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PHOTOPERIOD SENSITIVITY DURING SOYBEAN FLOWER DEVELOPMENT

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Acock M. C. and Acock B. *Photoperiod sensitivity during soybean flower development*. BIOTRONICS 24, 25-34, 1995. Flowering in field-grown soybean [*Glycine max* (L.) Merr.] is difficult to predict because the influences of photoperiod (P) and temperature are not well understood. The purpose of this research was to improve our understanding of how the photoperiod-sensitive and -insensitive phases of flower development are controlled by P. Controlled-environment studies were conducted in which 'Johnston' (maturity group VIII) soybean plants were switched from Ps between 12 h and 14.75 h to a P of 22 h. All chambers were maintained at $25 \pm 1^\circ\text{C}$. The P experienced by plants before they were switched to 22 h did not influence the length of the photoperiod-sensitive phase of flower development for $P \leq 13.5$ h. For $P > 13.5$ h, there was a linear increase in the number of days needed for P to cause flower induction (i. e. irreversible flower development) as P increased. The length of the photoperiod-insensitive phase also showed an increase when P during the photoperiod-sensitive phase was > 13.5 h. One of the reasons why it has been so difficult to predict flowering times in soybean is because the P experienced during the photoperiod-sensitive phase of flower development also affects the length of the photoperiod-insensitive phase.

Key words: *Glycine max* (L.) Merr; photoperiodic induction.

INTRODUCTION

Flowering times of field-grown soybeans are difficult to predict (2, 7). One reason for this difficulty is that temperature and photoperiod (P) are highly variable in the field and flowering response to these factors is not understood completely. The plant does not appear to be sensitive to P at all times during its development.

To account for the interaction between the plant and its environment, modelers have divided the development of the plant into various phases. Jones and Laing (5) recognized three phases of development between sowing and flowering: (a) sowing to primary leaf, (b) primary leaf to flower initiation (when morphologically distinct flower initials are present in the meristem), and (c) flower initiation to anthesis. They assume all phases are sensitive to temperature. The latter two phases are also sensitive to P. Hodges and French (4) described four phases from sowing to anthesis. Only the phase from the end

of juvenility to flower initiation was sensitive to P. Juvenility is an early vegetative phase during which the plant cannot be induced to flower. Flower induction is said to occur when flower development is irreversible. Wilkerson *et al.* (8) examined P effects under constant temperature and concluded that the interval between emergence and anthesis should be divided into four phases: (a) a juvenile phase (absent in some cultivars), (b) a photoperiod-sensitive inductive phase, (c) a second photoperiod-sensitive post-inductive phase, and (d) a photoperiod-insensitive post-inductive phase. This interpretation of soybean flower development was based, in part, on experiments in which soybean plants were transferred from a 9-h (highly inductive) P to a 22-h (low or non-inductive) P at regular time intervals. Using this technique, Wilkerson *et al.* (8) were able to establish the lengths of the photoperiod-sensitive and photoperiod-insensitive phases for several cultivars.

In this study, we wanted to find out how the durations of these photoperiod-sensitive and -insensitive phases depended on the P under which the flowers were induced. Using the same procedure described by Wilkerson *et al.* (8), except that a range of fixed photoperiods were used for inducing P, we studied the influence of P on the lengths of the photoperiod-sensitive and -insensitive phases of soybean flower development for one cultivar: 'Johnston.'

