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

ZHONGCHUN WANG*, MARY C. ACOCK and BASIL ACOCK

USDA-ARS, Remote Sensing and Modeling Laboratory, Beltsville, MD 20705, USA

Received: 12 March 1997 Accepted: 2 July 1997

Development up to flowering in opium poppy (*Papaver somniferum* L.) has been divided into four phases from emergence to anthesis which mark changes in its sensitivity to photoperiod: a photoperiod-insensitive juvenile phase (JP), a photoperiod-sensitive inductive phase (PSP), a photoperiod-sensitive post-inductive phase (PSPP) and a photoperiod-insensitive post-inductive phase (PIPP). To predict flowering time under field conditions, it is essential to know how these phases are affected by temperature. Plants were grown in artificially-lit growth chambers and received three different temperature treatments: 15/10, 20/15 and 25/20 °C in a 12 h thermoperiod. Plants were transferred within each temperature regime from a non-inductive 9 h to an inductive 16 h photoperiod or vice versa at 1–4 d intervals to determine the durations of the four phases. Temperature did not affect the duration of the first two phases (i.e. JP lasted 3–4 d and PSP required 4–5 d). The most significant effect of temperature was on the duration of PSPP which was 28, 20 and 17 d at 15/10, 20/15 and 25/20 °C, respectively. The temperature effect on PSPP was small (maximum difference of 3 d between treatments) and the data too variable to indicate a significant trend. Our results indicate that PSPP is the only phase that clearly exhibits sensitivity to temperature.

Key words: Days to flower, opium poppy, *Papaver somniferum* L., phases of flower development, photoperiod, temperature.

INTRODUCTION

The onset of flowering in the opium poppy (*Papaver somniferum* L.) is influenced by photoperiod (Acock, Wang and Acock, 1996). The critical photoperiod (the photoperiod below which flowering is delayed) for opium poppy is near 16 h (Gentner, Taylorson and Borthwick, 1975; Acock et al., 1996). However, flower development of poppy plants is not sensitive to photoperiod throughout the period from sowing to first flowering (Wang, Acock and Acock, 1997). Wang et al. (1997) divided the interval between emergence and first flower into four phases: (1) a photoperiod-insensitive (juvenile) phase (JP), in which poppy plants were insensitive to photoperiod during the first 4 d after emergence; (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 post-inductive phase (PSPP), in which plants required approx. nine additional inductive cycles for flowering to occur without delay; and (4) a photoperiod-insensitive post-inductive phase (PIPP), in which flowering time was no longer influenced by photoperiod. Further studies indicated that the duration of JP was a function of photoperiod (Wang et al., unpubl. res.). Plants transferred from a 9 h to an 11-, a 12-, or a 14-h photoperiod had a longer JP and required more inductive cycles (i.e. longer PSP and PSPP) before they reached the start of PIPP than those transferred to a 16 h photoperiod.

Photoperiod alone cannot adequately predict flowering time because temperature also influences floral development. The optimum daily mean temperature for poppy growth and development is between 16–20 °C (Acock, Pausch and Acock, 1997). Low temperatures delay poppy development (Bernath and Tetenyi, 1981). However, whether temperature affects all four phases has not been established. The current experiment was designed to determine how the durations of these phases change when plants are grown at different temperatures. The specific objectives of the experiment were: (1) to determine whether the duration of JP depends on temperature; (2) to identify phases of floral initiation and development that are temperature sensitive; and (3) to determine the magnitude of the influence of temperature for each phase of development. The data obtained will provide essential information required for predicting flowering time of poppy plants in field conditions.

MATERIALS AND METHODS

Plant culture and treatments

Seeds of *Papaver somniferum* (cv. album DC) were sown in 3·75 l black plastic pots filled with a Jiffy Mix growing medium (Jiffy Products, Batavia, IL, USA) consisting of Canadian sphagnum peat and vermiculite (1:1, v/v). Dolomitic lime was added to adjust the pH of the medium to 6·0. Six ‘reach-in’ controlled environment chambers (Environmental Growth Chambers, Inc., Chagrin Falls, OH, USA) were used, with 34 pots in each chamber. Each chamber was provided with a combination of six high
pressure sodium and six metal halide lamps that were arranged alternately in three rows. Photosynthetic photon flux density inside the growth chambers was maintained at 1000±100 \( \mu \text{mol m}^{-2} \text{s}^{-1} \) at the top of the plant canopy by adjusting a high intensity discharge dimmer. Stern’s Miracle-Gro fertilizer (15:0N-13:1P-12:4K) was applied weekly to each pot in 250 ml of irrigation water at a nitrogen concentration of 175 mg l\(^{-1}\) during the first 3 weeks after emergence and then applied twice a week during the remaining experimental period. Plants were watered as needed during the experiment and thinned to one per pot 20 d after emergence (DAE).

