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Field Crops Research 92 (2005) 53–59

Field Crops Research

www.elsevier.com/locate/fcr

Comparison of vegetative development in soybean cultivars for low-latitude environments

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Received 6 April 2004; received in revised form 23 August 2004; accepted 26 August 2004

Abstract

Soybean production has been expanded into northern Brazil by the introduction of long-juvenile genes. These genes cause flowering to be delayed but specific changes in the sensitivity of plant development to temperature and photoperiod have not been resolved in these commercial cultivars. This study was undertaken to resolve possible changes in long-juvenile plants associated with rates of plant emergence, leaf appearance, and flowering. Eight cultivars, including three long-juvenile cultivars, were sown each week throughout a year in a plastic greenhouse so that the plants would develop under differing temperature and photoperiod. While there were differences among cultivars in the cumulative temperature required for plant emergence and the rate of leaf appearance, these differences were not necessarily associated with the long-juvenile trait. An extended duration to flowering was confirmed for the three long-juvenile cultivars but this delay was not associated with any difference in sensitivity to temperature and photoperiod. The trait that distinguished the long-juvenile cultivars was a much lower maximum development rate towards flowering than that found in the other cultivars. However, cultivar differences were identified among the long-juvenile cultivars indicating the possibility of further selection of genotypes to fit specific environments in low-latitude regions.
Published by Elsevier B.V.

Keywords: Soybean; Flowering date; Emergence date; Phyllochron interval

1. Introduction

Soybean (*Glycine max* Merr.) production has rapidly expanded into low-latitude (<25°) regions, including areas near the equator. In the Cerrado of Brazil, for example, there is 204 million hectare (Mha) of land with 52 Mha already in agriculture and another 75 Mha available for agricultural development. Rapid expansion of soybean into these low-latitudes areas was made possible by the discovery and incorporation of long-juvenile genes that delayed flowering and maturity (Hartwig and Kiihl, 1979). Without the long-juvenile genes, soybean plants grown at low-latitudes flower very soon after emergence resulting in very short plants that are difficult to harvest mechanically and have low yields.

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0378-4290/$ – see front matter. Published by Elsevier B.V.
doi:10.1016/j.fcr.2004.08.008

While the qualitative consequences of incorporating the long-juvenile gene into soybean are obvious, there has been little quantitative assessment of the response of commercial long-juvenile cultivars to environmental variables. Sinclair et al. (1991) included in their analysis of flowering date of soybean the long-juvenile line PI 159225, which has been a genetic source for the long-juvenile trait. They found the response in this cultivar to temperature and photoperiod was similar to other cultivars. The critical difference in the long-juvenile genotypes was that its overall maximum development rate to flowering was much less than all other cultivars. Subsequently, Sinclair and Hinson (1992) reported an analysis of the differences in flowering of 15 isoline pairs developed using PI 159925 as a parent. While the overall maximum development rate was decreased in 14 of the 15 lines, their analysis also indicated that both the temperature and photoperiod coefficients were systematically changed in the long-juvenile isolines. Quantitative responses of vegetative development to environmental variables have not been reported for commercial long-juvenile cultivars.

The objective of this investigation was to quantify the vegetative development characteristics of long-juvenile cultivars, commercially grown in the Cerrados region of Brazil, and compare these with five cultivars that are grown in higher latitude regions of Brazil. Three developmental periods were examined for greenhouse plants grown year round: (1) the interval from sowing to emergence, (2) phyllochron interval, and (3) sowing to flowering.

2. Materials and methods

2.1. Experiment

2.1.1. Cultivars

Eight soybean cultivars were selected to reflect a range of maturity characteristics. Three cultivars were selected as having no long-juvenile traits; two being relatively early maturity (Bragg and IAS-5); and one late maturity (BR-15) under short daylength conditions. Two cultivars were selected because they were identified as having delayed flowering, Parana and OCEPAR 8, which is a selection from Parana. Two additional cultivars, OCEPAR 9 and Paranagoiana were natural mutations of Parana expressing the long-juvenile trait. A third cultivar expressing the long-juvenile trait was BR-27, which is a descendant of a cross between Bragg and a selection of a natural long-juvenile mutant of Hardee.

