varying numbers of 24-h long day photoperiods supplemented with FR light prior to return to 12-h short day photoperiods without supplemental FR light. Control, continuous 12-h short days (▲), 1 long day (+), 2 long days (●), 3 long days (▽), 5 long days (△), 7 long days (×), and continuous 24-h long days (○).

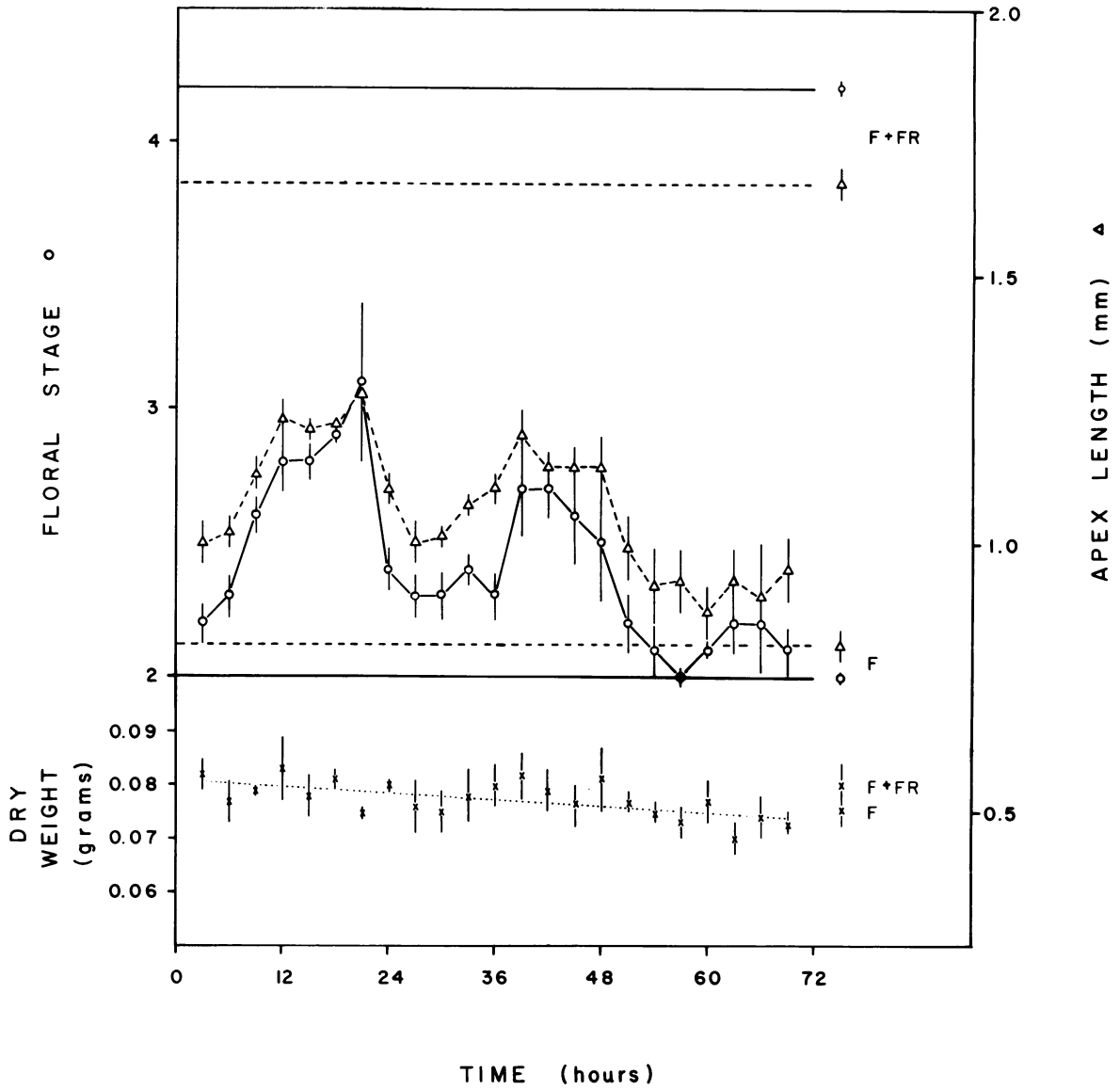

FIG. 6. Effect on floral stage (○), apex length (△), and dry weight (×) of 6 h of FR light added at various times to a continuous 72-h daylight fluorescent period which was inserted to interrupt 12-h photoperiods. Points are plotted at the center of the 6-h treatment.

reaction. We interpret the response as one mediated through the HIR of phytochrome (5). The quantitative nature of the response, its mediation by intermediate photoequilibrium states of phytochrome, and its enhancement against a background of continuous light support this conclusion. In order to test this hypothesis, a more detailed examination of both the irradiance and wavelength dependence of the response will be required. The sensitivity and stability of the response to a single inductive period suggest that this test may be reasonably accomplished using this system.