MATERIALS AND METHODS

Plants were grown in one of six identical reach-in controlled-environment chambers (Environmental Growth Chambers, Inc.). Temperature was maintained at $25 \pm 1^\circ\text{C}$ for all chambers. Seeds of soybean cultivar 'Johnston' (maturity group VIII) were sown in 15-cm plastic pots. After emergence, seedlings were thinned to one or two per pot. The growing medium consisted of 0.5 m^3 vermiculite and 0.5 m^3 sphagnum peat moss amended with 4.03 kg dolomitic lime, 1.06 kg micromax (containing, in g (100 g)^{-1} : 12.0 S, 0.1 B, 0.5 Cu, 12.0 Fe, 2.5 Mn, 0.05 Mo, and 1.0 Zn), and 5.57 kg of a 6-month slow-release fertilizer containing 14-6.1-11.6 (N-P-K). Plants were watered by hand as needed. Chambers were programmed to provide 1000-1500 $\mu\text{mol s}^{-1} \text{ m}^{-2}$ PAR from metal halide and high pressure sodium lamps. Time to first open flower was recorded. A flower was considered open when the petals had separated. Because of controlled environment space limitations, transfer experiments were run on two separate occasions covering the photoperiodic range from 12 to 14.75 h. The 13-h P was common to both experiments.

Experiment 1

Plants were grown in a P of either 13, 13.75, or 14.25 h and then transferred to a 22-h P. The day of transfer was recorded as days after VC stage (DAVC). VC stage was determined using Fehr and Caviness (3) criteria. VC stage was used as a starting point because the end of juvenility in 'Johnston' coincided with VC stage at the temperature used in this study (1). Plants grown in the 13-h P were transferred on 3, 5, 6, 13, 15, or 17 DAVC. Plants grown in the

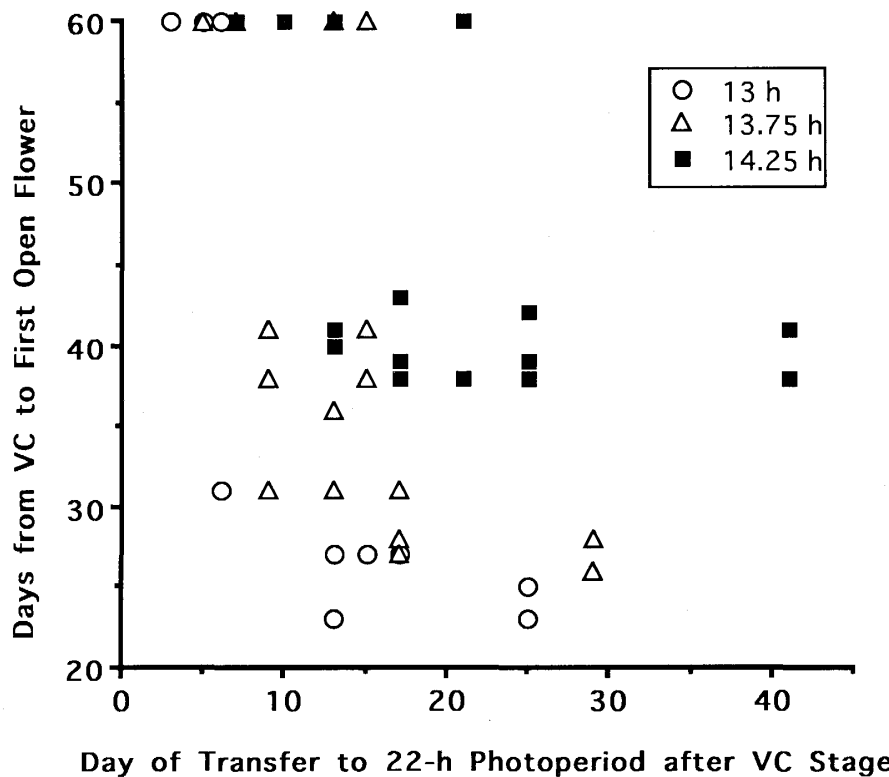


Fig. 1. Number of days from VC stage to first open flower for 'Johnston' soybean plants grown at 25°C plotted against days in either 13, 13.75, or 14.25-h photoperiods before being transferred to a 22-h photoperiod. Experiment ended on day 60. Plants shown as flowering at 60 days had not actually flowered.