Three temperature treatments, 15/10, 20/15 and 25/20 °C, at a 12 h thermoperiod (0800–2000 h), were applied to the six chambers (one temperature treatment for two chambers). The range of temperatures selected are common for most poppy growing regions worldwide during the growing season. For each temperature treatment, one chamber was programmed at a photoperiod of 9 h from 0800 to 1700 h, and the other programmed at a photoperiod of 16 h from 0800–2400 h. The 9 h photoperiod was chosen as a non-inductive photoperiod because it is short enough to keep plants vegetative (Acock et al., 1996). The 16 h cycle was chosen as an inductive photoperiod because it exceeds the critical photoperiod for poppy (Acock et al., 1996) and also because it can be compared with previous results (Wang et al., 1997).

**Transfer plans**

The plants were transferred, three at a time, from a 9 h to a 16 h photoperiod or vice versa within each temperature regime at different intervals.

For the plants transferred from a 9 h to a 16 h photoperiod within each temperature treatment, transfers began on the day of seedling emergence (0 DAE) and were made at 1 d intervals until 5 DAE, after which time transfers were made at 2 to 4 d intervals up to 28 DAE. Three plants in the 9 h photoperiod at each temperature were never transferred and were used as controls. After a plant was transferred from a 9- to a 16 h photoperiod, it was grown in the new 16 h photoperiod until the first flower opened.

For the plants transferred from a 16 h to a 9 h photoperiod within each temperature regime, transfers were made at 2 to 3 d intervals from 6 to 30 DAE. Three more transfers from 30 to 42 DAE were made at 4 d intervals for plants grown at 15/10 °C. Three plants in the 16 h photoperiod at each temperature were never transferred and used as controls. After a plant was transferred, it was grown in the 9 h photoperiod until the first flower opened or the experiment was terminated at 93 DAE.

The day of emergence was defined as the day when the two cotyledons had unfolded (Wang et al., 1997). The dates on which seedlings emerged and the first flower opened were recorded for each plant.

**Phase determination**

Linear equations were chosen to describe the relationship between the days to flower and the days to transfer from one photoperiod to another at each temperature. The determination of the four phases from emergence to anthesis was similar to the methods described by Wilkerson et al. (1989) and reported previously (Wang et al., 1997). The duration of JP for each temperature was determined by transferring plants at different intervals from the non-inductive 9 h to the inductive 16 h photoperiods after seedling emergence. The end of JP was estimated by intersection of two linear equations. One linear equation with a zero gradient had intercept values of the average flowering times for plants grown continuously in a 16 h photoperiod at each temperature. The second linear equation with a non-zero gradient was obtained using the flowering times from the 9- to the 16-h transfers. The flowering times from the first few transfer dates that decreased the \( r^2 \) value of the equation were omitted from the second equation.

The duration of PSP for each temperature treatment was determined by transferring plants at regular intervals from the inductive 16 h to the non-inductive 9 h photoperiod after seedling emergence. By subtracting the estimated duration of JP from the minimum number of days required for rapid flowering, the minimum duration of PSP was estimated.

The end of PSPP was defined as the earliest day before anthesis when flowering time was no longer influenced by photoperiod, i.e. flowering times were the same as 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 16 h photoperiod control groups at each temperature.

The standard errors of the means (\( n = 3 \)) for days to flower were calculated and presented for each transfer in each temperature treatment. Due to the relatively large difference in the duration of PIPP at 25/20 °C when compared to our previous experiments (Wang et al., 1997), values obtained from the 16 h to the 9 h transfers at 25/20 °C were combined (\( n = 12 \)) over four separate experiments to generate the relationship between the days to flower and the days to transfer.