LITERATURE CITED

1. ALTMAN PL, DS DITTMER 1964 Biology Data Book. Federation of American Societies for Experimental Biology, Bethesda, Md
2. BODSON M, RW KING, LT EVANS, G BERNIER 1977 Photosynthesis and flowering in the long day plant *Sinapis alba*. Aust J Plant Physiol 4: 467–478
3. BONNETT OT 1935 The development of the barley spike. J Agric Res 51: 451–457
4. BORTHWICK HA, SB HENDRICKS, MW PARKER 1948 Action spectrum for photoperiodic control of floral initiation of a long day plant, Wintex barley (*Hordeum vulgare*). Bot Gaz 110: 103–118
5. BORTHWICK HA, SB HENDRICKS, MJ SCHNEIDER, RB TAYLORSON, VK TOOLE 1969 The high-energy light action controlling plant responses and development. Proc Nat Acad Sci USA 64: 479–486
6. EVANS LT 1976 Inflorescence initiation in *Lolium temulentum* L. XIV. The role of phytochrome in long day induction. Aust J Plant Physiol 3: 207–217
7. EVANS LT, HA BORTHWICK, SB HENDRICKS 1965 Inflorescence initiation in *Lolium temulentum* L VII. The spectral dependence of induction. Aust J Biol Sci 18: 745–762
8. EVANS LT, RW KING 1969 Role of phytochrome in photoperiodic induction of *Pharbitis nil*. Z Pflanzenphysiol 60: 277–288
9. FRIEND DJC 1968 Spectral requirements for flower initiation in two long-day plants, rape (*Brassica campestris* cv. ceres), and spring wheat (*Triticum* × *aestivum*). Physiol Plant 21: 1185–1195
10. FRIEND DJC 1969 *Brassica campestris* L. *In* LT Evans, ed, The Induction of Flowering, Some Case Histories. Cornell University Press, Ithaca, NY, pp 364–375
11. GOLDBERG B, WH KLEIN 1974 Radiometer to monitor low levels of ultraviolet irradiance. Appl Opt 13: 493–496
12. GOLDBERG B, WH KLEIN 1977 Variations in the spectral distribution of daylight at various geographical locations on the earth's surface. Sol Energy 19: 3–13
13. HARTMANN KM 1966 A general hypothesis to interpret "high energy phenomena" of photomorphogenesis on the basis of phytochrome. Photochem Photobiol 5: 349–366
14. HENDRICKS SB, HA BORTHWICK 1963 Control of plant growth by light. *In* LT Evans, ed, Environmental Control of Plant Growth. Academic Press, New York, pp 233–263
15. HOLLAND RWK 1969 The effects of red and far-red light on floral initiation in *Lolium temulentum* and other long-day plants. PhD thesis. Univ of Reading, UK
16. HOLLAND RWK, D VINCE 1971 Floral initiation in *Lolium temulentum* L.: the role of phytochrome in the responses to red and far-red light. Planta 98: 232–243
17. HOLMES MG, H SMITH 1977 The function of phytochrome in the natural environment. I. Characterization of daylight for studies in photomorphogenesis and photoperiodism. Photochem Photobiol 25: 533–538
18. HOLMES MG, H SMITH 1977 The function of phytochrome in the natural environment. II. The influence of vegetation canopies on the spectral energy distribution of natural daylight. Photochem Photobiol 25: 539–546

19. JABBEN M, GF DEITZER 1978 A method for measuring phytochrome in plants grown in white light. Photochem Photobiol 27: 127–131
20. KING RW, BG CUMMING 1972 The role of phytochrome in photoperiodic time measurement and its relation to rhythmic time keeping in *Chenopodium rubrum*. Planta 108: 39–57
21. LANE H, HM CATHEY, LT EVANS 1965 The dependence of flowering in several long day plants on the spectral composition of light extending the photoperiod. Am J Bot 52: 1006–1014
22. LANG A, G MELCHERS 1943 Die photoperiodische Realktion von *Hyoscyamus niger*. Planta 33: 653–702
23. MONTIETH JL 1975 Spectral distribution of light in leaves and foliage. *In* H Smith, ed, Light and Plant Development, Butterworth London, pp 447–460
24. PARKER MW, SB HENDRICKS, HA BORTHWICK 1950 Action spectrum for the photoperiodic control of floral initiation of the long-day plant *Hyoscyamus niger*. Bot Gaz 111: 242–252
25. PARKER MW, SB HENDRICKS, HA BORTHWICK, NJ SKULLY 1946 Action spectrum for the photoperiodic control of floral initiation of short day plants. Bot Gaz 108: 1–26
26. QUEDADO RM, DJ FRIEND 1978 Participation of photosynthesis in floral induction of the long day plant *Anagallis arvensis* L. Plant Physiol 62: 802–806
27. SCHNEIDER MJ, HA BORTHWICK, SB HENDRICKS 1967 Effects of radiation on flowering of *Hyoscyamus niger*. Am J Bot 54: 1241–1249
28. SHROPSHIRE WA 1972 Phytochrome, a photochromic sensor. *In* AC Giese, ed, Photophysiology, Vol 7. Academic Press, New York, pp 34–67
29. SHROPSHIRE WA 1973 Photoinduced parental control of seed germination and the spectral quality of solar radiation. Sol Energy 15: 99–105
30. SMITH H, MG HOLMES 1977 The function of phytochrome in the natural environment. III. Measurement and calculation of phytochrome photoequilibria. Photochem Photobiol 25: 547–550
31. STOLWIJK JAJ, JAD ZEEVAART 1955 Wavelength dependence of different reactions governing flowering in *Hyoscyamus niger*. Vehr K Akad Wet 58: 386–396
32. WAGNER E 1975 The nature of photoperiodic time measurement: energy transduction and phytochrome action in seedlings of *Chenopodium rubrum*. *In* H Smith, ed, Light and Plant Development. Butterworth London, pp 419–433