13.75-h P were transferred on 5, 7, 9, 13, 15, or 17 DAVC. Plants grown in the 14.25-h P were transferred on 7, 10, 13, 17, 21, or 25 DAVC. There were three plants per transfer. Experiment 1 was repeated with transfers made every day to day 10 then every other day until flowering for 13-h P and every other day for 13.75-h and 14.25-h P to day 19 then every third day until flowering.

Experiment 2

Plants were grown in Ps of 12, 13, and 14.75 h. Four plants each from the 12 and 13-h P treatments were transferred into a 22-h P beginning at VC stage at daily intervals until 10 DAVC and then at 2-day intervals. For the 14.75-h P treatment, two plants were transferred into a 22-h P at daily intervals beginning at 10 DAVC and then at 2-day intervals from 30 DAVC.

RESULTS AND DISCUSSION

Data from the transfer experiments are plotted in Figs. 1 and 2. From these data all three phases of flower development described by Wilkerson *et al.* (8) can be distinguished: a photoperiod-sensitive, a photoperiod-sensitive post-inductive,

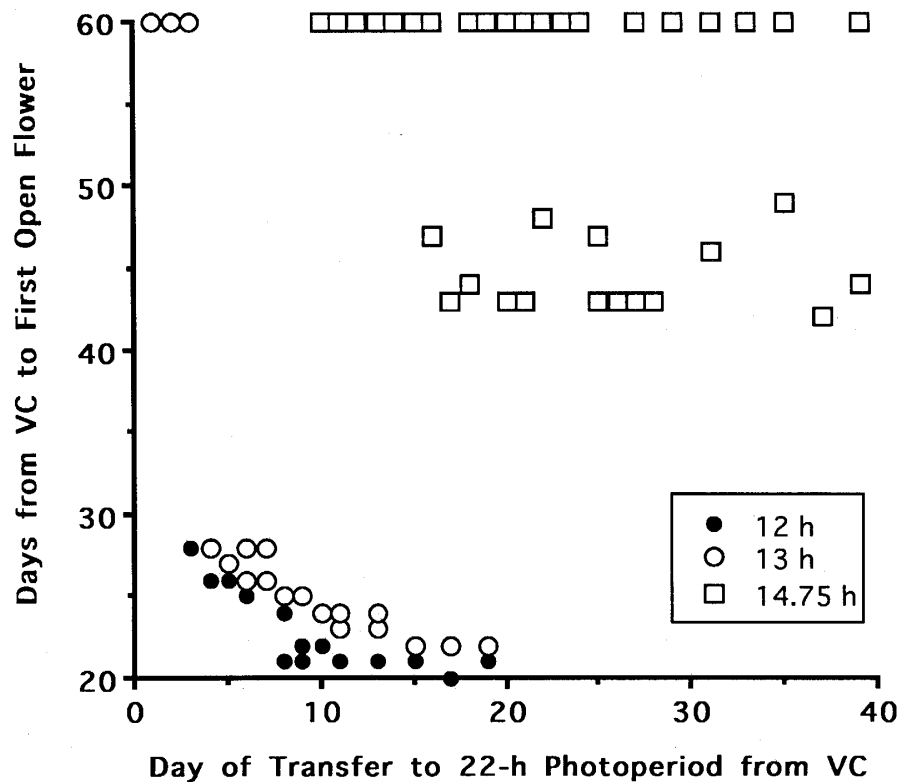


Fig. 2. Number of days from VC stage to first open flower for 'Johnston' soybean plants grown at 25°C plotted against days in either 12, 13, or 14.75-h photoperiods before being transferred to a 22-h photoperiod. Experiment ended on day 60. Plants shown as flowering at 60 days had not actually flowered.

and a photoperiod-insensitive phase.

