Testing for Early Photoperiod Insensitivity in Soybean

Zhongchun Wang,* Vangimalla R. Reddy, and Mary C. Acock

ABSTRACT

To accurately model the flowering process in soybean, it is essential to identify photoperiod-sensitive and photoperiod-insensitive phases of development. Despite extensive studies, there remains some disagreement about when soybean plants first become sensitive to photoperiod. The length of the juvenile phase from emergence has been found to differ for the same cultivar. This experiment tested the hypothesis that the early phase in soybean development is truly photoperiod-independent. Soybean plants [*Glycine max* (L.) Merr. cv. Hutcheson; Maturity Group V] grown in controlled environments at a constant air temperature of 26°C were transferred from a noninductive 22-h photoperiod to an inductive 8-, 10-, 12-, or 14-h photoperiod at 2- to 5-d intervals after seedling emergence (defined as the day when the cotyledons appeared above the soil surface). The duration of the so-called juvenile phase was shown to be photoperiod-dependent, the photoperiod effect being nonlinear. Soybean plants became sensitive to an 8-, 10-, 12-, and 14-h photoperiod at −1, 0, 1, and 9 d after seedling emergence, respectively. Based on these and other results, we conclude that there is no juvenile phase in Hutcheson soybean, and that photoperiod sensitivity begins when seedlings are exposed to light, but the rate of progress towards flowering depends on the photoperiod experienced.

Accurately predicting days to flower in soybean [*Glycine max* (L.) Merr.] is important because the time between emergence to flowering determines plant size and thus affects dry matter production and final crop yield (Shanmugasundaram and Tsou, 1978; Wang et al., 1997b). The environmental factor that most influences the floral development rate of soybean is photoperiod.

Development from sowing or emergence to anthesis in soybean, a quantitative short-day plant, has been divided into several phases based on its sensitivity to photoperiod. Roberts and Summerfield (1987) divided the time from sowing to first flower into three phases: (i) a preinductive phase, during which plant development is insensitive to photoperiod; (ii) an inductive phase, during which developmental rates are influenced by photoperiod; and (iii) a postinductive phase, during which the time to first flower is once again unaffected by photoperiod. Wilkerson et al. (1989) divided the interval between emergence and first flower into four phases: (i) a photoperiod-insensitive vegetative phase; (ii) a photoperiod-sensitive inductive phase; (iii) a photoperiod-sensitive postinductive phase; and (iv) a photoperiod-insensitive postinductive phase. Various phases of soybean phenology have also been defined by other researchers (Jones and Laing, 1978; Hodges and French, 1985).

Despite extensive studies, there remains some confusion about when soybean plants first become sensitive to photoperiod. It is widely accepted that the early phase of soybean development is not influenced by photoperiod and can therefore be described as a juvenile phase (Shanmugasundaram and Tsou, 1978; Hodges and French, 1985; Ellis et al., 1992). The juvenile phase described in this study is the length of photoperiod-insensitivity beginning from emergence. It is equivalent to the photoperiod-insensitive vegetative phase defined by Wilkerson et al. (1989). Variations in the duration of the juvenile phase have been reported for the same soybean cultivar. For instance, 'Davis' soybean grown at a constant air temperature of 26°C was found to be sensitive to a 9-h photoperiod at 4 d after seed wetting (Wilkerson et al., 1989), whereas Davis grown in a 12-h photoperiod at air temperatures of 30/20°C day/night (mean daily air temperature = 25°C) was not sensitive until 18 d after sowing (Ellis et al., 1992). We hypothesize that the difference in early photoperiod insensitivity (4 vs. 18 d) could have resulted from the different inductive photoperiods (9 vs. 12 h) applied, and if this was true, then the early phase of soybean development may not be photoperiod-insensitive as supposed. Results on opium poppy (*Papaver somniferum* L. subsp. *somniferum*; syn. var. *album* DC.), a quantitative long-day plant, showed that the duration of the so-called juvenile phase depended on the inductive photoperiod into which the plant was transferred (Wang et al., 1998). We concluded that the evidence of a juvenile phase in opium poppy was questionable. The results in opium poppy led us to examine the widely accepted assumption of a juvenile phase in soybean.