2.1.2. Experimental design

The experiment was carried out in a plastic greenhouse at Embrapa Soybean, Londrina-PR, Brazil (Lat 23°11′ S). The vegetative development of soybean was observed year round in 54 weekly sowings between 16 November 1990 and 22 November 1991. Consequently, the plants developed under a range of daylengths (10 h 34 min to 13 h 25 min) and temperature. Temperature was recorded in the greenhouse every 2 h using a thermohygrograph (Lambrecht, Gottingen, Germany). Extreme temperature varied through the year from a minimum of 17.5 °C in the winter to a maximum of 35.5 °C in the summer.

Each week, eight seeds were sown in each of three replicate pots for each cultivar. The pots contained 5.5 L of a mixture of 10% medium coarse sand, 25% organic compost, and 65% field soil (Latossolo Roxo distrofico). The soil was watered twice daily to ensure there was no stress from water-deficit. Within each weekly sowing, pots were arranged in a randomized complete block.

The interval in days from sowing to emergence was recorded. Emergence was defined as the day when the angle between the hypocotyl and the segment, to which the cotyledons were attached, was greater than 90°. Once the seedlings reached the V1 stage (Fehr and Caviness, 1977), each pot was thinned to only two plants.

The day at which the first open flower appeared at any node (R1 stage, Fehr and Caviness, 1977) on each plant was recorded. In addition, the number of nodes and the height of the plants were recorded at flowering. The average of the observations in each pot, i.e. two plants, was used as the datum for a replication.

2.2. Models for data analyses

2.2.1. Sowing to emergence

Temperature (T) is likely to be the main factor that determines the daily rate of development from sowing to emergence (ER, d^{-1}) since the plant material is buried in the soil for much of the time. Therefore, the

ER is defined as a function of temperature minus a base temperature (T_b).

$$\mathrm{ER} = e \times (T - T_b) \tag{1}$$

By definition, the sum of ER over the period from sowing to emergence is 1.0. Therefore, the value of the coefficient e can be calculated based on measured duration between sowing and emergence (d, days) and mean temperature (T_m) for this period. That is,

$$\sum \mathrm{ER} = 1.0 = de(T_m - T_b) \tag{2}$$

rearranging,

$$\frac{1}{d} = e(T_m - T_b). \tag{3}$$

An estimate for the value of T_b was obtained by doing a linear regression of $1/d$ against T_m by combining data from all cultivars. This regression resulted in a highly significant correlation ($r^2 = 0.33$) and the intercept defining T_b was equal to 7.0 °C. Linear regressions were performed for each cultivar of $1/d$ against T_m in which T_b was held constant at 7.0 °C to determine the value of e for each cultivar.

2.2.2. Phyllochron

The rate of phyllochron development (PR, d^{-1}) has been shown to be linearly dependent on temperature (Sinclair, 1984) resulting in an expression similar to Eq. (1).

$$\mathrm{PR} = p(T - T_b), \tag{4}$$

where p is the coefficient for phyllochron development rate (node C^{-1}). The base temperature for phyllochron was derived from observations of Thomas and Raper (1983) on the rate of leaf appearance over a range of temperatures. Combining all data from five photoperiod treatments in their experiment, a value of 11.2 °C was calculated for the base temperature for phyllochron development. A value of 11 °C for T_b was assumed in these analyses.

Since by definition the value of PR is equal to 1.0 for rate of production of each node, the total node number (N) is defined by the following equation:

$$N = \sum \mathrm{PR} = p \sum (T - T_b). \tag{5}$$

Therefore, the number of nodes observed at stage R1 was plotted against $\sum(T - T_b)$ for each cultivar to solve for p.

