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EFFECT OF CHANGING DAYLENGTH ON FLOWER INITIATION AND DEVELOPMENT IN TWO SOYBEAN CULTIVARS

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ACOCK M. C., BUNCE J. A. and ACOK B. *Effect of changing daylength on flower initiation and development in two soybean cultivars.* BIOTRONICS **23**, 93–104. 1994. To predict time to flowering in field-grown soybean [*Glycine max* (L.) Merrill], it is essential to know how floral initiation and development are affected by changing daylengths. There is some evidence that both the rate of change in daylength and the direction of that change affect flowering. The purpose of this research was to establish how increasing and decreasing daylengths of various magnitudes influenced progress toward floral initiation (R0) and progress in floral development (R0 to R1). Seeds of 'Johnston' (MG VIII) and 'Clark' (MG IV) were sown every two weeks in a greenhouse at 39° N latitude in which temperature was controlled at 25℃ day and night. The time from the end of juvenility to floral initiation (R0) and the floral development phase (time from R0 to first open flower, R1) were recorded for each cultivar. R0 was determined by apical dissection at 45× magnification. Most of the variation in the time to floral initiation in 'Johnston' could be accounted for by a constant value when daylengths were below ≈ 13 h and a linear increase when mean daylengths exceeded 13 h. The time to R0 in increasing daylengths was not different from the time to R0 in decreasing daylengths when the magnitudes of the daylengths during the floral initiation phase were similiar. The length of the floral development phase in 'Johnston' was longer when mean daylengths exceeded 13 h, suggesting that the floral development phase was also sensitive to photoperiod. However, the end of sensitivity to photoperiod coincided with R0 when mean daylengths were ≤13 h, suggesting that photoperiod during the floral development phase did not influence development equally over the time to R1. There were small but significant increases in time to R0 and in the length of floral development in 'Clark' as daylength increased, but no effect of direction of change in daylength was apparent in either phase. Photoperiod sensitivity during floral development was not established unequivocally. At least part of the period between R0 and R1 was not sensitive to photoperiod. Time to flowering could be explained without invoking an effect of change in direction of daylength.

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

INTRODUCTION

Much of the work on photoperiod in soybean [*Glycine max* (L.) Merrill] has been done in controlled-environment facilities where daylength is controlled at a set value (*5, 8, 9*). Field-grown soybeans experience photoperiods of various lengths, various rates of change, and two directions of change. One or more of these variations may affect flowering. In field studies, Constable and Rose (*2*) found that the inclusion of a term for rate of change in daylength in their multiple regression equation improved predictions of flowering time in a number of cultivars. They also noted that "...for similiar daylength and temperature in spring and autumn sowings, vastly different rates of development were observed. .."(p. 66), suggesting an effect of the direction of change. Garner and Allard (*4*) plotted flowering time against sowing date for soybeans grown in a temperature -controlled greenhouse and got an asymmetrical response curve over the growing season for 'Biloxi' (MG VIII) and 'Peking' (MG IV). These response curves showed that times to flowering in increasing daylengths were longer than the times to flowering in decreasing daylengths, even when the magnitudes of the daylengths were similiar.

Soybean crop simulation models predict flowering in the field based on certain suppositions about the influences of photoperiod at various developmental stages. Most crop models (*1, 6, 7*) assume that the end of juvenility comes at the V1 stage (*3*), with the appearance of the first trifoliolate leaf. Recent work by Wilkerson et al. (*9*) has demonstrated that the end of the juvenile phase could vary from VE to V5 depending on cultivar.

Modelers have agreed on when the juvenile phase ends, but the period over which floral development is sensitive to photoperiod has been an area of disagreement as modelers have struggled to find mechanisms that would fit flowering data. Some crop modelers (*1, 6*) have separated the time from the end of juvenility to first flower into two phases: the floral initiation phase and the floral development phase. The first phase ends with the appearance of a morphologically distinct flower bud in the apical meristem. This phase is assumed to be under photoperiod control. The second phase, which is the development of the flower bud until the petals open, R1, is temperature dependent but not photoperiod dependent. Other crop modelers (*7*) have used the same phases to describe flower development but have made both phases responsive to photoperiod. Recent work by Wilkerson et al. (*9*) has demonstrated that both approaches could be partly true. They tested six cultivars and two isogenic breeding lines and found that floral development was photoperiod sensitive in its early stage, but later development (6.3 to 8.7 d before anthesis) was found not to be sensitive to photoperiod.

