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Research Article

Inheritance of a long juvenile period under short-day conditions in soybean

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Abstract

The long juvenile period (LJP) characteristic of soybean (*Glycine max* L. Merrill) cultivars delays flowering under short-day conditions. This trait may be important in increasing the adaptation range of soybean to low latitudes and provides greater flexibility for sowing times within the same latitude. The inheritance of the long juvenile period was studied in the MG/BR22 (Garimpo) soybean cultivar to provide knowledge to support the development of cultivars adapted to short day conditions. Four cultivars ('Paraná', 'Bossier', 'Bragg', and 'Davis') were crossed among each other and with MG/BR 22 ('Garimpo'). The study was conducted under short-day conditions (early sowing) in a greenhouse and in the field, in Londrina, Paraná, (23°22' south latitude). The parents and the F_1, F_2, and F_3 populations were assessed daily for flowering. The genotype ratios of 15:1 ($p > 0.95$, χ^2 test) and 8:7:1 ($p = 0.193$) for the F_2 and F_3 generations, respectively, obtained for the Paraná x Bossier cross indicated a case of digenic interaction with a duplicate recessive epistatic effect for the LJP character. Segregation of the F_2 population from the MG/BR 22 (Garimpo) x Paraná cross resulted in the expected ratio of 3:1 ($p = 0.166$, indicating that the MG/BR 22 (Garimpo) and Paraná cultivars differed at a single locus. Similarly, in the MG/BR 22 (Garimpo) x Bossier cross, a 3:1 ($p = 0.065$) segregation indicated that these two cultivars differed at a single locus for number of days to flowering. The Davis cultivar had the same gene for LJP as the Paraná cultivar *(aa).* The F_2 segregation of the classic flowering Bragg with MG/BR 22 (Garimpo) cross resulted in a 15:1 ($p = 0.138$) ratio, indicating that these two cultivars differed at two loci for flowering. The genotypes assigned to the cultivars were *aaBB* for Paraná, *AAbb* for Bossier and *aabb* for MG/BR 22 (Garimpo). A single locus in recessive homozygosis does not produce LJP.

Key words: long juvenile period, soybean, *Glycine max*, delayed flowering, short-days.

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Introduction

Soybean, a short-day plant, originated in China between latitudes 30° and 45° north. Cultivation of this plant under short-day conditions, out of season, or at low latitudes, results in cultivars with a characteristic response to an altered photoperiod, namely, early flowering, low plant height, and low grain yield.

Until the end of the 1960s, commercial cultivation of soybean was limited by photoperiod barriers, which restricted this species to latitudes above 22°. In Brazil, soybean cultivation was restricted to the southern part of the country for a long time because of dependence on cultivars introduced from the United States. The photoperiod barrier was overcome at the end of the 1970s with the introduction of the long juvenile period (LJP) trait. Mechanized soybean cultivation could finally be conducted in regions with less than 15° latitude (Neumaier and James, 1993).

Soybean breeding programs for lower latitudes were the starting point for subsequent commercial soybean cultivation in the `fallow' season (dry season or winter). Currently, if temperatures are not too low and if there is adequate irrigation, soybean cultivation is possible in the savannah region of Brazil in the fallow season (Spehar *et al*. 1993). Brazil pioneered soybean cultivation at latitudes less than 20°. The contribution of the central western region and of the state of Bahia to the total cultivated area increased from 5.5% in the 1973/74 season to 39.0% in the 1992/93 season. The contribution of this region in the total production increased from 5.1% to 40.0% in 19 years (Roessing and Guedes, 1993).

A greater knowledge of the genetic mechanisms controlling LJP would assist in developing soybean genotypes with a wider range of sowing dates suitable for lower latitudes. Genetic control of flowering and maturity time in soybeans under short-day conditions is controlled by recessive alleles (Kiihl, 1976; Hartwig and Kiihl, 1979; Tisselli Jr, 1981; Toledo and Kiihl, 1982 ab; Carpentieri-Pípolo, 2000). We examined the inheritance of LJP conditioned by

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the complementary effects of gene recombination among cultivars with classic flowering in order to screen for genetic variability that would be useful for developing cultivars adapted to different regions of Brazil.