2.2.3. Sowing to flowering

Major et al. (1975) proposed a multiplicative function to describe for soybean the daily development rate to flowering (FR)

$$\mathrm{FR} = \mathrm{FR}_{\max} \times f(T) \times f(P), \tag{6}$$

where $f(T)$ and $f(P)$ are functions with values ranging from 0 to 1 based on daily temperature and photoperiod, respectively. The variable $\mathrm{FR}_{\max}$ defines the maximum rate of development to flowering. Eq. (6) has been used successfully to describe flowering in a number of soybean cultivars (Sinclair et al., 1991; Grimm et al., 1993).

Horie et al. (1986) used an exponential function in rice (*Oryza sativa* L.) to describe $f(T)$ and this function was also applied to soybean by Sinclair et al. (1991). However, Grimm et al. (1993) found that an exponential function was not needed for soybean and concluded that the following linear function for $f(T)$ described well the temperature response of all soybean cultivars.

$$f(T) = \frac{(T - 3.0)}{(25.8 - 3.0)} \quad \text{for } 3 < T < 25.8 \tag{7}$$

$$f(T) = 1.0 \quad \text{for } T > 25.8 \tag{8}$$

A preliminary test with the data collected on the cultivars used in this study showed that the above functions also described well the responses of the cultivars used in this study. Eqs. (7) and (8) were evaluated by calculating a daily mean T from the measures of greenhouse temperature recorded every 2 h. Any temperature that exceeded 25.8 °C was simply set equal to 25.8 °C. A mean temperature for the entire period from sowing to flowering was calculated based on daily mean values.

The sensitivity to daylength was described by Grimm et al. (1993), using an exponential function:

$$f(P) = 1 - \exp(c \times (P - P_c)) \quad \text{for } P < P_c, \tag{9}$$

where P is equal to daylength and P_c is the critical daylength above which no development towards flowering occurs. Daily photoperiod was calculated using the approach described by Goudriaan (1982). In this approach, the day of year and latitude is given as well as an assumed solar elevation of -6° to define the beginning and end of the day. The mean photoperiod for the experimental period from sowing to flowering was calculated from daily values.

Since by definition, the cumulative FR at flowering has a value of 1.0,

$$\mathrm{FR} = 1.0 = d \times \mathrm{FR}_{\max} \times f(T) \times f(P), \tag{10}$$

where d equals the observed duration from sowing to flowering. Rearranging Eq. (10),

$$\frac{1}{d(f(T))} = \mathrm{FR}_{\max} \times [1 - \exp(c \times (P - P_{\mathrm{c}}))]. \tag{11}$$

Hence, a nonlinear regression of the combined variable on the left-hand side of the Eq. (11) against P gave values for $\mathrm{FR}_{\max}$, c, and P_{c}.

2.2.4. Statistical analysis

Linear and non-linear regressions were done using Prism statistical analyses (version 3, GraphPad Software Inc., San Diego, CA). The Newman–Keuls test of Prism was used to do paired comparisons between cultivars.

3. Results

3.1. Sowing to emergence

Even though the resolution for emergence date was not good relative to the total length of time required from sowing to emergence (commonly < 7 d), highly significant correlations were found between the inverse of duration and temperature (Eq. (3)) for all cultivars. The inverse of the coefficient e defining the temperature sum for emergence ranged from 35.5 to 40.1 °C (Table 1). There was no apparent difference between the long-juvenile cultivars and the normal cultivars. While there were significant differences among cultivars in the emergence coefficient, the practical significance is limited. A difference among cultivars of less than 5 °C in the temperature sum required for emergence would likely translate into only a few hours unless the ambient temperature approached the base temperature.

3.2. Phyllochron

The description of the rate of phyllochron development (p) was well described by Eq. (5) as illustrated in Fig. 1. The regressions for each cultivar were highly significant and r^2 values ranged from 0.66 to 0.92 (Table 2).