Our objective was to experimentally test the hypothesis that the early phase of development in soybean just after emergence is truly photoperiod-independent.

MATERIALS AND METHODS

Plant Culture and Treatments

Seeds of Hutcheson soybean, a determinate Maturity Group V cultivar, were sown in 3.75-L black plastic pots (three seeds per pot) filled with a Jiffy Mix growing medium (Jiffy Products,[1] Batavia, IL) consisting of Canadian sphagnum peat and vermiculite (1:1, v/v). Hutcheson soybean was selected because it is a common cultivar grown in many soybean growing areas. To ensure satisfactory nodule formation and N_2 fixation, the seeds were coated with the N_2–fixing bacteria (*Bradyrhizobium japonicum*). The growing medium was amended with a slow-release fertilizer of Osmocote (14.0–6.1–11.6 N–P–K) (Scotts-Sierra Horticultural Products, Marysville, OH) at a rate of 3 g L^{-1}. Dolomitic lime was added to adjust the pH of the medium to 6.0.

Six controlled environment chambers (Environmental Growth Chambers, Chagrin Falls, OH) were used. Fifty-six pots were placed in two of the six chambers, and four pots

USDA-ARS, Remote Sensing and Modeling Laboratory, BARC West, Beltsville, MD 20705-2350. Received 11 Aug. 1997. *Corresponding author (zwang@asrr.arsusda.gov).

Published in Agron. J. 90:389–392 (1998).

---

[1] Trade name and company name are included for the benefit of the reader and do not imply any endorsement or preferential treatment of the product by USDA-ARS.

Abbreviations: DAE, days after emergence.

were placed in each of the four remaining chambers. Each chamber was provided with a combination of six high-pressure sodium and six metal-halide lamps, which were arranged alternatively in three rows. The air temperature in all six chambers was controlled at 26 ± 0.5°C both day and night. Photosynthetic photon flux density inside the growth chambers was maintained at 1000 ± 100 μmol m^{-2} s^{-1} at the top of the plant canopy. Plants were watered as needed and thinned to one per pot at the cotyledon stage (VC) (i.e., at 2 to 3 days after emergence [DAE]). Emergence day was defined as the day when the cotyledons appeared above the soil surface.

Photoperiod and Transfer Schedule

The two chambers that had 56 pots in each chamber were set at a photoperiod of 22 h from 0800 to 0600 h. The remaining four chambers, which had four pots per chamber, were set at a photoperiod of 8 h (0800–1600 h), 10 h (0800–1800 h), 12 h (0800–2000 h), and 14 h (0800–2200 h), respectively. The 22-h treatment was chosen as a noninductive photoperiod because the cultivar studied remained vegetative. The 8-, 10-, 12-, and 14-h treatments were chosen as various inductive photoperiods, and plants grown in these four photoperiods were expected to show different sensitivities to photoperiod during their growth and development.

The plants were transferred, three at a time, from a 22-h to an 8-, 10-, 12-, or 14-h photoperiod. Transfers began on the day of seedling emergence (0 DAE). To optimize the number of transfers for the space available and at the same time to accurately estimate the duration of the juvenile phase, the first six transfers after emergence were made at 2-d intervals for the 8-, 10-, and 12-h treatments and at 3-d intervals for the 14-h treatment. The remaining transfers were made at 3- to 5-d intervals, up to 35 DAE. Four plants remained in the 22-h chambers at the end of the experiment. After a plant was transferred, it was grown in the new photoperiod until the R1 stage (i.e., the appearance of first open flower) (Fehr and Caviness, 1977). The four plants that were kept in the 8-, 10-, 12-, and 14-h photoperiods were used as controls. The experiment was terminated at 55 DAE.