The purpose of our study was to determine how naturally changing daylengths influence progress toward soybean flower initiation and progress in flower development and to generate equations to be incorporated into a crop simulator. The objectives were (a) to establish whether flower development (the period after floral initiation but before flower opening) was influenced by

photoperiod and (b) to determine whether the direction of change in daylength affected either flower initiation or development for two maturity groups (MG VIII and MG IV) that had previously exhibited asymmetry in times to flower over the growing season at 39°N. The study extended the classic experiment of Garner and Allard (*4*) by including observations on floral initiation, thus allowing for an examination of the effect of photoperiod during various phases of soybean flower development.

MATERIALS AND METHODS

Seeds were sown three to a 10–cm pot containing medium grade vermiculite. After emergence, seedlings were thinned to one plant per pot. Nutrients were supplied in irrigation water using a complete nutrient solution that consisted of 13.5 mM N, 1.0 mM P, 8.5 mM K, 4.0 mM Ca, 3.5 mM Mg, 4.5 mM S, 0.34 μM Zn, 4.5 μM Mn, 0.16 μM Cu, 110 μM Fe, 13.7 μM B, and 0.49 μM Mo. Apices were dissected under a binocular microscope using 15× and 45× magnification to determine time of floral initiation, R0. R0 was recorded when the first morphological features of a differentiated flower bud were observed in the mainstem apex.

Experiment 1

Seeds of 'Johnston' (MG VIII) and 'Clark' (MG IV) were germinated and grown in controlled–environment chambers at a photosynthetic photon flux density (PPFD) of 500 μmol m^{-2} s^{-1} in a 22–h photoperiod (flower non–inducing conditions) at 25±1℃ (day/night). Every other day beginning at emergence, VE, five plants were transferred to a 9–h photoperiod (flower inducing conditions) at the same temperature. Times to various stages of development (>50% of the plants) were recorded for each cultivar and for each transfer set.

Experiment 2

'Johnston' (MG VIII) and 'Clark' (MG IV) were grown in a greenhouse controlled at 25±2℃ (day/night). Seeds were sown at twice weekly intervals starting 21 February 1989 and continuing through 26 October 1989 in a greenhouse at Beltsville Agricultural Research Center, Beltsville, MD, at latitude 39°N. A minimum of seven plants of each cultivar were kept from each sowing date to record times to R1. Additional plants were grown and sacrificed to determine when R0 occurred. Planting date (P), day of emergence (VE), cotyledon stage (VC), and other vegetative and reproductive stages (R0 and R1) were recorded for each cultivar. Growth stages were recorded when >50% of the plants had reached that stage.

Experiment 3

'Johnston' and 'Clark' seedlings were grown in two controlled–environment chambers maintained at 25±1℃ (day/night). Seedlings were grown at a PPFD of 500 μmol m^{-2} s^{-1} in a 14–h photoperiod until they reached the end of the

juvenile stage as determined by experiment 1. At this point, the growth chamber was programmed to decrease the photoperiod by 144 s each day. A change of 144 s each day was chosen because it was near the peak for the maximum naturally occurring change in daylength at Beltsville. Time to R0 was recorded, and the photoperiods at which these occurred for the two cultivars were noted. To compare the time to reach R0 for increasing photoperiods, 25 plants from each cultivar were grown at the photoperiod obtained at the end of the first treatment until they reached the end of the juvenile phase. Then the plants were subjected to increasing daylengths (144 s per day), and time to reach R0 was recorded. The same general procedure was followed to determine the effect of direction of changing daylength on the time interval between R0 and R1. Twenty-five plants from each cultivar were grown in a 14-h photoperiod until they reached R0; then the photoperiod was decreased by 144 s each day. Time to reach R1 was recorded for each cultivar, and the photoperiod at the end of this phase was recorded. Subsequent groups of plants were grown at these photoperiods until they reached R0, and then photoperiod was increased by 144 s each day. Times to R0 and R1 were recorded.

Experiment 4

Fifty-one plants were grown in controlled-environment chambers in a 9-h photoperiod at 26℃ (day/night) in a minimum of 800 μmol m^{-2} s^{-1} supplied by equal numbers of metal halide and high pressure sodium lights. Every day from 2 to 14 days after VE, three plants were transferred to a 22-h photoperiod at 26℃ (day/night). Then transfers were made every other day until all plants had flowered. Three plants remained in a 9-h photoperiod until R1. Time to R1 was recorded for all plants that flowered before the end of the experiment.