Table 1
Regression results for Eq. (3) to evaluate the coefficient e describing plant emergence rate

Cultivars	e (cum. temp.)$^{-1}$	$1/e$ (cum. temp.)
Normal development		
Bragg	0.027	36.7 c
IAS-5	0.025	40.1 a
BR-15	0.028	35.5 d
Delayed flowering		
Parana	0.025	39.9 a
OCEPAR 8	0.026	38.7 b
Long-juvenile		
OCEPAR 9	0.026	38.5 b
BR-27	0.027	37.5 bc
Paranagoiana	0.027	37.5 bc

Values in column with differing letters are significantly different ($p < 0.05$).

There were significant differences among cultivars in phyllochron development rate (Table 2). Two cultivars with the extreme values of p are illustrated in Fig. 1 in which $1/p$ (phyllochron duration expressed as temperature sums) equaled 47.7 °C for BR-15 and 64.2 °C for BR-27. Consequently, the rate of node production for BR-27 was 35% slower than BR-15. Slower node production is likely to lead to fewer nodes, as shown in Fig. 1, and consequently the production of fewer leaves.

While the two cultivars with the slowest rate of phyllochron development were long-juvenile, the

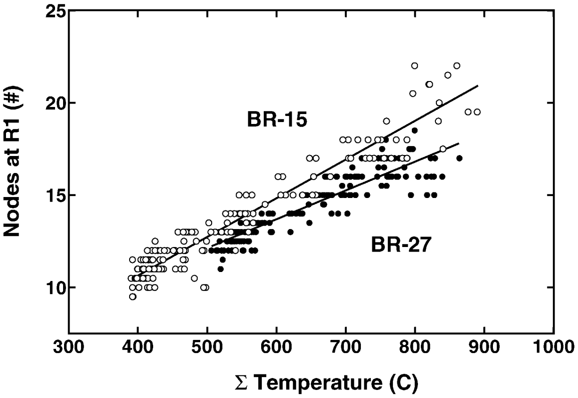

Fig. 1. Number of nodes at R1 stage plotted against the cumulative temperature (base temperature = 11 °C) for cultivars BR-15 and BR-27.

Table 2
Regression results for Eq. (5) to evaluate the coefficient p describing phyllochron interval

Cultivars	P (cum. temp.)$^{-1}$	$1/p$ (cum. temp.)	r^2
Normal development			
Bragg	0.019	53.0 bc	0.66
IAS-5	0.019	52.6 bc	0.77
BR-15	0.021	47.7 c	0.92
Delayed flowering			
Parana	0.019	52.2 bc	0.79
OCEPAR 8	0.020	50.3 bc	0.80
Long-juvenile			
OCEPAR 9	0.020	49.1 bc	0.78
BR-27	0.016	64.2 a	0.82
Paranagoiana	0.017	59.2 ab	0.69

Values in column with differing letters are significantly different ($p < 0.05$).

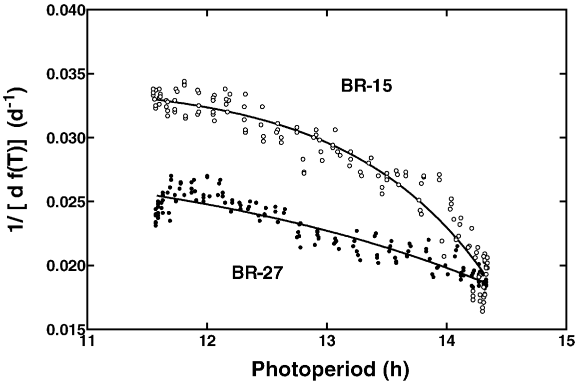

Fig. 2. Evaluation of Eq. (11) to define rate of development for cultivars BR-15 and BR-27 to flowering by plotting $1/[d \times f(T)]$ against mean photoperiod.

results do not indicate that slow phyllochron is a necessary consequence of the long-juvenile trait. There is substantial overlap among cultivars with several cultivars having $1/p$ equal to approximately 50 °C.

