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Effect of a Long-Juvenile Trait upon Flowering in Soybeans Grown in Short and Long Photoperiods

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Abstract

A delayed flowering response was identified in soybean [*Glycine max* (L.) Merr.] germplasm line PI 159925 when it was grown under short photoperiods. This flowering delay, referred to as a long-juvenile (LJ) trait, has been reported to be controlled by one, two, and three genes, in separate studies. The LJ trait may extend areas of adaptation and planting dates for latitudes < 35°. The objectives of this study were to (1) determine the genetic control of the LJ trait, and (2) determine if there is any association between flowering under short and long photoperiods. Cultivars Kirby and Perrin were crossed to PI 159925. Parents F_1, F_2, F_3, F_4 backcrosses to parents, and progeny of the respective backcrosses were evaluated in 1992 and 1993. Plantings were made twice in the field under long photoperiod (LP > 15 hours) and short photoperiod (SP < 13 hours) conditions at 33° N. latitude. Results suggest that the LJ trait is controlled by a single recessive nuclear gene. Heritability estimates greater than 86% favor early generation selection. The realized heritabilities were high enough to suggest that further gains from selection are possible. The mean of the F_2 plants derived from reciprocal crosses of Kirby X PI 159925 and Perrin X PI 159925 were similar, indicating that inheritance of the LJ trait was not maternally influenced. Correlation coefficients of 0.10 and 0.37 between flowering date under short and long photoperiods for the two crosses indicated that flowering time under long photoperiod was not a good criterion to predict the performance of the LJ trait under short photoperiod.

Introduction

Photoperiod influences the development of soybeans from time of emergence to anthesis (Bidja, 1988: Hartwig and Edwards, 1986). Soybeans are classified as photoperiod-sensitive, short-day plants and are assigned to maturity groups according to the time required to maturity at specified latitudes.

Hartwig (1970) suggested that soybeans grown under short-photoperiod conditions required a minimum of 45 days from emergence to flowering in order to develop enough vegetative mass to yield adequately.

Rennie et al.(1991) suggested the need for photoperiod-insensitive plants for Canada (high latitudes). Rachie and Plarre (1979) proposed the use of photoperiod-insensitive cultivars in the tropics (low latitudes). However, the production capability of this day-neutral character is doubtful in the field (Hinson, 1974).

A delayed flowering characteristic has been identified in several strains of soybeans (Hartwig and Kiihl, 1979). PI 159925, introduced from Peru in 1947, possesses a trait that delays flowering in soybeans under short-day (< 14 hours) conditions (Hartwig and Kiihl, 1979; Cregan and Hartwig, 1984).

This trait was referred to by Tisselli (1981) as a "long juvenile characteristic in soybeans."

The published literature contains estimates of one (Bidja, 1988; Hinson, 1989), two (Kilen and Hinson, 1990), and three (Hartwig and Kiihl, 1979) genes to be controlling the LJ trait.

In some previous inheritance studies, the source of the juvenile trait was a recovered line rather than the original germplasm accession. This diversity in genetic background may have altered segregation ratios. With this in mind, two cultivars that flowered at approximately the same time as PI 159925 when grown under long photoperiod conditions were selected as adapted parents for crossing. Any differences among the progeny from such crosses in time to flowering under a short photoperiod should be mainly the contribution of the gene or genes affecting the long-juvenile trait.

The primary objectives of this study were to (1) determine the genetic control of the LJ trait, and (2) determine if there is any association between flowering date under short and long photoperiods.

Materials and Methods

Kirby, a maturity group VIII cultivar, traces to one F_5 plant (F_6 line) from the modified backcross of 'Centennial' × [Forrest × ('Cobb' × D68-216)]. Perrin is a maturity group VIII cultivar that matures one day later than Kirby. It traces to an F_5 line selected from the cross 'Coker 488' × 'Braxton.' PI 159925, a plant introduction from Peru, is also a maturity group VIII type.

The parental materials were selected for their marked differences in flowering dates when grown under short photoperiod (less than 13 hours at 33° 26' N. latitude. However, these genotypes flower and mature within a difference of four to seven days, when grown under long photoperiod (more than 15 hours) conditions at 33° 26' N. latitude.