RESULTS AND DISCUSSION

Experiment 1

The photoperiod-sensitive period of growth started at VC stage for 'Johnston' and at VE stage for 'Clark' (Fig. 1). In both cultivars, it took a minimum of 19 days to reach R1 from the time the plants were placed in a 9-h photoperiod at constant 25℃ air temperature.

Experiment 2

Figure 2 is a stacked plot of days from the end of the juvenile phase to R0 and the floral development phase (days from R0 to R1) as a function of time of year when soybeans reached the end of juvenility. Time to R0 ranged from 10 to 17 days for 'Clark' and from 8 to 28 days for 'Johnston.' The floral development phase ranged from 8 to 15 days in 'Clark' and from 12 to 29 days in 'Johnston.' The increase in time from the end of the juvenile phase to R1 reached a peak when the juvenile phase ended on day 163 (12 June 1989) for 'Johnston' and day 160 (9 June 1989) for 'Clark.'

Some of the variability in time to R0 (Fig. 2) may have resulted from

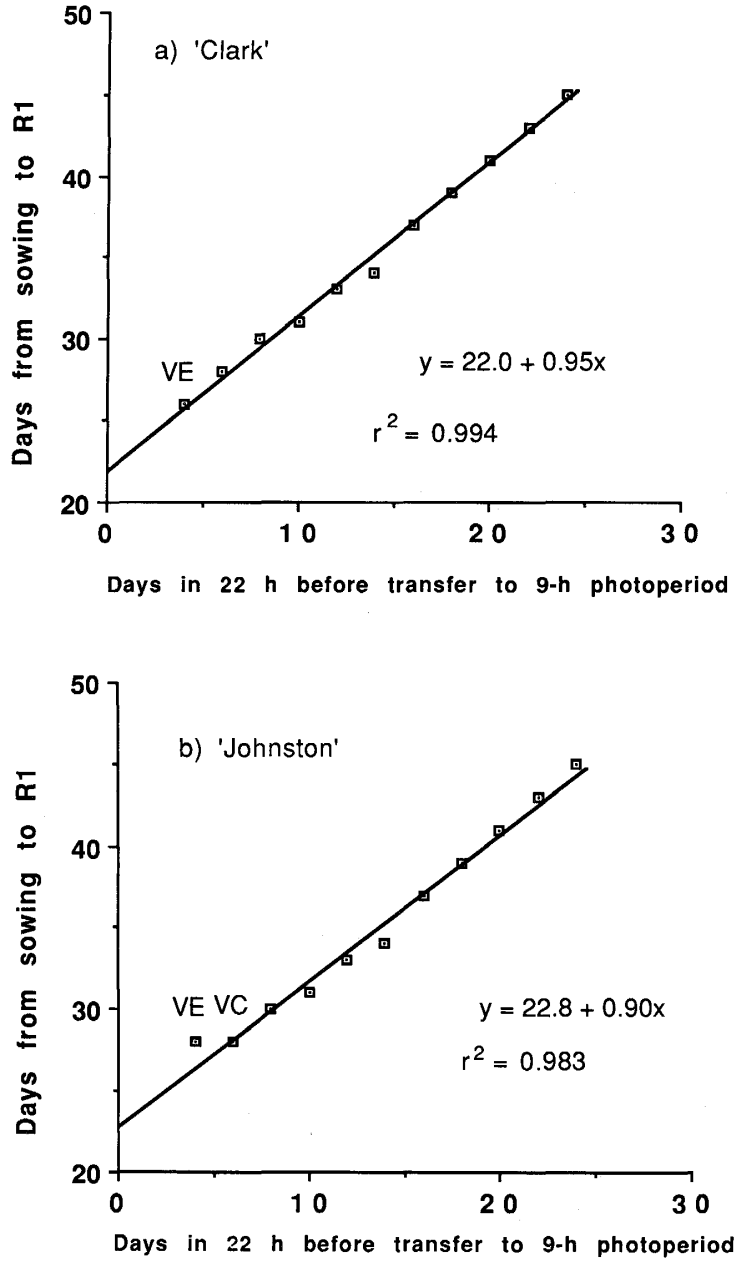


Fig. 1. Days from VE to R1 as a function of the day of transfer from a 22-h to a 9-h photoperiod for soybean cultivars. Transfer began two days after VE.