Days to R1 were recorded for each plant. The developmental stages were determined using Fehr and Caviness (1977) criteria.

Juvenile Phase Determination

The determination of the juvenile phase was similar to the methods described by Wilkerson et al. (1989) and by Wang et al. (1997a). Briefly, the duration of the juvenile phase in each photoperiod was determined by transferring plants at different times from the noninductive 22-h treatment to the inductive 8-, 10-, 12- or 14-h treatment. If the effect of the inductive photoperiod on the development to first flower could not be distinguished from the noninductive 22-h photoperiod, it was assumed that the plants were insensitive to photoperiod during this developmental phase.

The end of the juvenile phase was estimated by the intersection of two linear equations. One linear equation with a slope = 0 had intercept values of the average flowering times for plants grown continuously in an 8-, 10-, 12-, or 14-h photoperiod. The second linear equation with a slope ≠ 0 was obtained using the flowering times from the 22 to the 8-, 10-, 12-, or 14-h transfers. Observations on early transfers were omitted in establishing the second linear equation if they decreased the r^2–value of the equation.

Statistical Analyses

Statistical analysis was performed using SAS procedures (SAS Inst., 1989). Days to flower was analyzed as a linear dependence on the day of transfer from one photoperiod to another. The standard errors of the means ($n = 3$) for days to flower were calculated and presented for each transfer.

RESULTS AND DISCUSSION

There was a linear relationship between the days to flower and the days to transfer from the noninductive 22-h to the inductive 8-h photoperiod (Fig. 1a). The average flowering time for plants grown continuously in an 8-h photoperiod and at a constant air temperature of 26°C was 20 d, but was 47 d when plants were transferred at 26 DAE. The end of the juvenile phase, as estimated by the intersection of two linear equations, was −1 DAE. Since emergence day is defined as the day when cotyledons appear above the soil surface, the −1 d indicates that Hutcheson soybean was responsive to the 8-h photoperiod as soon as the seedlings emerged.

Similar trends were obtained for plants transferred from a 22-h photoperiod to a 10-h (Fig. 1b) or a 12-h (Fig. 1c) photoperiod. The end of the juvenile phase was estimated to be 0 and 1 DAE for plants transferred from a 22-h to a 10-h and a 12-h photoperiod, respectively. The transfer interval in this study was 2 d during the first few transfers. The 2-d difference in the duration of the juvenile phase among the three photoperiods tested might have reflected the photoperiod effect. It is unlikely that the 2-d difference is due to the imprecision of the estimate, since (i) the SE of the y-estimates at the intercepts is 0.21, 0.19, and 0.20 d for the 8-, 10-, and 12-h photoperiods, respectively, and (ii) the duration of the juvenile phase increased with increasing photoperiod.

Plants transferred from a 22- to a 14-h photoperiod showed a significantly different pattern from those transferred to an 8-, 10-, or 12-h photoperiod (Fig. 1d). The first few transfers (i.e., transfers at 0, 3, 6, and 9 DAE) did not show any delay towards flowering when compared with the 14-h control plants. The end of the juvenile phase was estimated to be 9 DAE (i.e., at growth stage V2).

These results indicated that the duration of the observed juvenile phase in soybean varied and depended on the length of the inductive photoperiod to which the plant was transferred. The durations of the juvenile phase were similar for those plants exposed to photoperiods shorter than or equivalent to the critical photoperiod (e.g., ≤12 h for cv. Hutcheson). Greater differences in the duration of the juvenile phase were found for those plants exposed to photoperiods longer than the critical photoperiod (e.g., 14 h). A similar photoperiod effect on the duration of the photoperiod-sensitive phase was also found for soybean cv. Johnston (Acock and Acock, 1995). The different durations of the juvenile phase for Davis soybean reported by Ellis et al. (1992) and Wilkerson et al. (1989) could have resulted from the different inductive photoperiods (9 vs. 12 h) applied, since the air temperatures in these studies were similar. Although the 8- and 12-h photoperiods were almost equally inductive to Hutcheson in our study, not all cultivars have the same critical photoperiod. Because Davis had a longer juvenile phase in transfers to a 12-h photoperiod, as reported by Ellis et al. (1992), and

