Phases of Development to Flowering in Opium Poppy (*Papaver somniferum* L.) under Various Inductive Photoperiods

Zhongchun Wang, Mary C. Acock, and Basil Acock

U.S. Department of Agriculture, Agriculture Research Service, Remote Sensing and Modeling Laboratory, Beltsville, MD 20705

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Abstract. Four phases of development from emergence to anthesis of the opium poppy (*Papaver somniferum* L.) are recognized based on transfer studies using 9- and 16-hour photoperiods: a photoperiod-insensitive juvenile phase (JP), a photoperiod-sensitive inductive phase (PSP), a photoperiod-sensitive postinductive phase (PSPP), and a photoperiod-insensitive postinductive phase (PIPP). The objective of this experiment was to determine how the durations of the photoperiod-sensitive phases changed when the plants were exposed to different photoperiods. Plants were grown in lamplight growth chambers with a 12-hour thermoperiod of 25 °C day/20 °C night. They were transferred from a noninductive 9-h to an inductive 12-, 14-, or 16-hour photoperiod or vice versa at 1- to 4-day intervals to determine the durations of the four phases. The average number of days to flower by plants grown continuously in a 16-hour photoperiod was 32 days. Days to flower were delayed by 10 days in the 14-hour photoperiod and by 36 days in the 12-hour photoperiod. The durations of the four phases were not equally affected by photoperiod. The first three phases were photoperiod-dependent, the photoperiod effect being nonlinear. The durations of JP, PSP, and PSPP were 3, 5, and 17 days in the 16-hour; 4, 8, and 23 days in the 14-hour; and 7, 14, and 40 days in the 12-hour photoperiod, respectively. The final phase was not sensitive to photoperiod (i.e., PIPP lasted 7 days regardless of photoperiod). Based on these results, we conclude that the so-called juvenile phase cannot be regarded as photoperiod-insensitive. To model the development of opium poppy under field conditions, a knowledge of daylength as early as seedling emergence may be necessary. The number of inductive cycles needed for floral induction and the rate of floral development largely depend on the photoperiod experienced.

Flowering time determines capsule size and thus affects gum yield of field-grown opium poppy (Acock et al., 1996b, 1997). To develop methods for estimating gum yield, one must know how long the plants have grown before flowering. Photoperiod is the environmental factor that has the most influence on the development rate of poppy (Acock et al., 1996a).

The opium poppy is a long-day plant with a critical photoperiod near 16 h (Acock et al., 1996a; Gentner et al., 1975). Plants grown in a 9-h photoperiod do not initiate flowers within 120 d after emergence (DAE), but those grown in a 16-h photoperiod flower in 32 DAE (Wang et al., 1997a). Based on the sensitivity of opium poppy plants to a 16-h photoperiod, Wang et al. (1997a, 1997b) divided the interval between emergence and first flower into four phases: 1) a photoperiod-insensitive (juvenile) phase (JP), in which plants were insensitive to

photoperiod during the first 3 to 4 DAE; 2) a photoperiod-sensitive inductive phase (PSP), in which plants required a minimum of four 16-h inductive cycles for rapid flowering; 3) a photoperiod-sensitive postinductive phase (PSPP), in which plants required 17 additional inductive cycles for flowering to occur without delay; and 4) a photoperiod-insensitive postinductive phase (PIPP), in which flowering time was no longer influenced by photoperiod. To predict flowering time of poppy plants grown in the field, one must know how the durations of these phases change with photoperiod and whether they are affected by temperature. Our recent study suggested that the duration of the third phase (PSPP) was strongly temperature-dependent, but all other phases were temperature-insensitive (Wang et al., 1997b). The influence of various photoperiods on the durations of the two photoperiod-sensitive phases of development has not been established.

The current experiment was designed to determine how the phases of development up to flowering change when plants are grown in various photoperiods. The specific objectives of the experiment were to 1) determine how each phase is affected by varying the photoperiod, and 2) obtain data needed for establishing quantifiable relationships to predict flowering time of plants in field conditions when daylength varies.