**RESULTS**

**Photoperiod-insensitive juvenile phase (JP)**

A linear equation was chosen to describe the relationship between the days to flower and the days to transfer from the non-inductive 9 h to the inductive 16 h photoperiod at 15/10 °C (Fig. 1). The average flowering time for plants grown continuously in a 16 h photoperiod at 15/10 °C was 46 d (Fig. 1). The first few transfers from 0 to 5 DAE did not affect flowering time when compared with the 16 h non-transferred plants. Later transfers delayed flowering times to approx. 52, 62 and 72 d when transfers were made at 10, 20 and 30 DAE, respectively. The end of JP, defined as the day at intersection of the two linear equations, was 4 DAE in the 15/10 °C treatment (Fig. 1).
There were also linear relationships between the days to flower and the days to transfer at 20/15 °C (Fig. 2) and 25/20 °C (Fig. 3). Using the same procedures described above, the end of JP was estimated to be 4 and 3 d for the 20/15 and 25/20 °C treatments, respectively. Estimates for the end of JP for each temperature, the minimum number of inductive days required for flower initiation, and the end of photoperiod influence on flowering are summarized in Table 1.

**Photoperiod-sensitive inductive phase (PSP)**

Plants grown at 15/10 °C and transferred from the inductive 16 h to the non-inductive 9 h photoperiod at 8 DAE flowered after 68 d, whereas no plants transferred prior to 8 DAE flowered during the course of the experimental period (93 DAE) (Fig. 4). It appeared that a 16 h photoperiod for 8 DAE was critical for poppy plants to initiate a rapid qualitative transition from vegetative to reproductive development. Subtracting the estimated duration of JP from the pivotal day (8 d) resulted in an estimated 4 d for PSP at 15/10 °C. Estimates of the durations

<table>
<thead>
<tr>
<th>Temperature (°C)</th>
<th>15/10</th>
<th>20/15</th>
<th>25/20</th>
</tr>
</thead>
<tbody>
<tr>
<td>Estimated end of the juvenile phase (DAE*)</td>
<td>4</td>
<td>4</td>
<td>3</td>
</tr>
<tr>
<td>Minimum number of days required for rapid flower initiation (DAE)</td>
<td>8</td>
<td>8</td>
<td>8</td>
</tr>
<tr>
<td>Estimated end of photoperiod influence on flowering (DAE)</td>
<td>36</td>
<td>28</td>
<td>25</td>
</tr>
<tr>
<td>Total number of days required for flowering (DAE)</td>
<td>46</td>
<td>37</td>
<td>32</td>
</tr>
</tbody>
</table>

* DAE, days after emergence.
Table 2. Estimates of durations of the juvenile phase (JP), the photoperiod-sensitive inductive phase (PSP), the photoperiod-sensitive post-inductive phase (PSPP) and the photoperiod-insensitive post-inductive phase (PIPP) in poppy plants grown at 15/10, 20/15 and 25/20 °C

<table>
<thead>
<tr>
<th>Phases</th>
<th>Estimated durations at different temperatures (d)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>15/10 °C</td>
</tr>
<tr>
<td>JP</td>
<td>4</td>
</tr>
<tr>
<td>PSP</td>
<td>4</td>
</tr>
<tr>
<td>PSPP</td>
<td>28</td>
</tr>
<tr>
<td>PIPP</td>
<td>10</td>
</tr>
<tr>
<td>Total</td>
<td>46</td>
</tr>
</tbody>
</table>

of these four phases for each temperature regime are summarized in Table 2.

The minimum number of inductive day/night cycles required for rapid flowering also appeared to be 8 DAE for plants grown at 20/15 (Fig. 5) and 25/20 °C (Fig. 6) (Table 1). Thus, the minimum duration of PSP was estimated as 4 and 5 d at 20/15 and 25/20 °C, respectively (Table 2).

Photoperiod-sensitive post-inductive phase (PSPP)

The rate of flower development for plants transferred from the 16 h to the 9 h photoperiod at 15/10 °C was enhanced as the number of inductive cycles increased (Fig. 4). The days to flower decreased from 68 d for plants transferred at 8 DAE to 58 d for plants transferred at 20 DAE. The time before anthesis when plants were no longer sensitive to photoperiod, i.e. the point of the intersection between two linear equations, was calculated to be 36 d (Table 1). Thus, by subtracting the durations of JP and PSP, the minimum duration of PSPP was estimated as 28 d (Table 2).

Similar trends were obtained in the 20/15 (Fig. 5) and 25/20 °C treatments (Fig. 6). Plants were no longer sensitive to photoperiod at 28 d for 20/15 °C and at 25 d for
25/20 °C (Table 1). Therefore, the minimum duration of PSPP was estimated as 28 d at 15/10 °C, 20 d at 20/15 °C and 17 d at 25/20 °C (Table 2).