Photoperiod-Sensitive Phase

The photoperiod-sensitive phase was called complete when the minimum number of days or day/night cycles needed to induce flowering had been provided. Because transfers were not made every day, and the three replicate plants did not always behave the same, the end of the photoperiod-sensitive phase of soybean flower development could only be placed within certain limits. The lower limit was determined by the last transfer from inducing to non-inducing conditions in which none of the replicates flowered. The upper limit was determined by the earliest transfer in which one or more of the replicates produced an open flower. In the 14.25-h treatment (Fig. 1) no plants transferred on 10 DAVC flowered but two plants transferred on 13 DAVC flowered. Thus the end of the photoperiod-sensitive phase for 'Johnston' in this treatment occurred between 10 and 13 DAVC. A few plants in the same treatment failed to flower even though they were transferred as late as 21 DAVC. A possible reason for this is discussed later.

The data in Fig. 3 are derived from data shown in Figs. 1 and 2. The two

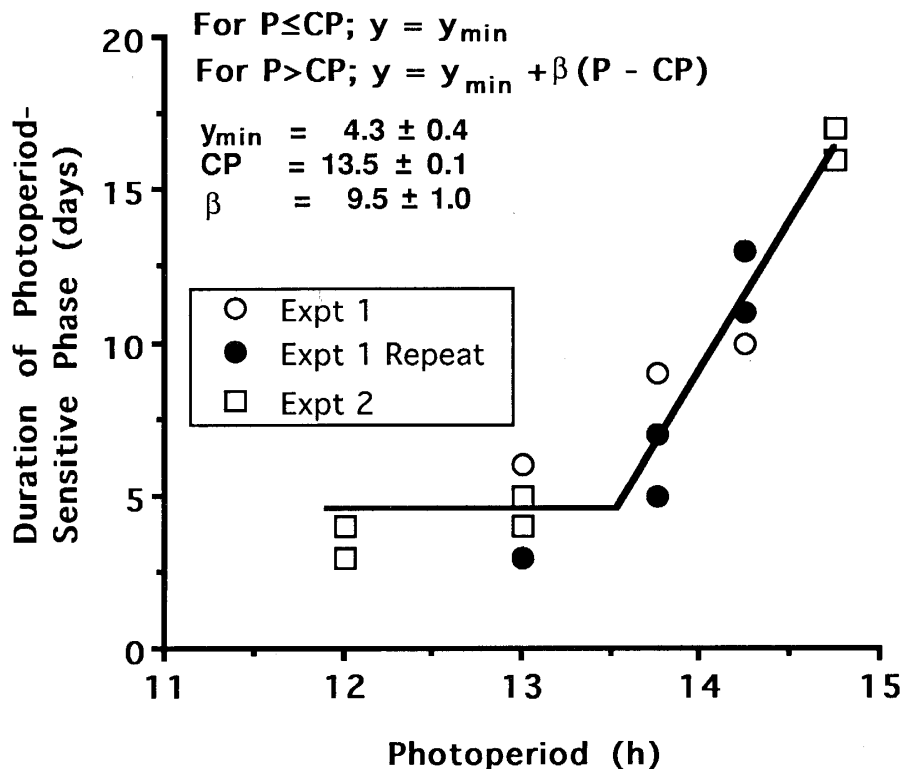


Fig. 3. Duration of the photoperiod-sensitive phase of flower development in 'Johnston' plotted against photoperiod before transfer. The two observations made for each set of plants tested define the upper and lower limits of the end of the photoperiod-sensitive phase.

values for each photoperiodic observation describe the upper and lower limits of the photoperiod-sensitive phase at that P, as measured by our experiments. The data are interpreted as a plateau-linear dependence of the photoperiod-sensitive phase on P which is approximated by two lines intersecting at a point we call the critical photoperiod (CP). Values for the parameters: y_{min} , CP, and β were found using the Levenberg-Marquardt method (6) of nonlinear optimization (Fig. 3). β describes the change in the duration of the photoperiod-sensitive phase per unit change in P. The length of the photoperiod-sensitive phase of flower development (y) can be calculated from the following formulae:

$$y = \begin{cases} y_{min}, & P \leq CP \\ y_{min} + \beta * (P - CP), & P > CP. \end{cases}$$

Since the length of the photoperiod-sensitive phase of soybean flower development is not constant, we can only use extreme inducing conditions such as the 9-h P used by Wilkerson *et al.* (8) to determine y_{min} . To predict the length of the photoperiod-sensitive phase over a range of P, we must also know CP and β .