Soybean cultivars, 'Kirby' and 'Perrin,' were crossed with a germplasm accession, PI 159925, possessing the LJ trait. Reciprocals of each cross were made. Kirby (P_1), Perrin (P_2), PI 159925 (P_3), F_1; F_2; reciprocal F_2 (F_2-recp); F_3; F_4; backcrosses to Kirby and Perrin, ($BC_1P_1P_3F_1$ and $BC_1P_2P_3F_1$); backcrosses to PI 159925, ($BC_1P_3P_1F_1$ and $BC_1P_3P_2F_1$); and the respective backcross selfed generations ($BC_1P_1P_3S_1$, $BC_1P_2P_3S_1$, $BC_1P_3P\ _1S_1$ and $BC_1P_3P_2S_1$) were evaluated during 1992 and 1993. For ease of discussion, the Kirby × PI 159925 cross will be identified as cross 1, and Perrin × PI 159925 as cross 2.

Crosses were made on field-grown plants in the summer of 1990, at the Mississippi Agricultural and Forestry Experiment Station Delta Branch, Stoneville, MS. F_1 plants were grown in a greenhouse with artificially extended daylength during the winter of 1991. The F_2 plants along with some F_1's were grown in the field under natural light in the summer of 1991.

In 1992 parents and progeny derived from crosses 1 and 2 were sown in the field at two sites at different planting dates (May 28 and September 1) under natural photoperiod.

One-hundred sixty-one F_2 plants and 340 F_3 lines from cross 1, and 155 F_2 plants and 260 F_3 lines from cross

2, were planted in the field together with parents, F_1, $BC_1P_1P_3F_1$, $BC_1P_2P_3F_1$, $BC_1P_3P_1F_1$, and $BC_1P_3P_2F_1$ populations at Stoneville, MS on May 28, 1992. A plot consisted of a single row 2.8 m (9 feet) long with 0.9 m (36 inches) between rows and approximately 20 plants per row. Soil type was a Bosket very fine sandy loam (fine-loamy, mixed, thermic, Mollic Hapludalfs).

Plants emerged June 2, 1992 (long photoperiod, 15.15 hours). Flowering dates (days from emergence to at least one flower opened in 50% of the plants per row) and maturity (95% of the pods mature and defoliations occurred) were recorded three times weekly. The daily average temperature from emergence to flowering was 31.6 °C. For the short photoperiod (13.05 hours) experiment, remnant seeds from the F_2 populations and F_3 lines along with parents, F_1, and reciprocal F_2 were planted on September 1, 1992.

Plantings were made in a completely randomized design with two replications on the Mississippi State University Plant Science Research Center, Starkville, MS (Lat. 33° 26' N) in a Marietta fine sandy loam (fine-loamy, silicious, thermic Fluvaquentic Eutrochrepts) soil. Plots consisted of single rows 1.8 m (6 feet) long and 0.9 m (36 inches) apart. Approximately 25 seeds per row of F_3 lines were planted. Plots for the parents and F_2 populations contained approximately 20 seeds per row. Because of a limited amount of F_1 hybrid seeds, only 12 F_1 seeds from cross 1, and 5 seeds from cross 2 were planted. There were no reciprocal F_1 seeds available for these plantings.

The number of days to flower was recorded on the first 12 individual plants in a row for F_3 lines and parents; however, for F_1, F_2, F_2 reciprocal, $BC_1P_3F_1$, $BC_1P_2P_3F_1$, $BC_1P_3P_1F_1$ and $BC_1P_3P_2F_1$ plants, observations were taken on all individual plants. From emergence to flowering the average temperature was 13.6 °C.

In 1993 the plantings were repeated on two planting dates (June 2 and August 24) at the same two sites under long and short photoperiod previously described for 1992. The F_4 lines, grown in 1993, were from seeds produced on ramdomly chosen F_3 plants grown in the long photoperiod in 1992. Therefore, each F_4 line traced back to a single different F_2 plant.

Each cross was analyzed separately, using the SAS General Linear Models Procedure (SAS Institute, 1982). A 95% confidence interval (CI) was calculated for the two parents in each cross, to define the three maturity classes (early, intermediate, and late flowering). Chi-square analysis (Steel and Torrie, 1980) was used to test goodness-of-fit between observed and expected phenotypic ratios in segregating populations. Broad-sense heritability estimates were computed from variance components. Simple correlation coefficients for flowering time under LP and SP were also calculated. Maternal influence on the expression of the trait was tested by comparing the mean number of days to flower for reciprocal F_2 populations from each cross.

Realized heritability (H_R) was calculated according to the formula of Falconer (1981):

$$\mathbf{H_R = R/S}$$

where R is the response realized by selection and S is the selection differential. Standard errors for the estimates of realized heritability were calculated according to Prout's (1962) formula.

Expected genetic gain was calculated for 10% selection pressure using the formula of Allard (1960).