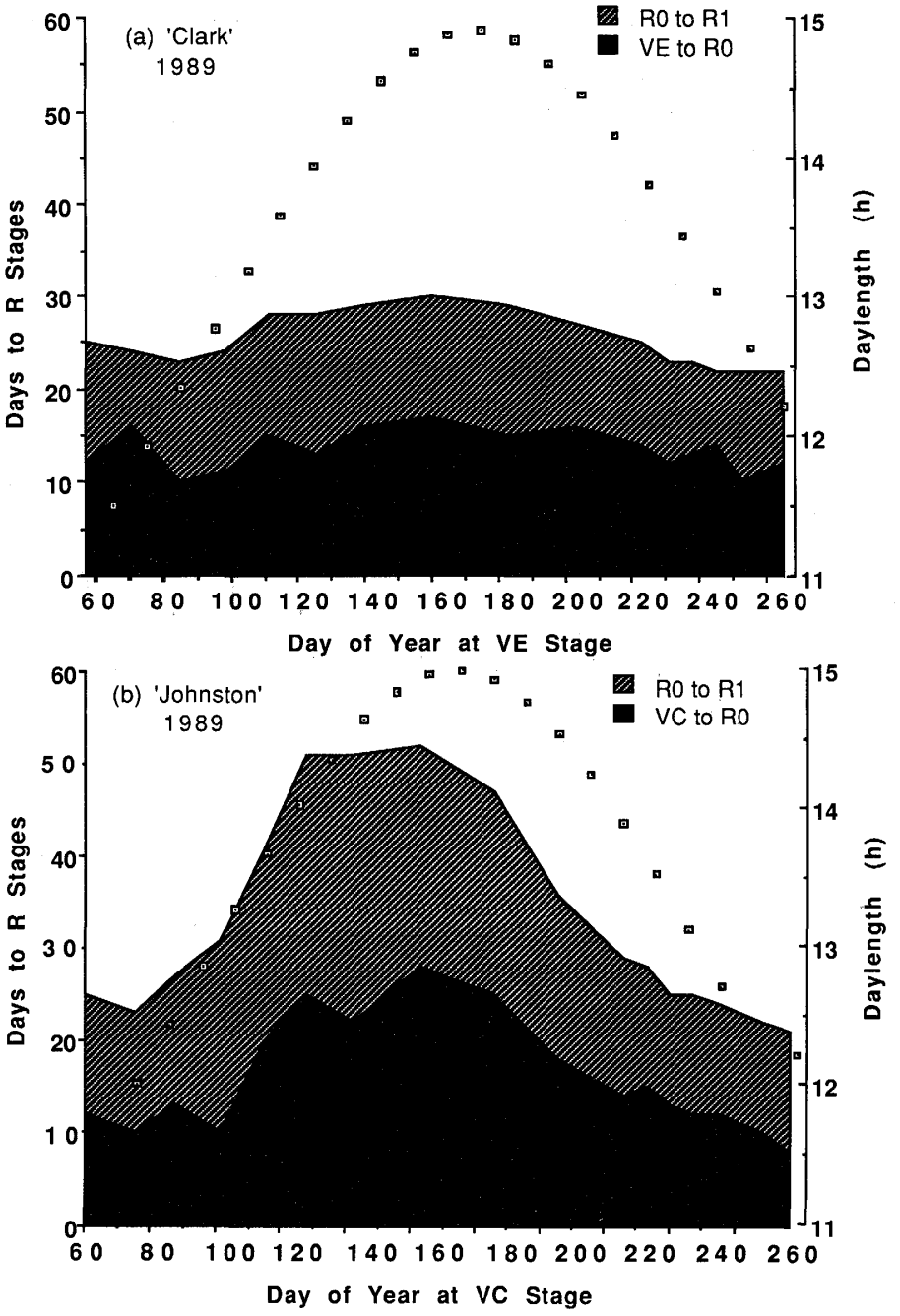


Fig. 2. A stacked plot of days from the end of the juvenile phase to floral initiation, R0, and from R0 to first open flower, R1, as a function of the day when juvenility ended for 'Johnston' and 'Clark' soybean cultivars.

difficulty in assessing when R0 had occurred. When photoperiods were <13-h, the appearance and differentiation of the flower bud were rapid (1-2 days) and unmistakable. When photoperiods exceeded 13-h in 'Johnston,' morphological changes were slow, and assessing the time to reach a floral stage with comparable morphological characteristics across all sowing dates was not always easy. R0 was said to have occurred when pollen sacs were first observed as small spheres in the flower bud.

The time to R0 and the length of the floral development phase in 'Johnston' increased rapidly as daylengths exceeded 13 h (Fig. 3). There was no evidence that either time to R0 or the length of the floral development phase was affected by the direction of change in daylength (Fig. 3). There were small but significant increases in the time to R0 and in the length of the floral development phase in 'Clark' over all daylengths experienced (Fig. 4). There was no evidence in 'Clark' that change of the direction of daylength affected results.