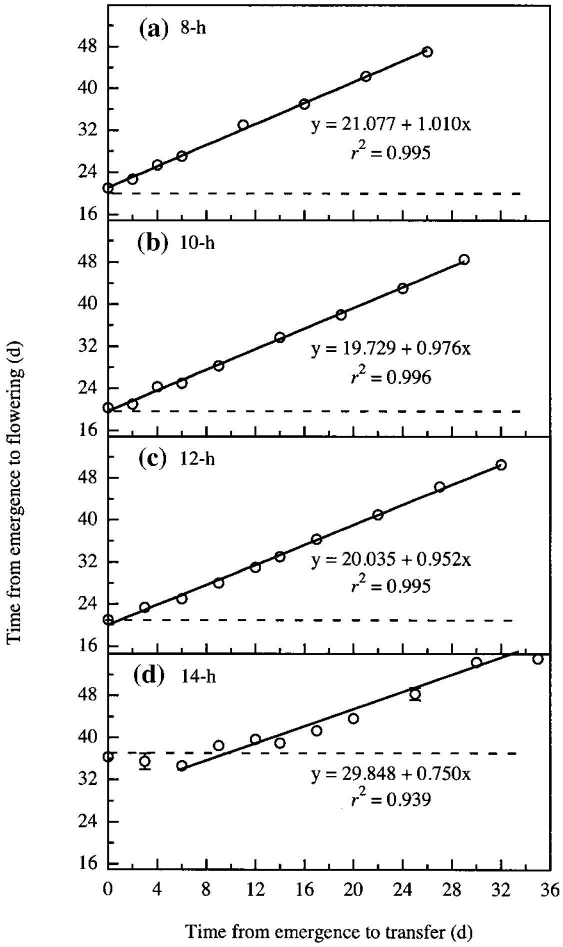

Fig. 1. Time from emergence to flowering as a function of time from emergence to transfer for soybean plants transferred from a 22-h photoperiod to one of (a) 8 h, (b) 10 h, (c) 12 h, or (d) 14 h. Horizontal broken lines indicate time to flowering (in days) for plants that remained in the given photoperiod: 20 d for (a), 20 d for (b), 21 d for (c), and 37 d for (d). Error bars indicate standard error (n = 3), where larger than symbol size.