Results and Discussion

Table 1 presents the means and standard errors for the number of days after emergence to flower when the populations were grown in the field under long and short photoperiods in 1992. All populations exhibited a longer period of vegetative growth when cultivated under a long photoperiod than when grown under a short photoperiod.

The differences in days to flowering between long and short photoperiods were 7.6 days for PI 159925, 26.3

days for Kirby, and 24.7 days for Perrin (Table 1), indicating a reduced sensitivity to photoperiod for PI 159925. Mean numbers of days to flowering for the F_1, F_2, F_2-recp, F_3, $BC_1P_1P_3F_1$ and $BC_1P_2P_3F_1$ populations fell between the early parent and mid-parent value, but most were closer to the early parent value (Table 1). Mean number of days to flowering for the F_2 reciprocal populations did not differ significantly, indicating that there was no maternal effect in either cross 1 or 2 for the expression of the LJ trait under short photoperiods.

Correlation coefficients for flowering response of late F_3 lines grown under long photoperiods with F_3 lines grown under short photoperiods were positive but had very small value, 0.10 and 0.37 for cross 1 and 2, respectively. This indicated that there was little association between selection under long photoperiod and short photoperiod. Hartwig and Kiihl (1979) and Parvez and Gardner (1987) also suggested that flowering response under long-day conditions was not a good predictor of behavior of the LJ trait under short-day conditions. Therefore, all analyses for determining the genetic control of the LJ trait were performed on flowering data from plants grown in short photoperiods.

Table 1. Means and standard errors of parents, mid-parents, F_1, F_2, F_2-recp, F_3, BC_2F_1, BC_2F_1, and BC_3F_1 populations for days after emergence to flower under long (LP) and short (SP) photoperiod conditions in 1992.

Population	Length of Photoperiod		Difference
	LP	SP	
	days		
Kirby	63.8 ± 3.2	37.5 ± 2.0	26.3
PI 159925	72.1 ± 1.0	64.5 ± 1.5	7.6
Mid-parent	67.7 ± 2.8	51.0 ± 1.0	16.5
Cross 1 F_1	62.3 ± 2.1	48.3 ± 2.3	14.4
Cross 1 F_2	63.2 ± 5.6	46.3 ± 3.6	16.9
Cross 1 F_2-recp	63.4 ± 5.7	49.3 ± 5.5	14.7
Cross 1 F_3	65.7 ± 4.8	53.7 ± 9.1	12.0
Cross 1 $BC_1P_1P_3F_1$	61.1 ± 4.4		
Cross 1 $BC_1P_3P_1F_1$	70.5 ± 4.4		
Perrin	63.1 ± 3.5	38.1 ± 1.3	24.7
PI 159925	72.2 ± 1.7	64.3 ± 1.5	7.9
Mid-parent	67.1 ± 3.4	51.2 ± 1.0	15.9
Cross 2 F_1	61.7 ± 2.3	45.6 ± 1.8	16.1
Cross 2 F_2	64.4 ± 5.9	45.8 ± 3.3	16.4
Cross 2 F_2-recp	63.7 ± 5.2	44.9 ± 7.4	18.8
Cross 2 F_3	63.7 ± 5.2	50.7 ± 8.7	13.0
Cross 2 $BC_1P_2P_3F_1$	60.7 ± 1.7		
Cross 2 $BC_1P_3P_2F_1$	68.5 ± 4.9		

Table 2. Segregation of F_2 plants and F_3 lines from two crosses for flowering response under short photoperiod conditions in 1992.

Cross 1	Phenotypes		Total
	Early	Late	
Observed	120	44	164
Expected (3:1)F_2	123	41	164
Observed	250	90	340
Expected (3:1)F_3	255	85	340
Chi-square (3:1) F_2 = 0.29 ($0.50 < P < 0.75$)			
Chi-square (3:1)[*] F_3 = 0.35 ($0.50 < P < 0.75$)			

Cross 2	Phenotypes		Total
	Early	Late	
Observed	121	46	167
Expected (3:1)F_2	125	42	167
Observed	201	59	260
Expected (3:1)F_3	195	65	260
Chi-square (3:1) F_2 = 0.59 ($0.25 < P < 0.50$)			
Chi-square (3:1)[*] F_3 = 0.63 ($0.25 < P < 0.50$)			

[*] ratios constructed as (Early + Intermediate):Late

The F_2 populations grown in the short photoperiod resulted in the following flowering response:

In cross 1, 120 (73.2%) plants flowered from 34 to 35 days after emergence and 44 plants (26.8%) flowered later than 54 days. In cross 2, 121 plants (72.5%) flowered from 34 to 54 days after emergence and 46 plants (27.5%) flowered later than 54 days. These late-flowering F_2 plants could not be progeny tested to determine if they were homozygous, because the plants were killed by frost before seeds could be harvested. Chi-square test gave a better fit to a 3 early:1 late ratio (one gene model) than other models tested (Table 2).