Plant culture. Seeds of *Papaver somniferum* (var. album DC) were sown in 3.75-L pots filled with a Jiffy Mix growing medium (Jiffy Products, Batavia, Ill.) consisting of 1 Canadian sphagnum peat : 1 vermiculite (v/v). Dolomitic lime was added to adjust the pH of the medium to 6.5. Thirty-five pots were placed in each of six reach-in controlled environment chambers (Environmental Growth Chambers, Inc., Chagrin Falls, Ohio). Temperatures during the entire experimental period were controlled at 25 ± 1 °C during the first 12 h (0800–2000 HR), and at 20 ± 1 °C for the next 12 h (2000–0800 HR) in all six chambers. Each chamber was provided with six high-pressure sodium and six metal halide lamps that were alternated in three rows. Photosynthetic photon flux (PPF) was maintained at 1100 ± 100 μmol·m⁻²·s⁻¹ at the top of the plant canopy by adjusting a high-intensity discharge dimmer and/or bench height. Stern's Miracle-Gro fertilizer (15.0N–13.1P–12.4K) was applied twice a week to each pot in 200 mL of irrigation water at an N concentration of 175 mg·L⁻¹ beginning at 7 DAE. Plants were watered as needed during the experiment.

Photoperiod and transfer intervals. The photoperiod was 9 h (0800–1700 HR) in three chambers and 12 (0800–2000 HR), 14 (0800–2200 HR), and 16 h (0800–2400 HR), respectively, in the remaining three. The plants were transferred, three at a time, from a 9-h to a 12-, 14-, or 16-h photoperiod or vice versa at various intervals. The 9-h was chosen as a noninductive photoperiod because it is short enough to keep plants vegetative (Acock et al., 1996a). The 16-h was chosen as a highly inductive photoperiod because photoperiods of >16 h have an effect on flowering time similar to that of the 16-h photoperiod (Acock et al., 1996a). The 12- and 14-h photoperiods were chosen because plants grown in those photoperiods were expected to flower later than those grown in a 16-h photoperiod (Acock et al., 1996a). Thus, plants grown on the shorter photoperiods were expected to show different sensitivities during some or all phases of growth if such differences existed compared with those grown in a 16-h photoperiod.

Plants were transferred from a 9-h to a 12-, 14-, or 16-h photoperiod on the day of seedling emergence (0 DAE) and at 1-d intervals thereafter until 6 DAE, after which transfers were made at 2- to 4-d intervals up to 28 DAE. Three plants in the 9-h photoperiod chamber were not transferred and used as controls. Following transfer, plants were grown in the new photoperiod until the first flower opened.

Plants were transferred from a 12-, 14-, and 16-h to a 9-h photoperiod at 6 DAE, and were made at 1- to 4-d intervals thereafter until 64, 40, and 28 DAE, respectively. The 6 DAE was chosen as the first transfer date because of space limitations and because previous experiments (Wang et al., 1997a) had indicated no transfer effects in the 16-h photoperiod before 8 d. Three plants in each of the 12-, 14-, and 16-h photoperiods were not transferred and used as controls. After transfer,

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plants were grown in the 9-h photoperiod until the first flower opened or until the experiment was terminated at 154 DAE.

Seedlings emerged 5 to 6 d after sowing. The day of emergence was defined as the day when the two cotyledons had unfolded. Plants were thinned to one per pot at 20 DAE. The flowering date (i.e., the date when the first flower on a plant opens) was recorded for each plant.

Phase determination. The method used for determination of the four phases from emergence to anthesis was similar to that described by Wilkerson et al. (1989) and reported previously (Wang et al., 1997a). The duration of JP was determined by transferring plants at various intervals from the noninductive 9-h to the inductive 12-, 14-, or 16-h photoperiod. If the inductive photoperiod had no effect relative to that of the 9-h photoperiod, we assumed that the plants were insensitive to photoperiod during this developmental stage. The end of JP was estimated by intersection of two linear equations. One linear equation with a slope = 0 had intercept values equivalent to average flowering times for plants grown continuously in a 12-, 14-, or 16-h photoperiod. The second linear equation with a slope $\neq 0$ was obtained using the flowering times from the 9- to the 12-, 14-, or 16-h transfers. The flowering times from the first few transfer dates that reduced the r^2 value of the equation were omitted from the second equation.

The duration of PSP was determined by transferring plants at regular intervals from the inductive 12-, 14-, or 16-h to the noninductive 9-h photoperiod after seedling emergence. The minimum duration of PSP was estimated by subtracting the estimated duration of JP from the minimum number of days required for rapid flowering. The term "rapid flowering" was used to distinguish those plants that flowered with no or relatively little delay from those that flowered eventually, but after much delay.