Experiment 3

Experiment 3 was designed to control the magnitude and the direction of photoperiod experienced by soybean plants from the end of juvenility to R0 and from R0 to R1, rather than just observing and interpreting changes over the growing season. If the direction of photoperiod were to have an influence on flowering time, the expectation was that flowering time would increase in increasing daylengths.

The standard error for time to flower was small, but the determination of R0 is a destructive observation and could have varied by one day. Therefore, treatment means in Table 1 were judged to be different when one extra day made no difference to the significance. The direction of change in photoperiod had little influence on time to R0 for 'Johnston' or 'Clark.' However, for the

Table 1. Mean days to floral initiation (VE to R0 for 'Clark', VC to R0 for 'Johnston') and to floral development (R0 to R1) when photoperiods were increased or decreased by 144 s each day.*

Cultivar	Development Phase	Photoperiod			
		Decreasing	Increasing	Decreasing	Increasing
		Daylength at start time (hh:mm:ss)		Length of phase days	
'Johnston'	VC to R0	14:00:00	13:31:12	13.4 a	11.8 a
	R0 to R1	14:00:00	13:21:36	16.6 a	13.1 b
'Clark'	VE to R0	14:00:00	13:29:12	12.0 a	12.0 a
	R0 to R1	14:00:00	13:40:48	8.8 a	10.6 a

* Row means followed by the same letter are not significantly different (t-test, $p<0.05$).

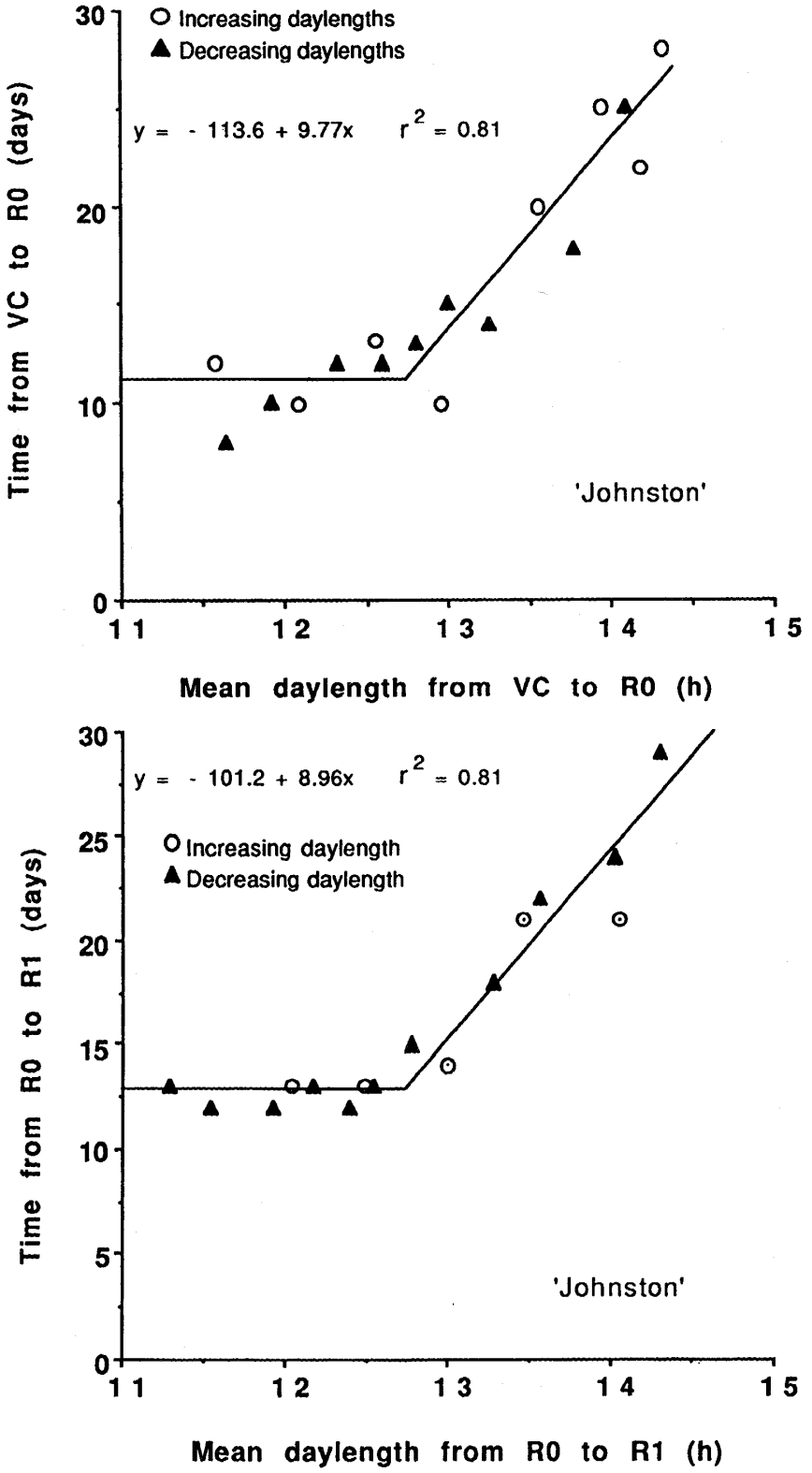
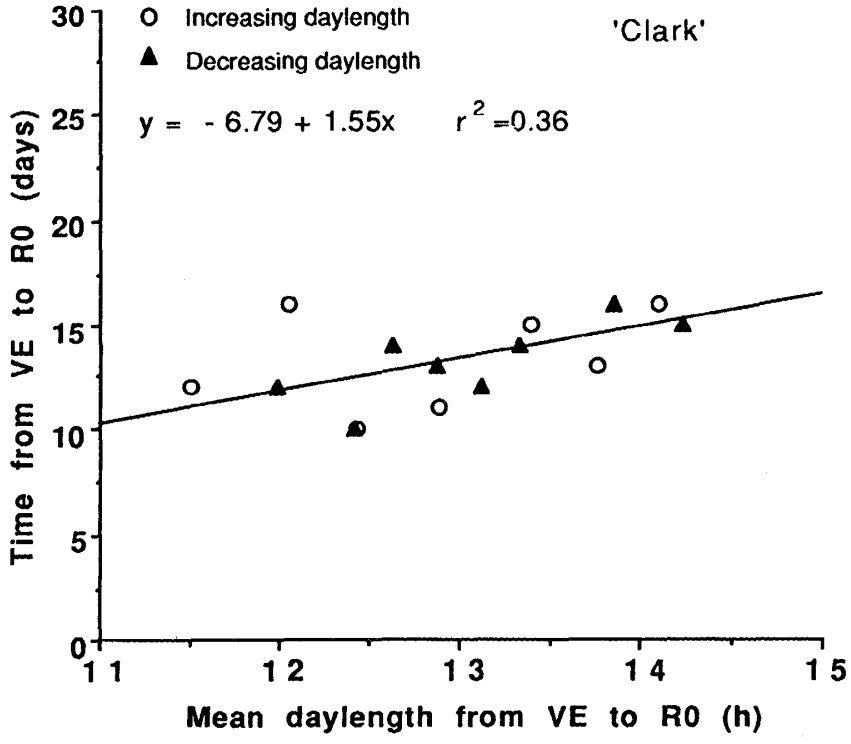