The F_3 lines were separated into early, intermediate, and late-flowering cases by calculating a 95% confidence interval for the early and late-flowering parent in each cross. Using this separation for cross 1, 49 F_3 lines were classified as early flowering (<= 45 days), 90 F_3 lines were classified as late flowering (>= 58 days, and 201 F_3lines were classified as intermediate flowering 46 to 57 days). For cross 2, 55 F_3 lines were classified as early flowering (<= 44 days), 59 F_3 lines were classified as late (>= 58 days) and 146 F_3 lines were classified as intermediate flowering (45- to 57-days) class. For both crosses, the observed number of late F_3 lines grown under a short photoperiod was relatively close to the expected number if the LJ trait were controlled by a single gene. However, the separation of early flowering from intermediate flowering lines was not as precise, with a deficiency of early lines from that expected in both crosses.

In view of these variations in the early class, the early and intermediate classes were combined to test for a 3:1 F_2 ratio (one gene model). When this was done, an acceptable fit to a 3:1 ratio was achieved (Table 2). The one gene model gave the best fit of all models tested (data not shown).

The second-year experiments, planted August 24, 1993 at Starkville, had very poor emergence because of drought conditions. The tests were terminated 61 days after emergence because of killing frost on October 30, 1993.

Means and standard errors for days after emergence to flowering when grown under the short photoperiod in

1993 are presented in Table 3. Mean numbers of days to flowering for F_1, F_2, and F_4 populations were not significantly different from the calculated mid-parent value for both crosses. These data did not support the single-gene model proposed for 1992 data. It may be because variation was so large that differences could not be detected, or that a more complex system may be involved in flowering; however, the $BC_1P_1P_3S_1$, $BC_1P_2P_3S_1$, $BC_1P_3P_1S_1$ and $BC_1P_3P_2S_1$ means differed significantly from the mid-parent value. It was observed that when the hybrid from each cross was backcrossed to the late parent, PI 159925, and selfed, late flowering individuals were found. However, when the backcross was made to the early parents in each cross and selfed, it resulted in early flowering individuals under short photoperiod (Table 3).

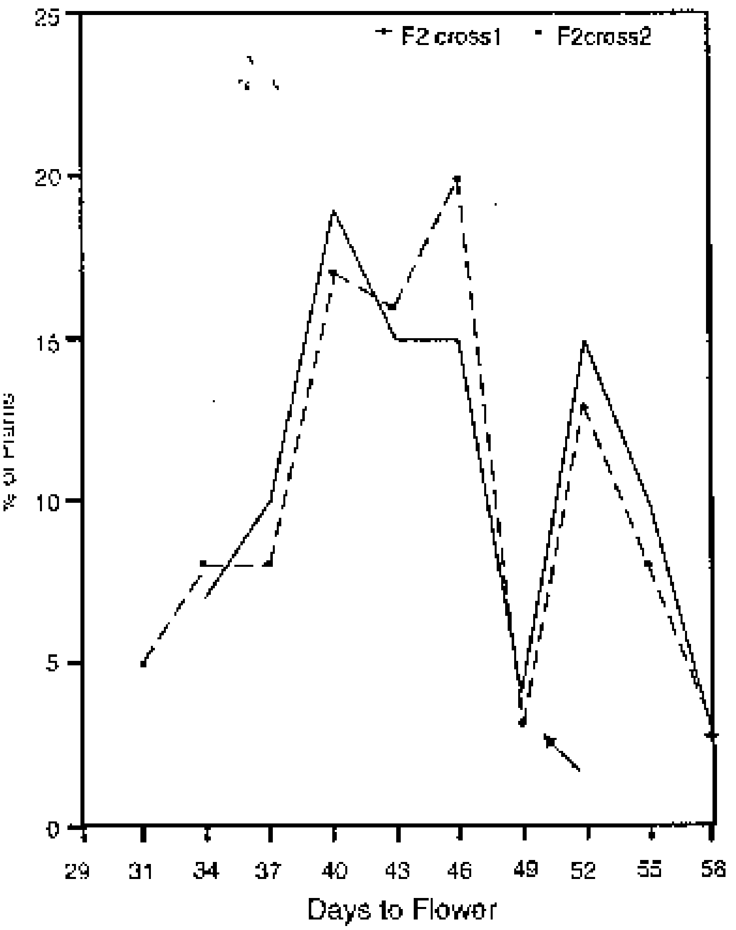
In cross 1 and 2, F_2 distributions were bimodal without discrete classes for the Starkville planting under short photoperiod conditions in 1993 (Figure 1). Average temperature during emergence to flowering period was 14.7 °C. In the absence of discrete classes, F_2 plants were arbitrarily divided into early and later flowering classes. The separations were made at the low point on the distribution curves (Figure 1). A summary of the division of F_2 plants into classes is presented in Table 4.