The end of PSPP was identified as the earliest day prior to anthesis when flowering time was no longer influenced by photoperiod, i.e., flowering times were the same as those of controls. The duration of PSPP was then derived by subtracting the estimated durations of the first two phases (JP and PSP) from the day when PSPP ended.

The minimum duration of PIPP before the first flower opened was calculated by subtracting the minimum days for the first three phases (JP, PSP, and PSPP) from the days to flower in the control groups.

For plants transferred from the 16- to the 9-h photoperiod, values from four separate experiments were combined ($n = 12$) to generate the relationship between the days to flower and the days to transfer. Two of these four experiments have already been described (Wang et al., 1997a, 1997b).

Results and Discussion

Photoperiod-insensitive juvenile phase (JP). There was a linear relationship between the days to flower and the days to transfer from

the noninductive 9-h to the inductive 12-, 14-, and 16-h photoperiods (Fig. 1A–C). The average flowering time for plants grown continuously in a 16-h photoperiod was 32 d (Fig. 1C). Transfers between 0 and 3 DAE had no effect, but later transfers significantly delayed flowering time. Thus, the end of JP, as estimated by the intersection of two linear equations, was 3 DAE (Fig. 1C). A similar result was obtained in a previous experiment (Wang et al., 1997a).

The average flowering time was 42 d for plants grown continuously in a 14-h photoperiod (Fig. 1B) and 68 d in a 12-h photoperiod (Fig. 1A). Using the same procedures described above, the end of JP was estimated as 4 and 7 DAE for plants transferred from a 9- to a 14-h and a 12-h photoperiod, respectively. Estimates for the end of JP for each photoperiod, the minimum number of inductive days required for rapid flower initiation, and the end of photoperiodic influence on flowering

Fig. 1. Days from emergence to flower as a function of days from emergence to transfer for poppy plants transferred from a 9-h to a (A) 12-, (B) 14-, or (C) 16-h photoperiod. The horizontal broken lines indicate the average number of days to flower for plants that remained in a 12-, 14-, or 16-h photoperiod. The flowering times from the first few transfer dates that showed no sensitivity to photoperiod were omitted from the regression lines.

Table 1. Estimates for the end of the juvenile phase and minimum number of inductive day/night cycles required for floral development of opium poppy plants in 12-, 14-, or 16-h photoperiods.

	Photoperiod (h)		
	12	14	16
Estimated end of the juvenile phase (DAE) ^a	7	4	3
Minimum time required for rapid flower initiation (DAE)	21	12	8
Estimated end of photoperiod influence on flowering (DAE)	61	35	25
Total number of days required for flowering (DAE)	68	42	32

^aDAE = days after emergence.

Fig. 2. Days from emergence to flower as a function of days from emergence to transfer for poppy plants transferred from a (A) 12-, (B) 14-, or (C) 16-h photoperiod to a 9-h photoperiod. The horizontal broken lines indicate the average number of days to flower for plants that remained in a 12-, 14-, or 16-h photoperiod. The flowering times from the last few transfer dates that showed no sensitivity to photoperiod were omitted from the regression lines.

are summarized in Table 1. A separate experiment showed that plants transferred from a 9- to an 11-h photoperiod did not demonstrate any transfer effect until 10 DAE (Wang et al., unpublished data). These results indicate that the duration of the observed JP, as defined by transferring plants from a noninductive to an inductive photoperiod, varied with the length of the latter. Plants transferred to the 16-h photoperiod had the shortest JP, followed by those transferred to the 14-, 12-, and 11-h photoperiods. Thus, the so-called JP appears to be photoperiod-sensitive.

Photoperiod-sensitive inductive phase (PSP). Transferring plants from an inductive to a noninductive photoperiod delayed or totally inhibited flowering (Fig. 2). Plants transferred from a 16-h to a 9-h photoperiod at 8 DAE flowered at 48 DAE (Fig. 2C), whereas plants transferred 2 d earlier did not flower (data not shown) during the 154-d experimental period. Thus, a 16-h photoperiod for 8 DAE

was critical for plants to make a rapid, qualitative transition from vegetative to reproductive development, confirming previous findings (Wang et al., 1997a, 1997b). By subtracting the estimated duration of JP (3 d) from the pivotal day (8 d), the minimum number of inductive day/night cycles (i.e., the minimum duration of PSP) required for flowering was estimated to be 5 d. Estimates of durations of four phases for each photoperiod are summarized in Table 2.