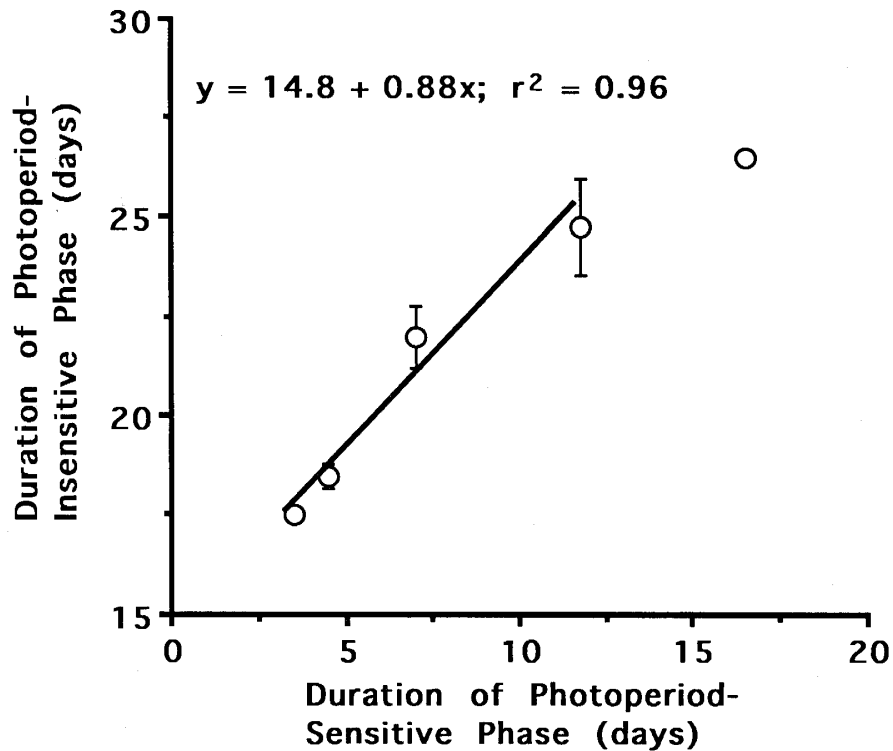


Fig. 4. Duration of the photoperiod-insensitive phase of flower development in 'Johnston' plotted against the length of the photoperiod sensitive phase (the number of days from VC stage to first open flower minus the calculated length of the photoperiod-sensitive phase).

Photoperiod-Insensitive Phase

The mean number of days required to produce open flowers after the end of the photoperiod-sensitive phase, which is referred to (with some reservations to be described later) as the photoperiod-insensitive phase, is plotted against the length of the photoperiod-sensitive phase in Fig. 4. The data indicate a linear relationship up to 14.25-h. Data are too limited to draw any conclusions about the nature of the relationship beyond 14.25-h.

The linearity of this relationship suggests that the plateau-linear dependence that characterizes the relationship between the length of the photoperiod-sensitive phase and P can also be applied to the photoperiod-insensitive phase. This is an important interpretation for modelers: that the length of the photoperiod-insensitive phase depends on the P experienced during the photoperiod-sensitive phase. A physiological explanation for this relationship will require further investigation. However, we have observed that as photoperiods increase beyond CP, the number of flowers developing per node also increases. The plant appears to be switching from fast development of a few flowers in short photoperiods to slower development of more flowers in long photoperiods. The relationship between the photoperiod-sensitive and photoperiod-insensitive phases of flower development may eventually be shown