Material and Methods

Ten F_2 populations developed from crosses between conventional juvenile types (‘Paraná’, ‘Bossier’, ‘Davis’, and ‘Bragg’) and the LJP carrier MG/BR-22 (Garimpo) (Table I) were obtained. The crosses included the diallel crosses between the four conventional juvenile types and the crosses of each of the four conventional juvenile types and the LJP carrier MG/BR-22 (Garimpo) (Table II). The F_1, F_2, and F_3 generations, including some reciprocals, were evaluated. The study was conducted from December 1992 to March 1995, on the experimental station at the Embrapa - Soybean National Research Center, Londrina, in the state of Paraná (23°22’ south latitude), Brazil.

The genotypes were sown in a greenhouse at seven day intervals from November 1992 to March 1993 to allow hybridization (through concomitant flowering) and hand pollinated among cultivars with different cycles. The F_1 plants were grown in a greenhouse in the winter of 1993 to obtain seeds for the F_2 population. The plants received additional artificial incandescent and fluorescent light 6 h per day for 26 days after emergence. The seeds collected from the F_1 plants (F_2 seeds) were divided into three samples. One sample was assessed in the 93/94 season in a greenhouse (Experiment I), the second sample was assessed in the field in the 93/94 season (Experiment II), and the third sample was kept in a cold room and assessed in the 94/95 season (Experiment III).

The F_2 population of each cross in experiment I was sown in 15 vases with seven seeds each. Two pots with each parent and one vase with the F_1 population were sown for each treatment. The parents and their F_1 and F_2 generations were assessed daily for flowering. The flowering date was recorded when the first flower opened on the plant.

In Experiment II, the parents and F_2 populations were sown in the field on September 29, 1993, which is earlier than the normal sowing date, to provide short-day conditions. Four 5-m rows with 10 seeds/m were sown for each cross. Row spacing was 0.50-m. A single 5-m row was sown for each parent. Flowering was assessed daily on all the plants in the plot. The date of flowering was recorded for individual plants as the first day an open flower appeared on the plant.

The F_2 population was assessed in Experiment III to complement the F_2 segregation data obtained in the 93/94 season. The remnant seeds from the 92/93 season which had been kept in cold storage were used. Each cross was sown in 7.5-m rows with four replications and each parent was sown in a single 7.5-m row with four replications.

The F_3 population was sown in 2-m rows with 10 seeds/m spaced 0.5 apart; the seeds in each row came from a single F_2 plant. Each parent was sown in 2-m rows with 10 seeds/m. Flowering was assessed daily after the opening of the first flower. In all experiments, plants were classified as early flowering plants (conventional-juvenile) (CJ) or late flowering (LJP) by comparing the flowering date distribution of the respective early flowering plants and LJP parental lines. The dates were categorized and flowering categories established using the narrow flowering range of the parents. Long Juvenile Period (LJP) was considered when the genotypes showed more than 46 d to flowering. A chi-square test for the distribution of plant frequencies versus the days to flowering characteristic was used to check the genetic hypotheses of monogenic, digenic, and polygenic inheritance (Snedecor and Cochran, 1980).

Results and Discussion

The temperatures during Experiment I (greenhouse) varied from 16.5 °C to 34.3 °C and in Experiment II (field) from 14.3 °C to 27.1 °C. A significant shortening in the number of days to flowering was observed in the plants in Experiment I, compared to those of Experiments II and III (Tables I and II). The populations and cultivars in Experiments I and II were sown at the same time, but in Experiment I (greenhouse), the temperature, particularly at night, was relatively higher than in the field. The main cause of early flowering may thus be temperature. The influence of

Table I - Means, standard deviation (SD), and range of the number of days to flowering of the soybean parent cultivars in experiments under short-day conditions.