Chi-square analysis showed that segregation for early and late types fit a 3:1 ratio better than other models tested (Table 4). Heritability estimates computed from variance components were 86.0% and 87.9% for cross 1 and 2, respectively. Early generation selection for this trait should be successful, particularly if PI 159925 is the common donor parent. Hinson (1989), Tisselli (1981), Bidja (1988), and Hanson and Webber (1962) reported high heritability values for flowering time in soybeans.

Table 3. Means and standard errors of parents, F_1, F_2, F_4, BC_1 P_1P_3 S_1, BC_1 P_3P_1 S_1, BC_1 P_2P_3 S_1, and BC_1 P_3P_2 S_1 populations for days from emergence to flower under short photoperiod conditions, 1993.

Population	Days from emergence to flower
Kirby	35.5 ± 2.5
PI 159925	61.0 ± 1.0
Mid-parent	48.3 ± 1.0
Cross 1 F_1	43.3 ± 4.2
Cross 1 F_2	44.9 ± 6.7
Cross 1 F_4	46.8 ± 9.7
Cross 1 $BC_1P_1P_3S_1$	42.5 ± 2.9
Cross 1 $BC_1P_3P_1S_1$	54.4 ± 2.5
Perrin	35.0 ± 2.5
PI 159925	60.6 ± 1.0
Mid-parent	47.8 ± 1.0
Cross 2 F_1	43.0 ± 4.2
Cross 2 F_2	43.0 ± 4.2
Cross 2 F_4	44.9 ± 10.1
Cross 2 $BC_1P_2P_3S_1$	41.2 ± 5.1
Cross 2 BC_1 P_3P_2 S_1	51.0 ± 1.7

Figure 1. Distribution of days to flower for F_2 plants under short photoperiod conditions, 1993. Arrow shows arbitrary separations of classes.



The realized heritabilities (60.9 ± 7.6 and 73.1 ± 6.1 for crosses 1 and 2, respectively) were high enough to suggest that further gains from selection are possible. The percentages of expected gain were about the same in each cross. However, the percentage of observed gain was smaller (13.4%) for cross 1 than for cross 2 (19.5%).

The observed gain (realized response) was larger for cross 2 (9.9 days) than for cross 1 (7.15 days). The difference between expected and observed gain was larger for cross 1 than for cross 2. This was probably due to the fact that the mean number of days to flowering (53.7) for the F_3 population from cross 1 was larger than the mean for cross 2 (50.7). Additionally, data for F_4 populations were terminated at 61 days after emergence. Therefore, the assignment of a flowering date of 61 days after emergence was a minimal estimate of what the true flowering date would have been without a killing frost.

The results from the Chi-square analyses performed on F_2 and F_3 populations were consistent with a 3 early:1 late, suggesting that the LJ trait from PI 159925, grown in short photoperiods in 1992 and 1993, is controlled by s single recessive nuclear gene. The mean number of days to flowering for the F_1, F_2, reciprocal F_2, F_3, F_4, $BC_1P_1P_3S_1$, and $BC_1P_2P_3S_1$ populations fell between early parent and mid-parent values, most were closer to the early parent value in each cross. The relatively large percentage of plants or lines from segregating populations having the LJ trait, the high heritability estimates, and the high estimates of expected genetic gains suggest that the LJ trait is not controlled by a complex genetic system.

Table 4. Segregation of F_2 plants from two crosses for flowering response under short photoperiod

conditions, 1993.

Cross 1	Phenotypes		Total
	Early	Late	
Observed	45	22	67
Expected (3:1)	50	17	67
Chi-square (3:1) = 1.97 (0.10 < P < 0.25)			

Cross 2	Phenotypes		Total
	Early	Late	
Observed	57	20	77
Expected (3:1)	58	19	77
Chi-square (3:1) = 0.069 (0.75 < P < 0.90)			

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