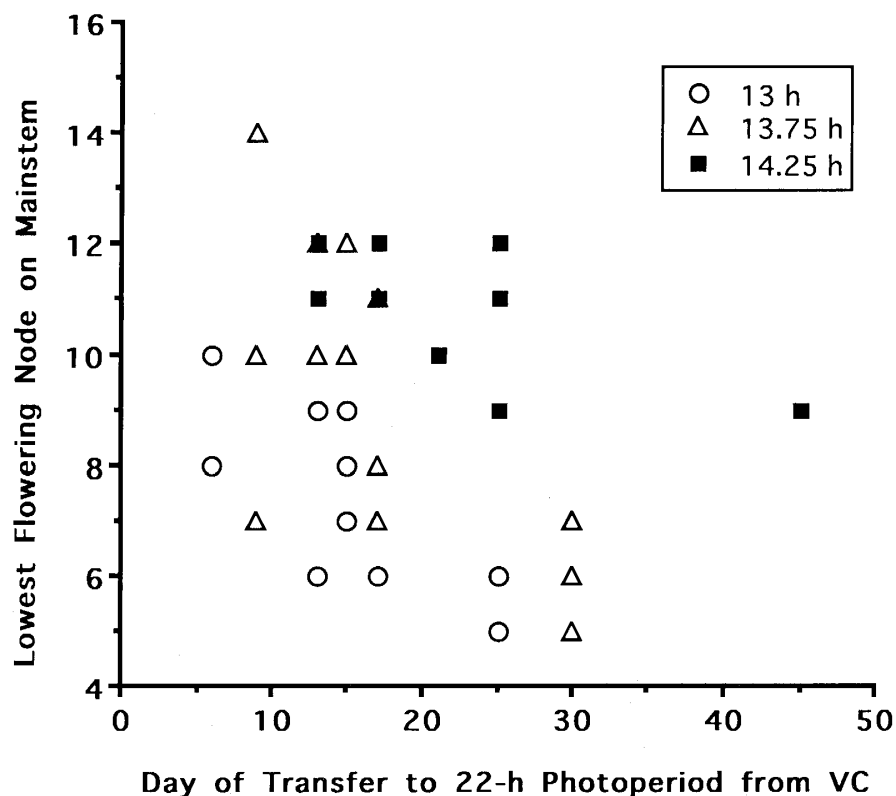


Fig. 5. The lowest node on the mainstem where flowers opened, plotted as a function of the number of days after VC stage that 'Johnston' soybean plants were kept at 13, 13.75, and 14.25-h photoperiods before being transferred to a 22-h photoperiod.

to be a consequence of the number of flowers formed during the photoperiod-sensitive phase and subsequently developed during the photoperiod-insensitive phase.

Of course, the interpretation of the data as a plateau-linear dependence of each flower development phase on P is only an approximation and based on data from a relatively few fixed P s. More observations at various P s can establish the adequacy of this interpretation. Whether the approximation holds when more observations are made or not, the description will feature a relationship which changes little at $P < 13.5$ and rapidly at $P > 13.5$ for the cultivar 'Johnston'.

Photoperiod-sensitive post-inductive phase.

A close examination of the data points in Figs. 1 and 2 will reveal that early transfers flowered later. Generally, the plants that received only a few photoperiodic cycles took longer to reach anthesis than plants that experienced more cycles of the same P before transfer to 22 h. These observations can be taken as evidence of a photoperiod-sensitive post-inductive phase of flower development as described by Wilkerson *et al.* (8). In this phase, the plants are