Fig. 3. Days (a) to floral initiation, R0, and (b) from R0 to first open flower, R1, as a function of mean daylength for 'Johnston' (MG VIII) soybean.



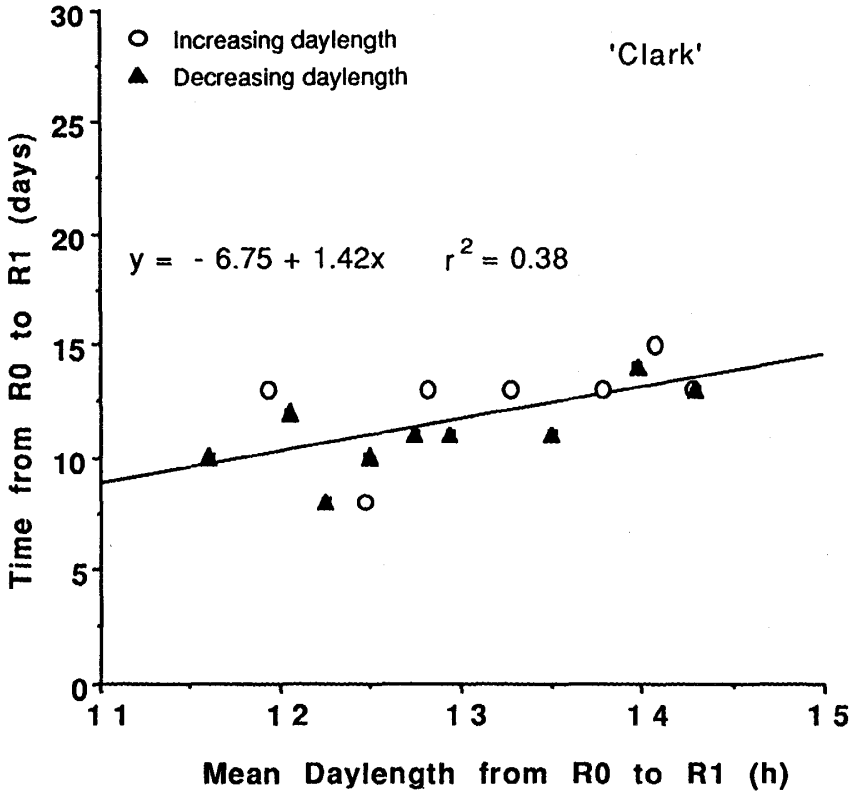


Fig. 4. Days (a) to floral initiation, R0, and (b) from R0 to first open flower, R1, as a function of mean daylength for 'Clark' (MG IV) soybean.

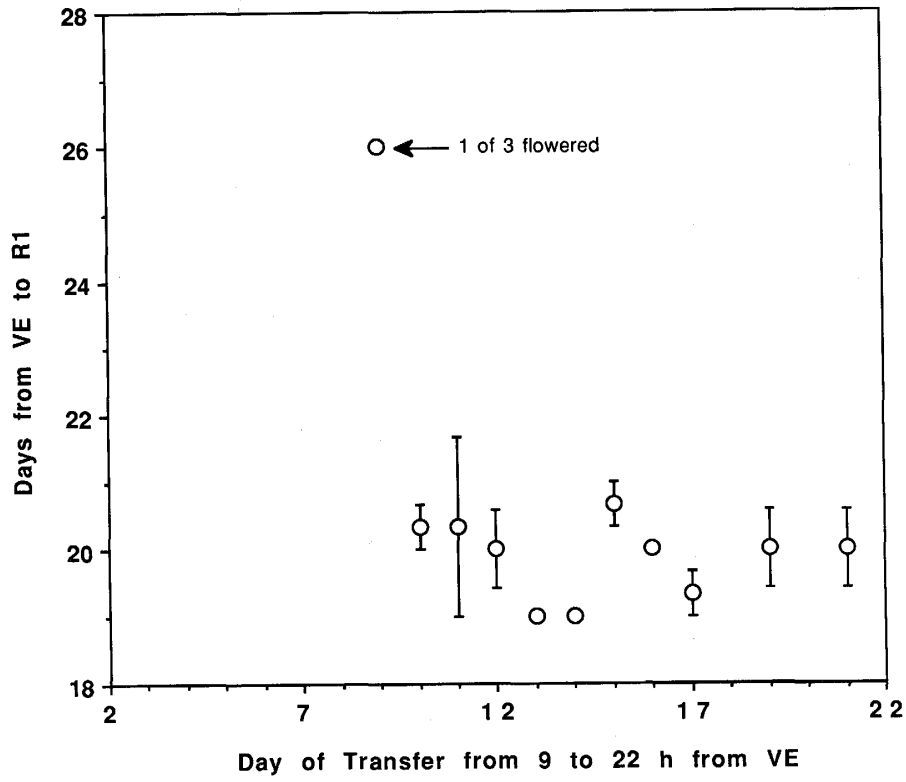


Fig. 5. Days from emergence, VE, to first open flower, R1, as a function of day of transfer from a 9–h to a 22–h photoperiod for 'Johnston' soybean.

floral development phase, there was a significant decrease in time from R0 to R1 in 'Johnston' as the photoperiod increased.

In experiment 3, an assumption was made that floral development was responsive to photoperiod until R1. Wilkerson et al. (*9*) have shown this assumption is not correct for some cultivars. In experiment 4, using an experimental paradigm similar to that of Wilkerson et al. (*9*), we tested 'Johnston' for photoperiod insensitivity before first open flower. One of the three plants flowered when given a 9–h photoperiod for 9 days before transfer to a 22–h photoperiod (Fig. 5). All three plants that were given a 9–h photoperiod for 10 days or more before transfer to a 22–h photoperiod, flowered at the same time as plants that remained in a 9–h photoperiod until R1. Results were interpreted to mean that the time to first flower in 'Johnston' was unaffected by the 22–h photoperiod 12 days before first open flower (Fig. 5). This observation helps to explain the results of experiment 3. When the change in photoperiod was controlled from R0 to R1, plants experiencing increasing daylengths would have also experienced shorter daylengths during their photoperiod–sensitive stage compared with plants given decreasing daylengths.