		Experiment I			Experiment II			Experiment III		
Genotypes	Loci*	Mean ± SD	CV%	Range	Mean ± SD	CV%	Range	Mean ± SD	CV%	Range
Paraná	*aa*	27.3 ± 1.5	0.05	25-29	36.3 ± 1.0	2.75	35-38	38.4 ± 2.4	6.25	36-42
Bossier	*bb*	33.1 ± 1.1	0.03	32-36	39.9 ± 2.1	5.26	35-43	43.9 ± 2.5	5.69	40-47
Bragg	-	24.8 ± 0.8	3.22	24-26	28.1 ± 0.7	2.49	27-29	30.5 ± 2.3	7.59	28-33
Davis	*aa*	29.1 ± 0.6	2.06	28-30	37.9 ± 0.8	2.11	36-39	40.6 ± 3.6	8.87	33-47
MG/BR-22 (Garimpo)	*aabb*	35.9 ± 1.5	4.18	34-38	51.4 ± 2.0	3.89	47-54	53.6 ± 2.2	4.10	51-56

*Loci segregation. CV% (Coeficient of Variation) = SD/Mean.

Table II - Means, standard deviation (SD), and range of number of days to flowering of F_1 and F_2 soybean populations in three experiments under short-day conditions.

			Experiment I			Experiment II			Experiment III		
Cross	Loci*	Generation	Mean ± SD	CV%	Range	Mean ± SD	CV%	Range	Mean ± SD	CV%	Range
1-Paraná x	AB	F_1	27.5 ± 1.1	4.0	26-29						
Bossier		F_2	28.6 ± 3.0	10.4	23-38	34.3 ± 5.5	16.0	27-47	40.3 ± 7.4	18.4	30-61
2- Paraná x	*A*	F_1	26.1 ± 0.8	3.0	25-27						
Bragg		F_2	26.1 ± 1.4	5.4	23-32	30.5 ± 2.7	8.8	27-38	35.8 ± 5.9	16.5	27-70
3- Paraná x	-	F_1	27.4 ± 0.5	1.8	27-28						
Davis		F_2	28.5 ± 1.2	4.2	26-31	36.7 ± 1.9	5.1	29-41	41.3 ± 4.2	10.2	34-63
4- Davis x	*A*	F_1	25.4 ± 0.7	2.7	24-26						
Bragg		F_2	25.9 ± 1.3	5.0	23-30	30.7 ± 3.2	10.4	27-40	33.8 ± 4.6	13.6	28-51
5- Bragg x	B	F_1	25.0 ± 0.4	1.6	24-26						
Bossier		F_2	27.2 ± 3.7	13.6	23-38	30.7 ± 5.3	17.2	27-43	36.5 ± 7.4	20.3	28-65
6- Davis x	*AB*	F_1	26.5 ± 0.5	1.8	26-27						
Bossier		F_2	28.8 ± 3.7	12.8	23-41	35.1 ± 5.9	16.8	27-48	40.8 ± 8.0	19.6	28-61
7- MG/BR22	*B*	F_1	27.4 ± 0.8	2.9	27-29						
x Paraná		F_2	28.8 ± 3.3	11.4	24-43	41.4 ± 5.6	13.5	34-59	48.3 ± 7.2	14.9	37-68
8- MG/BR-22	*A*	F_1	34.7 ± 1.0	2.8	33-36						
x Bossier		F_2	34.4 ± 1.8	5.2	30-40	42.4 ± 2.2	5.2	35-47	51.3 ± 7.5	14.6	30-68
9- MG/BR22	*AB*	F_1	26.2 ± 0.4	1.5	26-27						
x Bragg		F_2	27.6 ± 2.8	10.1	24-37	35.7 ± 6.0	16.8	27-48	40.1 ± 7.4	18.4	28-63
10-MG/BR22	*B*	F_1	29.6 ± 1.9	6.4	29-30						
x Davis		F_2	31.7 ± 3.4	10.7	27-42	39.3 ± 2.5	6.4	34-49	45.9 ± 6.7	14.6	34-63

*Loci segregation. CV% (Coeficient of Variation) = SD/Mean.

temperature on flowering in soybean has been reported by several authors. Higher night temperatures have a significant effect on the induction of flowering which occurs during the dark, and leads to earlier flowering (Easton, 1924; Parker and Bortwick, 1950; Major *et al*., 1975; Summerfield *et al*., 1975; Shibles *et al*., 1976; Oliveira, *et al*. 1999).