**Photoperiod-insensitive post-inductive phase (PIPP)**

The minimum duration of PIPP before the first flower opened was calculated to be 10, 9 and 7 d at 15/10, 20/15 and 25/20 °C, respectively (Table 2). This was derived by subtracting the minimum days for the first three phases from the days to flower in the 16 h photoperiod control groups at each temperature.

**DISCUSSION**

Our results indicate that the durations of the first two phases, JP and PSP, were relatively constant and did not change within the temperature range tested. Plants transferred from a 9- to a 16-h photoperiod within each of the 15/10, 20/15 and 25/20 °C treatments first demonstrated transfer effects 3–4 DAE and required a minimum of 4–5 inductive cycles for the plant to flower. This result confirmed previous findings that plants grown at 25/20 °C required at least four inductive cycles in a 16 h photoperiod before they would flower rapidly (Wang et al., 1997).

After the minimum inductive cycles for flowering were given, additional inductive cycles, i.e. PIPP, hastened flowering. The duration of PSPP was strongly temperature-dependent and was the only phase that demonstrated a significant decrease in duration with an increase in temperature. Plants grown at 15/10 °C required 8 and 11 more inductive cycles to reach the final phase (PIPP) than those grown at 20/15 and 25/20 °C, respectively.

Temperature also seemed to affect PIPP. The duration of PIPP estimated at 15/10 °C was 1 and 3 d longer than those at 20/15 °C and 25/20 °C, respectively. However, the duration of this phase at 25/20 °C was too variable among the four separate experiments to confirm that the difference among the three temperature treatments was significant. We observed that plants grown at 15/10 °C required 1 to 3 more days from the peduncle hook stage (USDA,ARS, System Research Laboratory, 1992) to flower opening than those grown at 25/20 °C. This indicates that the duration of PIPP is not completely insensitive to temperature.

The results in opium poppy differed significantly from those reported in rice, a short-day plant (Collinson et al., 1992). In four rice cultivars tested in glasshouses, the cooler temperature (28/20 °C) prolonged the durations of JP and PIPP when compared to the warmer temperature regime (32/26 °C), whereas the cooler temperature shortened the duration of the photoperiod-sensitive inductive phase (equal to the duration of PSP and PSPP in our study) in one cultivar, but slightly prolonged this phase in another cultivar (Collinson et al., 1992). Our results in opium poppy also differed from those reported in soybean, another short-day plant where the duration of JP was also temperature-dependent (Jones and Laing, 1978; Hodges and French, 1985). It is not clear why the duration of JP in opium poppy does not change with temperature compared with rice and soybean. Unlike rice and soybean, opium poppy is a cool rather than a warm season crop and may require very low temperatures before differences are observed. Since our lowest temperature treatment (15/10 °C) did prolong the duration of PSPP and delay flowering time when compared with the higher temperatures (20/15 and 25/20 °C), the 15/10 °C treatment should have been sufficiently low to demonstrate a temperature effect on JP.

To maintain the same daily temperature for all transfers within a temperature treatment it was necessary to maintain some fixed thermoperiod for the two (9 and 16 h) photoperiods. Such an asynchrony between photoperiod and temperature has been reported to influence floral initiation in some cultivars of sorghum, a short-day plant (Morgan, Guy and Pao, 1987). Asynchrony of thermoperiods with photoperiods promoted floral initiation compared with controls with synchronous thermoperiods and photoperiods. It is important to know from our experiment whether the timing of the thermoperiod also influenced floral initiation in opium poppy, a long-day plant. Such information is important for the development of a model to estimate poppy growth and floral development, and deserves study in order to clarify the effects of temperature on developmental phases.

In summary, the average number of days to flower by plants grown continuously in a 16 h photoperiod was 32 d at 25/20 °C. Flowering was delayed by 5 d at 20/15 °C and by 14 d at 15/10 °C. However, the durations of the four phases were not equally affected by temperature. The first two phases, JP and PSP, were not shown to be temperature-dependent. The third phase, PSPP, was the most sensitive to temperature, but the temperature effect on this phase was non-linear. The maximum difference in the duration of PIPP was 3 d for the three temperature treatments and the data too variable to indicate a significant trend. Our results indicate that low temperatures delayed flowering mainly because they prolonged the duration of PSPP.

**ACKNOWLEDGEMENTS**

We thank Mr Robert Jones for his excellent technical assistance.

**LITERATURE CITED**