The time required for rapid flowering was found to be 12 and 21 DAE in the 14- and the 12-h photoperiods, respectively (Table 1; Fig. 2 A and B). Thus, the minimum durations of PSP were estimated as 8 and 14 d in the 14- and 12-h photoperiod, respectively (Table 2). No pivotal day for rapid flowering was found for plants transferred from an 11- to a 9-h photoperiod (Wang et al., unpublished data). In the shorter photoperiods, the distinction between inductive and noninductive responses becomes

Table 2. Estimates of durations (days) of the juvenile phase (JP), the photoperiod-sensitive inductive phase (PSP), the photoperiod-sensitive postinductive phase (PSPP), and the photoperiod-insensitive postinductive phase (PIPP) in opium poppy plants in 12-, 14-, or 16-h photoperiod.

Phase	Photoperiod (h)		
	12	14	16
JP	7	4	3
PSP	14	8	5
PSPP	40	23	17
PIPP	7	7	7
Total length (DAE) ^a	68	42	32

^aDAE = days after emergence.

unclear and variation in plant response to photoperiod masks any difference that might exist between a 9- and 11-h photoperiod.

Photoperiod-sensitive postinductive phase (PSPP). The rate of flower development for plants transferred from a 16- to a 9-h photoperiod was enhanced when the plant received more inductive cycles (Fig. 2C). The time before anthesis when plants were no longer sensitive to photoperiod, i.e., the point of intersection between the two linear equations, was calculated to be 25 d (Table 1). If plants received the 16-h photoperiod for <25 DAE, flowering time was delayed. By subtracting the estimated durations of the first two phases (JP and PSP) from 25 d, the minimum duration of PSPP was estimated as 17 d (Table 2).

Similar trends were obtained for plants transferred from a 14-h (Fig. 2B) or a 12-h photoperiod (Fig. 2A) to a 9-h photoperiod. The intersection (the day when plants were no longer sensitive to photoperiod) was calculated to be 35 DAE in the 14-h and 61 DAE in the 12-h photoperiod (Table 1). Therefore, the minimum duration of PSPP was estimated as 23 d in the 14-h photoperiod and 40 d in the 12-h photoperiod (Table 2). The results indicate that the duration of PSPP is a nonlinear function of photoperiod.

Photoperiod-insensitive postinductive phase (PIPP). The minimum duration of PIPP before the first flower opened was calculated to be 7 d for all three photoperiods (Table 2). This was derived by subtracting the minimum days for the first three phases from the days to flower in the control plants. The final phase (PIPP) of floral development in opium poppy appears to be photoperiod-independent. The results are similar to those reported in soybean, a short-day plant (Upadhyay et al., 1994).

In conclusion, the average number of days to flower for plants grown continuously in a 16-h photoperiod was 32 d at 25/20 °C. Days to flower were delayed by 10 d in the 14-h photoperiod and by 36 d in the 12-h photoperiod. The durations of the four phases were not equally affected by photoperiod. The first three phases, JP, PSP, and PSPP, were photoperiod-dependent, and the effect of photoperiod was nonlinear. The final phase, PIPP, was not sensitive to photoperiod.

Results of transfers between a 9- to a 16-h photoperiod in our previous experiment (Wang

et al., 1997a), in which no induction occurred in the first 3 d of exposure to the long photoperiod, have been interpreted by us and other researchers (Ellis et al., 1992; Wilkerson et al., 1989) as a photoperiod-insensitive JP. However, the results of this experiment, which indicated that the duration of the so-called JP is a function of photoperiod, lead us to question this assumption. Variations in the duration of JP have been reported within cultivars of soybean (a short-day plant). For instance, the duration of JP for cv. Davis was found to be 4 d in a 9-h photoperiod (Wilkerson et al., 1989) and 18 d in the 12-h photoperiod (Ellis et al., 1992). We postulate that sensitivity to photoperiod in opium poppy (var. album DC) begins with emergence, but the rate of progress towards flowering depends on the photoperiod experienced.

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