The flowering means, standard deviations, and ranges of F_1 and F_2 populations were analyzed in three experiments (Tables I and II). Transgressive segregation for early flowering was observed in the Paraná x Bossier cross. Dominance for early flowering was detected in the F_1 generation. In studies on soybean flowering under short-day conditions, Kiihl (1976) and Hartwig and Kiihl (1979) showed that the LJP characteristic is recessive. In our three experiments, the F_2 populations had a multimodal distribution, with a greater number of early plants. The proportions obtained fitted the theoretical 15:1 ratio (conventional flowering: LJP ratio) as confirmed by the chi-square test, with probability values of $p = 0.25$, $p = 0.99$, and $p = 0.975$ for Experiments I, II, and III, respectively (Table III). These results suggested the action of two genes with independent distribution in which normal flowering was determined by genotypes with at least one dominant allele and LJP occurred only when the genotype was double recessive homozygous for two loci. Thus, the LJP trait in this cross was conditioned by duplicate recessive epistasis (Ramalho *et al*., 1994).

F_3 family segregation was assessed to confirm these results. The observed phenotypic ratio of 41:31:6 fitted the expected genotypic ratio of 8:7:1 proposed for the two loci which determine LJP in the Paraná x Bossier cross (Table IV). These results indicated that LJP has a digenic inheritance, with the LJP trait in this population conditioned by two double recessive genes. The existence of a gene for LJP in the Paraná cultivar was reported by Kiihl and Garcia (1989) and Miranda *et al*. (1990). However, this gene alone is not sufficient to cause an appreciable delay in flowering under short-day conditions.

Bonato and Vello (1999) studied the time for flowering and maturity in the cultivars Paranagoiana and SS-1 cultivars. They indicated that early flowering and maturity are controlled by a single dominant gene and the natural mutations that originated the cultivars Paranagoiana and SS-1 cultivars occur at the same locus of the cultivar Paraná cultivar. Results quite similar to these were obtained by Gilioli (1979), in four crosses, under photoperiods of 13 h 21 min, and by Ray *et al*. (1995) in plantings with days with 13 h 10 min and 14 h 02 min of light where they concluded that the LJP characteristic in PI 159925 accesses was controlled by a pair of recessive alleles identified as *jj and* Vargas (1996) in crosses involving the cultivars Doko,

Table III - Observed and expected phenotypic ratios of number of days to flowering in the F_2 populations.

Cross	Experiment	n.	CJ[1]		LJ[2]		Ratio	Chi-Square (χ^2)	Probability
			Obs.	Exp.	Obs.	Exp.			
1- Paraná x Bossier	I	361	342	338.4	19	22.6	15:1	0.6	0.454
	II	182	171	170.6	11	11.4		0.0	0.950
	III	225	212	210.9	13	14.1		0.1	0.760
2- Paraná x Bragg	I	407	296	305.3	111	101.8		1.1	0.295
	II	226	173	169.5	53	56.5	3:1	0.3	0.603
	III	366	261	274.5	105	91.5		2.7	0.100
4-Davis x Bragg	I	366	268	274.5	98	91.5	3:1	0.6	0.454
	II	235	173	176.3	62	58.8		0.2	0.699
	III	272	198	204	74	68		0.8	0.388
5-Bragg x Bossier	I	343	267	257.3	76	85.8	3:1	1.5	0.225
	II	210	158	157.5	52	52.5		0.0	0.950
	III	421	318	315.8	103	105.3		0.1	0.760
6-Davis x Bossier	I	283	262	265.3	21	17.68	15:1	0.7	0.421
	II	178	168	166.8	10	11.12		0.1	0.668
	III	176	160	165	16	11		2.4	0.100
7-MG/BR-22 x Paraná	I	316	249	237	67	79	3:1	2.4	0.100
	II	172	121	129	51	43		2.0	0.166
	III	52	35	39	17	13		1.6	0.207
8-MG/BR-22 x Bossier	I	402	299	301.5	103	100.5	3:1	0.1	0.760
	II	184	127	138	57	46		3.5	0.065
	III	63	44	47.3	19	15.8		0.9	0.356
9-MG/BR-22 x Bragg	I	360	348	337.5	12	22.5	15:1	5.2	0.031
	II	165	152	154.6	13	10.3		2.3	0.138
	III	236	215	221.3	21	14.8		2.8	0.096
10-MG/BR-22 x Davis	I	305	236	228.8	69	76.3	3:1	0.9	0.356
	III	342	266	256.5	76	85.5		1.4	0.242

[1]CJ indicates conventional juvenile flowering type. [2]LJ indicates long-juvenile flowering type. Obs.-observed phenotypic ratio. Exp.- expected phenotypic ratio. n. - total number of individuals.