3.3. Sowing to flowering

The rate of development for flowering decreased as the daylength lengthened (Fig. 2), as expected for this short-day species. However, the sensitivity to the change in daylength was different among cultivars. As illustrated in Fig. 2, the rate of decrease in the development rate was greater as daylength increased. On the other hand, BR-27 appeared to have nearly a linear response to daylength over the range of daylengths experienced by the plants in this experiment.

Nevertheless, Eq. (11) effectively represented the development of all cultivars for the period from sowing to flowering (Eq. (11)) although there were significant differences among cultivars in the model coefficients. There was a large variation in the maximum rate of development (FR_{max}) with values ranging from 0.023 d^{-1} for Paranagoiana to 0.039 d^{-1} for Bragg (Table 3). The three long-juvenile cultivars had FR_{max} values that were less than those of the normal lines. The distinction among cultivars for the coefficient c, which indicates the curvature of the response, was not so clear. Two long-juvenile

Table 3
Observed mean number of days from sowing to flowering and results of non-linear regression (Eq. (11)) describing response to photoperiod $f(P)$

Cultivars	Sow to flower (days)	FR_{max} (d^{-1})	c	P_c (hours)	r^2
Normal development					
Bragg	31.3 e	0.039 e	1.21 c	15.8 b	0.75
IAS-5	35.1 d	0.036 d	1.11 bc	15.8 b	0.73
BR-15	42.7 d	0.034 d	0.88 abc	15.3 b	0.94
Delayed flower					
Parana	35.3 d	0.035 d	1.46 c	15.4 b	0.78
OCEPAR 8	37.2 d	0.035 d	0.85 abc	15.9 b	0.86
Long-juvenile					
OCEPAR 9	46.8 c	0.026 b	1.08 bc	16.0 b	0.65
BR-27	51.7 b	0.030 c	0.34 a	17.2 ab	0.88
Paranagoiana	54.6 a	0.023 a	0.49 ab	17.9 a	0.57

Values in column with differing letters are significantly different ($p < 0.05$).

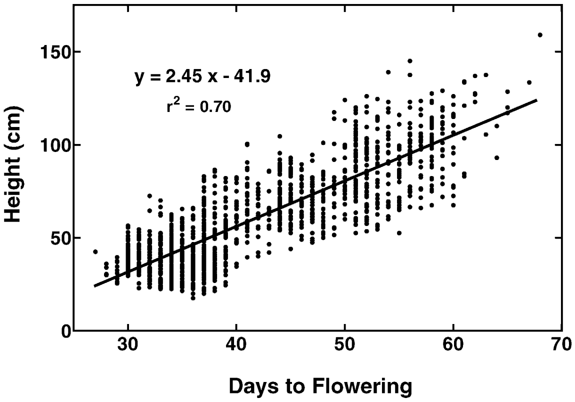

Fig. 3. Height of plant plotted against days to flowering for all cultivars combined.

cultivars, however, did have the smallest values of *c* reflecting less curvature in the response curve. Finally, the critical daylength above which the rate of development is equal to zero were not different among cultivars except for a large value for Paranagoiana.

3.4. Height

Not surprisingly, the time from sowing to flowering had a large influence on the final height of the plants. Delaying flowering allowed more nodes to be produced (Fig. 1) and hence the height of the plants was increased. A linear relationship was found across all cultivars between height and days to flowering (Fig. 3).

4. Discussion

The quantitative analysis presented here was undertaken to fully document the responses of several long-juvenile and delayed-flowering cultivars to variations in temperature and photoperiod in order to provide basic information to allow full exploitation of the long-juvenile trait in low-latitude regions.