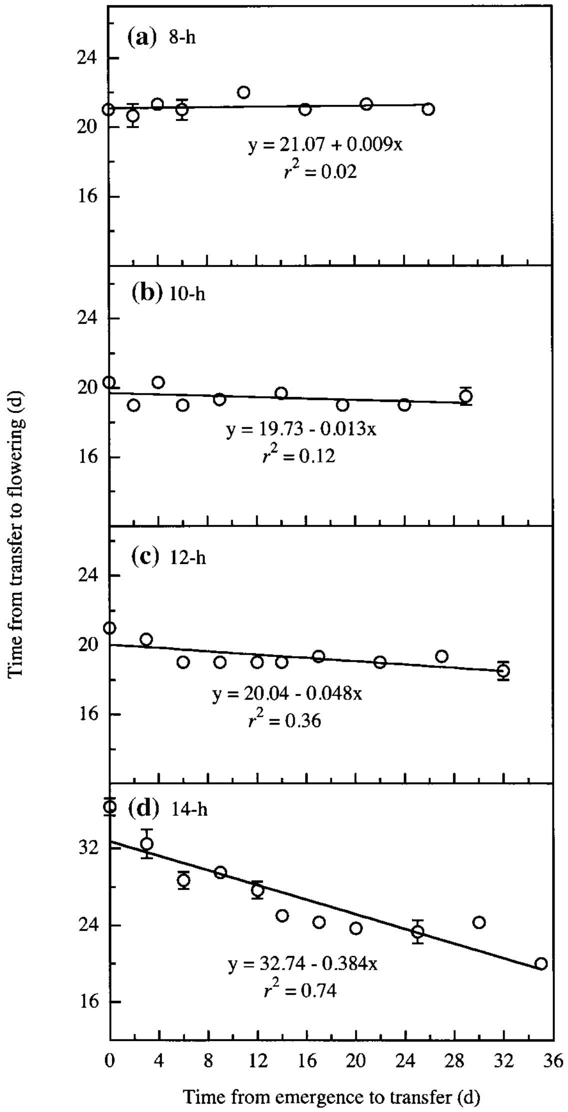

Fig. 2. Time from transfer to flowering as a function of time from emergence to transfer for soybean plants transferred from a 22-h photoperiod to one of (a) 8 h, (b) 10 h, (c) 12 h, or (d) 14 h. Error bars indicate standard error (n = 3), where larger than symbol size.

a shorter juvenile phase in transfers to a 9-h photoperiod, as reported by Wilkerson et al. (1989), it appears that Davis has a different sensitivity to photoperiod compared with Hutcheson. Observations on both cultivars are consistent with our findings in opium poppy that the duration of the so-called juvenile phase is dependent on the inductive photoperiod experienced (Wang et al., 1998).

Our results indicate that there is no juvenile phase in Hutcheson soybean, because seedlings were demonstrated to be sensitive to photoperiod as soon as they emerged. The apparent juvenile phase for plants transferred to the 14-h photoperiod simply reflects application of a less-inductive photoperiod.

When plants were transferred from a 22-h to an 8-, 10-, or 12-h photoperiod, the duration from transfer to flowering was 19 to 21 d, regardless of the plant age at transfer (Fig. 2a,b,c). The duration (≈30 d) during which plants remained in the 22-h photoperiod prior to transfer apparently did not significantly affect the time from transfer to flowering. The greater developmental rates towards flowering in the highly inductive 8-, 10-, and 12-h photoperiods probably had masked any effect of the 22-h photoperiod on floral development. However, for plants transferred from a 22- to a 14-h photoperiod, days from transfer to flower decreased from 36 to 20 d as transfer date increased from 0 to 35 DAE (Fig. 2d). The effect of the 22-h photoperiod on floral development became significant when plants were transferred to the less-inductive photoperiod of 14 h.

The duration of the juvenile phase has been shown to be cultivar-dependent (Shanmugasundaram and Tsou, 1978; Board and Settimi, 1988; Wilkerson et al., 1989; Upadhyay et al., 1994). Various durations of the juvenile phase have been reported in different soybean cultivars that had experienced a highly inductive 9-h photoperiod (Wilkerson et al., 1989). The observed difference in the duration of the juvenile phase among cultivars might have resulted from cultivar difference. However, based on our results it is also possible that these cultivars are all sensitive to photoperiod from emergence, but show different rates of progress towards flowering in response to a given photoperiod. To model the development of soybean under field conditions, it is necessary to know daylength as early as seedling emergence if there is no juvenile phase. Whether there is a juvenile phase or not for other cultivars needs to be reassessed. Using transfers from highly noninductive to highly inductive photoperiods is recommended for this reassessment. Eliminating the juvenile phase will reduce the number of phases required to adequately simulate floral development of soybean.