Table IV - Observed and expected phenotypic ratios of number of days to flowering in the F_3 populations.

Cross	n.	Homozygote		Segregation		LJ		Ratio	Chi-Square (χ^2)	Probability
		Obs.	Exp.	Obs.	Exp.	Obs.	Exp.			
1-Paraná x Bossier	78	31	29.3	41	43.9	6	4.9	8:7:1	3.3	0.193
2-Paraná x Bragg	45	12	11.3	25	22.5	8	11.3	1:2:1	1.3	0.531
4-Davis x Bragg	58	19	14.5	28	29	11	14.5	1:2:1	2.3	0.320
5-Bragg x Bossier	70	17	17.5	30	35	23	17.5	1:2:1	2.5	0.292
6-Davis x Bossier	78	32	29.3	39	43.9	7	4.90	8:7:1	2.87	0.237
7-MG/BR-22 x Paraná	88	16	22	48	44	24	22	1:2:1	2.2	0.336
8-MG/BR-22 x Bossier	91	21	22.8	47	45.5	23	22.8	1:2:1	0.2	0.911
9-MG/BR-22 x Bragg	51	21	19.1	27	28.7	3	3.2	8:7:1	1.8	0.408
10-MG/BR-22 x Davis	97	19	24.3	53	48.5	25	24.3	1:2:1	1.6	0.454

LJ - indicates long-juvenile flowering type. Obs.-observed phenotypic ratio. Exp.- expected phenotypic ratio. n. - total number of individuals.

BR-9 (Savana) and Davis cultivars, seeded at 23° 12' latitude south.

The Paraná cultivar has *aa* recessive alleles for LJP, but they do not have a pronounced effect under short-day conditions. Similarly, the Bossier cultivar has *bb* alleles. The segregation of their F_2 population resulted in the genotype ratio 9 *A-B-*, 3 *A-bb* and 3 *aaB-* with conventional flowering (early flowering under short-day conditions) and 1 *aabb* with late flowering (LJP). There were complementary gene effects or duplicate recessive epistatic effects for LJP under short-day conditions.

The early flowering: LJP ratios of Paraná x MG/BR-22 (Garimpo) in Experiments I, II and III (Table III) fitted the expected genetic ratio of 3:1 for segregation of a single dominant gene controlling the expression of the early flowering trait, or a pair of recessive alleles for LJP expression under short-day conditions. The chi-square tests yielded $p > 0.10$ for all the environments (Table III). This genetic hypothesis was confirmed in the assessment of the progenies from 88 F_2 plants taken randomly from the population (Table IV). The chi-square test value indicated fit to the expected genetic proportion of 1:2:1 and confirmed the single locus segregation of the cross flowering distribution. The MG/BR-22 (Garimpo), which originated from the Paraná x Bossier cross, has a pair of alleles *(aa)* in common with the Paraná cultivar so that the F_2 and F_3 generations segregate at a single locus *(bb*).