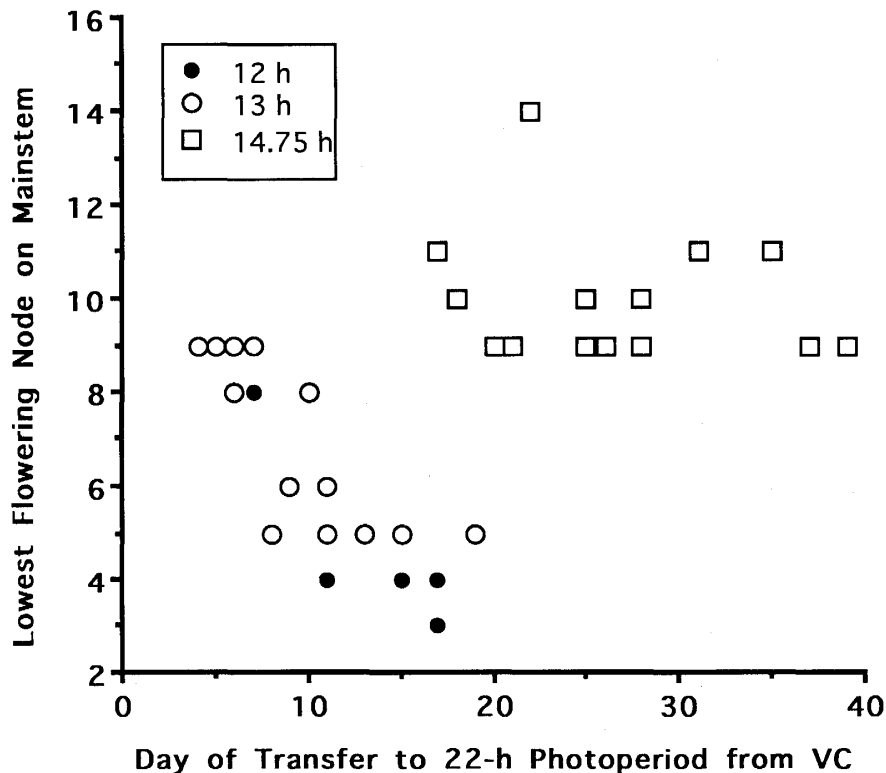


Fig. 6. The lowest node on the mainstem where flowers opened plotted as a function of the number of days after VC stage that 'Johnston' soybean plants were kept at 12, 13, and 14.75-h photoperiods before being transferred to a 22-h photoperiod.

already 'programmed' to flower so development is no longer dependent on P. On the other hand, progress toward flowering is slower in the earlier transfers. Only later transfers flower at the same time as those plants kept continuously in inducing P.

We found that plants transferred after a few inducing Ps flowered at younger nodes (higher nodes on mainstem) compared with plants kept for longer in inducing Ps before transfer (Figs. 5 and 6). Since some plants flowered first on branches, the nodes on the axillary branch where flowers occurred first were given a node number equivalent to the mainstem node of the same age in order to make comparisons easier (Figs. 5 and 6). If flowers opened at older nodes first, the time to flower was shorter than when flowers opened first on younger nodes (Fig. 7). Thus, the photoperiod-sensitive post-inductive phase of flower development could be linked to whatever mechanism caused the first flowers to open at different locations on the plant. Later transfers tend to open flowers at the same node as those kept continuously in inducing P.

One explanation for younger nodes flowering first when plants are given a minimum number of inducing cycles (Figs. 5 and 6) is that older nodes require more inducing cycles to initiate flowers compared with younger ones. We can