Long-juvenile and delayed-flowering traits had no consistent influence on seedling emergence rate. All cultivars in this study emerged rapidly requiring only a temperature sum of about 36–40 °C (base temperature of 7 °C) to reach unbending of the hypocotyls (Table 1). Therefore, there appears to be no negative consequences of the long-juvenile trait causing delayed crop emergence.

The lengthening of the phyllochron interval in two of the long-juvenile cultivars (Paranagoiana and BR-27) as compared to the other cultivars has not been previously reported. The slow development of leaf area in these two cultivars would generally be considered a negative trait resulting in decreased interception of solar radiation. One possibility to compensate for the slow appearance of leaves in some long-juvenile cultivars is to sow the crop with a higher plant population. Of course, careful consideration needs to be given to any potential negative influence of the high plant population during the later stages of crop development.

Cultivar OCEPAR 9 appears to have an advantage over the other two long-juvenile cultivars, especially BR-27, in that it produces leaves at the same rate as the normal cultivars. A key selection criterion in the development of new long-juvenile cultivars may be a short phyllochron interval to identify genotypes producing leaves as rapidly as normal cultivars. An interesting challenge would be to sort out the inheritance of the difference in phyllochron intervals within long-juvenile cultivars.

Long-juvenile and delayed-flowering cultivars were developed specifically to prolong vegetative development. Surprisingly, the two delayed-flowering cultivars used in this study failed to exhibit flowering characteristics different from the cultivars identified as having normal development. Since delays in flowering are relative, it may be that these two cultivars had delayed flowering only relative to the genetic populations from which they were originally identified.

The three cultivars with the long-juvenile trait clearly had, as expected, a longer period between sowing and flowering than the other five cultivars tested (Table 3). The critical distinguishing feature in these three cultivars was a smaller value of FR_{max}, which indicates a maximum development rate that was inherently slower than the other cultivars. The decrease in FR_{max} associated with the long-juvenile traits is consistent with the conclusion of Sinclair and Hinson (1992) concerning the overall slowed development rate observed in the isoline pairs they tested.

The critical photoperiod (P_c) was greater for Paranagoiana and BR-27 than all other cultivars.

The results for these two cultivars match the general observation of Sinclair and Hinson (1992) that P_c was increased by the long-juvenile trait. These results lead to the rather curious conclusion that under daylengths slightly longer than P_c for the normal cultivars, the long-juvenile cultivars could continue to progress to flowering and ultimately flower while the normal lines would not flower, i.e. the phenotype for the long-juvenile trait under this unique condition would be earlier flowering.

The long-juvenile trait is critically important at low-latitudes where daylength is always near 12 h. A low value of FR_{max} reflects a slow development of plants in progressing from sowing to flowering. As a result, the season is greatly extended for these cultivars resulting in the development of tall, full-size plants that can be readily harvested mechanically. Also, the extended vegetative phase gives the crop more opportunity to fix carbon and accumulate nitrogen, both of which are required to increase yield potential.

An especially important outcome of this study may be the observation that FR_{max} varied significantly among the long-juvenile cultivars. Consequently, it may be possible to select among long-juvenile germplasm for differences in length of development to match specific growth conditions. For example, the length of plant development of cultivars might be tailored specifically to the length of the wet season, or to differences in altitude and associated differences in temperature. Areas of high altitude with cooler temperatures that occur in the Cerrado may require long-juvenile cultivars with larger FR_{max} values so as to complete crop development within a desired time frame. Low altitude areas limited to the same time frame would likely require cultivars with lower values of FR_{max}.

This study demonstrated that genetic variation exists within the long-juvenile germplasm for phyllochron interval and maximum development rate to flowering, which could allow long-juvenile cultivars to be developed for environmental differences within low-latitude regions. Studies to identify additional genetic variation for these two traits and to describe their inheritance are relevant research topics for full exploitation of the long-juvenile trait in low-latitude areas.

Acknowledgements

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