The results of our study demonstrated that the floral development phase was sensitive to photoperiod. However, in mean daylengths <13–h, the period of

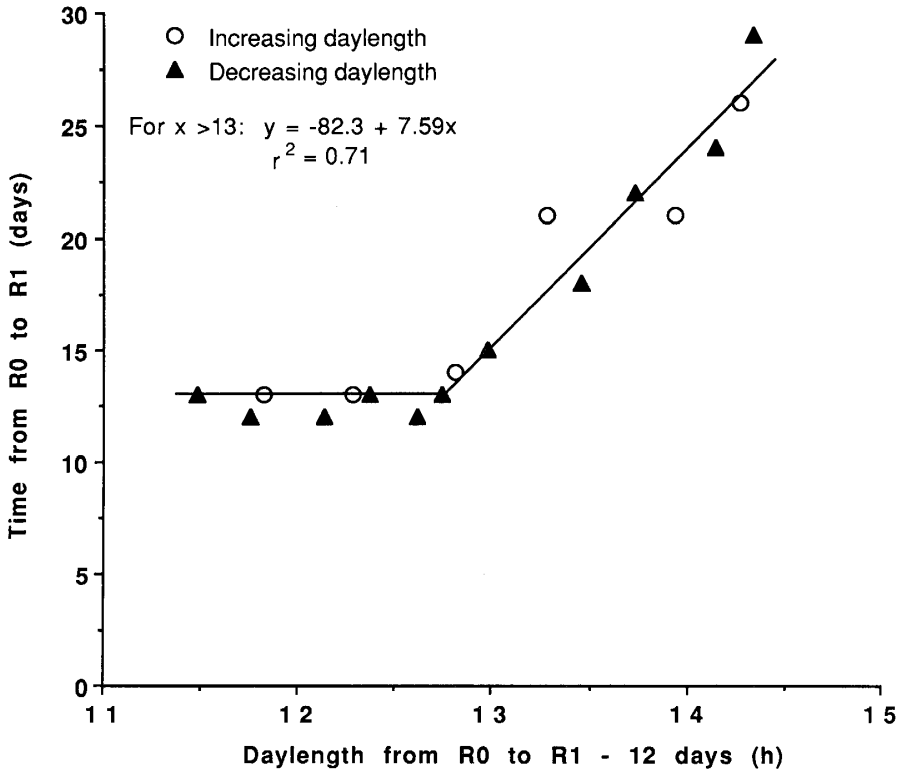


Fig. 6. Days from floral initiation, R0, to first open flower, R1, for 'Johnston' as a function of mean daylength from R0 to 12 days before first open flower.

photoperiod insensitivity for 'Johnston' (as judged by experiment 4) was very nearly equal to the length of the floral development phase. The sensitivity to photoperiod, as shown in Fig. 6, must be occurring early in the floral development phase.

There was no evidence that a change in direction of daylength affected time to R0 or the length of the floral development phase for either 'Clark' or 'Johnston'. Most of the variation in time to R0 and from R0 to R1 in 'Johnston' could be explained by a constant response time for daylengths <13-h and a linear increase in reponse time as daylengths increased beyond $\approx$ 13-h. Most of the variation in time to R0 and in the length of the floral development phase in 'Clark' could be explained as a linear increase with increased daylengths over the range observed at 39°N (9.43 h to 14.9 h).

CONCLUSIONS

When making predictions about flowering times for field-grown soybeans, it is essential to know (a) what the relative sensitivities to photoperiod are for the various cultivars, (b) the critical daylengths (photoperiods that mark a distinct change in flowering response time) for various cultivars, and (c) which growth

stages are sensitive to photoperiod. 'Clark' was found to be relatively insensitive to the photoperiods experienced at 39°N, whereas time to flowering in 'Johnston' rapidly increased as daylengths exceeded 13-h.

Our results showed that photoperiod sensitivity of the first flower in 'Johnston' began from VC stage and ended 12 days before R1. 'Clark' was photoperiod sensitive from VE stage, but because it was relatively insensitive to the daylengths over the range tested, the end of any photoperiod sensitivity to flower development was not determined.

The photoperiod-insensitive period of floral development in 'Johnston' was determined by transferring plants from a 9-h to a 22-h photoperiod. Whether the length of the photoperiod-insensitive phase can be assumed constant for a given cultivar or whether it depends on the inducing photoperiod is an important question to answer before we can accurately predict flowering time in field-grown soybeans.

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