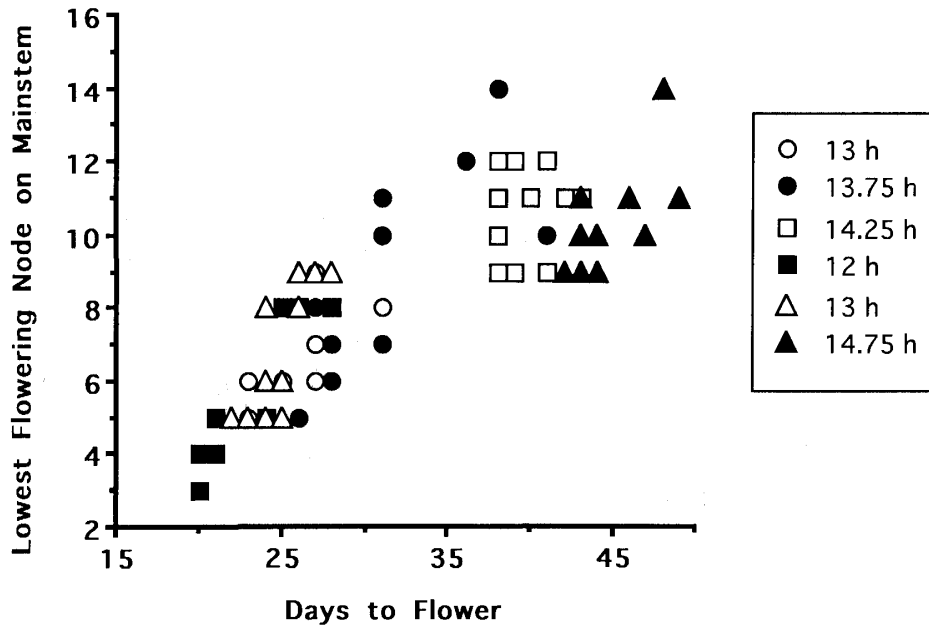


Fig. 7. The lowest node on the mainstem where first flowers appeared when soybean plants were given a variety of photoperiods (P) and days of exposure plotted as a function of days from VC stage to first open flower, R 1.

dismiss this explanation because plants given continuous inducing Ps will flower first at the older node (Figs. 5 and 6), indicating that the older node is the first to initiate flowers.

Another explanation is that flowerbuds are initiated at the older nodes, but either revert to vegetative buds or abort when P conditions turn unfavorable for flowering. Both flowerbud abortion and reversion were observed in our experiments. When examining meristems of soybean plants to determine when and where flower initiation occurred, it was not unusual to find flowerbuds that would abort at the touch of a probe while others were more tenacious. Also, some well-developed floral structures were observed to revert to vegetative growth after being transferred and kept in a 22-h P.

The node at which the first flower opened was highly variable (Figs. 5 and 6) but flowering always occurred at the younger nodes on early transfers. Therefore, our data are consistent with the idea that older nodes initiate flowers which either revert to vegetative buds or are aborted in non-inducing P conditions.

Flower abortion may explain the variability in flowering times between replicates of the same treatment. Some replicates never flowered. Plants that are given a minimum number of inducing P cycles have few meristems on the plant that are induced to flower. The abortion of one flowerbud can therefore be a substantial proportion of the floral meristems present on the plant and can have a significant effect on flowering time.

The picture that emerges is of a soybean plant with a dynamic supply of meristems that become sensitive to P and are induced to flower. Under fixed photoperiods, photoperiod histories among meristems are identical for the whole plant and flowering may be relatively uniform. However, under field conditions where photoperiods change, the soybean plant can have flowering meristems that have experienced a variety of photoperiod histories and the location of these meristems within the plant canopy may influence their ability to produce viable flowers.

CONCLUSIONS

These results offer new insights into the photoperiodic control of flowering in soybean. The lengths of the photoperiod-sensitive and -insensitive phases of flower development are not constant but are both a function of P. The duration of the photoperiod-sensitive phase can be described as a constant for $P \leq CP$ and an increasing linear function of P for $P > CP$ where CP is the critical photoperiod. The duration of the photoperiod-insensitive phase showed a similar dependence on P. Thus, the P that activates flowering can influence all phases of flower development, including the photoperiod-insensitive phase.

More investigations are needed to improve our understanding of the transition between the photoperiod-sensitive and -insensitive phases of soybean flower development and to determine the manner in which P affects flower development even in the photoperiod-insensitive phase.

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