CONCLUSIONS

The photoperiod effect on days to flower of Hutcheson soybean was nonlinear. The average number of days to flower for plants grown in an 8-, 10-, 12-, and 14-h photoperiod was 20, 20, 21, and 37 d after seedling emergence at a constant air temperature of 26°C. The effect of the highly noninductive photoperiod (22 h) on floral development was masked by the highly inductive photoperiods, but became significant when plants were transferred to the less-inductive photoperiods. The duration of the so-called juvenile phase in Hutcheson soybean was a nonlinear function of the photoperiod at transfer. Our results do not support the hypothesis that the early phase of development in Hutcheson soybean is insensitive to photoperiod, because the duration of the so-called juvenile phase depends on the photoperiod applied. These findings lead us to suggest that the duration of the juvenile phase may have been overestimated in some cultivars due to the longer, less-inductive photoperiods used in some experiments (e.g., a 13.5-h inductive photoperiod used by Board and Settimi (1988) and a 12-h inductive photoperiod used by Ellis et al. (1992). The intriguing question is: do some soybean cultivars have juvenile phases, or are all of them sensitive to photoperiod from the first exposure to light, differing only in the rate of progress towards flowering in response to a given photoperiod? In using the transfer method to identify a juvenile phase, we recommend transferring from highly noninductive to highly inductive photoperiods. This may lead to simplifying models of floral development by eliminating the photoperiod-insensitive juvenile phase in many if not all soybean cultivars.

ACKNOWLEDGMENTS

We thank Robert Jones and Yi Zhou for their excellent technical assistance.

REFERENCES

Acock, M.C., and B. Acock. 1995. Photoperiod sensitivity during soybean flower development. Biotronics 24:25–34.

Board, J.E., and J.R. Settimi. 1988. Photoperiod requirements for flowering and flower production in soybean. Agron. J. 80:518–525.

Ellis, R.H., S.T. Collinson, D. Hudson, and W.M. Patefield. 1992. The analysis of reciprocal transfer experiments to estimate the durations of the photoperiod-sensitive and photoperiod-insensitive phases of plant development: An example in soya bean. Ann. Bot. (London) 70:87–92.

Fehr, W.R., and C.E. Caviness. 1977. Stages of soybean development. Iowa State Univ. Coop. Ext. Serv. Spec. Rep. 80.

Hodges, T., and V. French. 1985. Soyphen: Soybean growth stages modeled from temperature, daylength, and water availability. Agron. J. 77:500–505.

Jones, P.G., and D.R. Laing. 1978. Simulation of the phenology of soybeans. Agric. Syst. 3:295–311.

Roberts, E.H., and R.J. Summerfield. 1987. Measurement and prediction of flowering in annual crops. p. 17–50. *In* J.G. Atherton (ed.) Manipulation of flowering. Butterworths, London.

SAS Institute. 1989. SAS user's guide. SAS Inst., Cary, NC.

Shanmugasundaram, S., and S.C.S. Tsou. 1978. Photoperiod and critical duration for flower induction in soybean. Crop Sci. 18:598–601.

Upadhyay, A.P., R.J. Summerfield, R.H. Ellis, E.H. Roberts, and A. Qi. 1994. Variation in the durations of the photoperiod-sensitive and photoperiod-insensitive phases of development to flowering among eight maturity isolines of soybean [*Glycine max* (L.) Merrill]. Ann. Bot. (London) 74:97–101.

Wang, Z., M.C. Acock, and B. Acock. 1997a. Phases of development to flowering in opium poppy (*Papaver somniferum* L.) under various temperatures. Ann. Bot. (London) 80:547–552.

Wang, Z., M.C. Acock, and B. Acock. 1998. Phases of development to flowering in opium poppy (*Papaver somniferum*) under various inductive photoperiods. HortScience 33 (in press).

Wang, Z., V.R. Reddy, and B. Quebedeaux. 1997b. Growth and photosynthetic responses of soybean to short-term cold temperature. Environ. Exp. Bot. 37:13–24.

Wilkerson, G.G., J.W. Jones, K.J. Boote, and G.S. Buol. 1989. Photoperiodically sensitive interval in time to flower of soybean. Crop Sci. 29:721–726.