The F_2 population in the Bossier x MG/BR-22 (Garimpo) cross in Experiment III had a flowering mean intermediate to the parents, but close to the MG/BR-22 (Garimpo) parent (Tables I and II). In Experiment III, F_2 segregation ranged from the early parent (Bossier) to later than MG/BR-22 (Garimpo), indicating transgressive segregation for late flowering. Because of the similarity of flowering in the parents, it was not possible to separate the F_2 generation into distinct classes. However, early flowering dominance over LJP was observed. In Experiment II, a unimodal F_2 population distribution was observed (no defined classes), whereas for Experiment III, the groups were not well defined and there was a concentration of early plants. Segregation in Experiment III fitted the 3:1 ratio (conventional flowering:LJP) (Table III). Plant frequency classes were not clearly defined in Experiment II. The result of the MG/BR-22 (Garimpo) x Bossier cross indicated that the LJP characteristic was controlled by a single recessive gene fitting the 3:1 ratio (Table III). Although the F_2 population in Experiment II had a continuous distribution, there were indications that the expression of the LJP characteristic may have been hidden in some genetic combinations and even in certain photoperiods. As mentioned above, the results of the Paraná x Bossier (fitting the 15:1 ratio) and MG/BR-22 (Garimpo) x Paraná (fitting 3:1 ratio) crosses confirmed the existence of a locus with common alleles and another locus with different alleles in both parents. MG/BR-22 (Garimpo) has two pairs of recessive alleles *(aabb*) and Bossier has only one pair of recessive alleles, which confirmed the expected segregation of a single locus (Table III). The segregation observed in the F_2 generation was confirmed by analysis of segregation in the F_3 plants. Ninety-one plants were randomly selected to obtain 91 F_3 families that segregated close to a 1:2:1 ratio for a single locus controlling LJP in this cross (Table IV).

The F_2 population of the MG/BR-22 (Garimpo) x Davis cross had a bimodal distribution in the three experiments (Tables I and II). A larger number of conventional flowering plants was observed. It was not possible to categorize the data of Experiment II as the F_2 plant frequency distribution was approximately normal, with few individuals in the parental juvenile MG/BR-22 (Garimpo) range. In Experiment III, 266 plants were classified as early flowering and 76 as having LJP (Table III). These values fitted a 3:1 ratio. The chi-square values of the F_2 population (Table III) for Experiments I and III were 0.9 ($p = 0.356$), and 1.4 ($p = 0.242$), respectively, indicating that a single locus determined the differences between the parental flowering. Ninety-seven F_2 derived progenies were tested to confirm this hypothesis. The observed ratio fitted the expected genotype ratio of 1:2:1 for segregation of a pair of recessive genes controlling the expression of the LJP trait under short day conditions (Table IV). Tisseli (1981) studied the inheritance of soybean flowering under short-day conditions and found that the Davis cultivar had a gene for the juvenile period. Kiihl and Garcia (1989) suggested that the Davis cultivar had the same gene for LJP as the Paraná cultivar, probably inherited from Ogden, a parent common to both of these cultivars.

The F_2 population in the MG/BR-22 (Garimpo) x Bragg cross in the three environments showed no transgressive segregation and had a clear bimodal distribution with a greater concentration of early-flowering F_2 individuals (Tables I and II). The absence of transgressive, late-flowering plants in MG/BR-22 (Garimpo) may exist because Bragg did not contribute any genes affecting this trait. As already mentioned, the Bragg cultivar has conventional flowering when sown under short-day conditions. The segregation of the F_2 population fitted a 15:1 ratio (conventional flowering:LJP) in Experiment II and III (Table III). This phenotypic ratio indicated the presence of two pairs of recessive alleles controlling the LJP trait in this cross. Analysis of the results of the MG/BR-22 (Garimpo) x Bragg cross showed the segregation of two genes with independent distribution, with early flowering determined by genotypes which have at least one dominant allele; LJP occurred only when the genotype was homozygous for recessive alleles of the two loci. This suggested a case of duplicate dominant epistasis (Ramalho *et al*., 1994). The results from the F_2 populations were confirmed by the F_2 progeny test in which 51 F_3 families were assessed. The frequency distributions agreed with the expected genetic ratio of 9:6:1 for the segregation of two loci (Table IV). These results confirmed the genetic hypothesis that the LJP characteristic in the MG/BR-22 (Garimpo) cultivar is controlled by two pairs of recessive alleles (*aabb)*.

The Bragg x Paraná cross in the F_2 population fitted the expected genetic hypotesis of Mendelian monogenic segregation (3:1 ratio) (Tables II and III). The flowering distribution in the F_2 generation was intermediate to that of the parents in Experiment II. The segregation of the F_2 population in Experiment III was multimodal and transgressive. Dominance of early over late flowering was observed in the three experiments. In the F_1 generation there was also dominance of early flowering over late flowering. In Experiment III, the F_2 generation showed transgressive segregation for later flowering. The flowering category in

Experiments II and III fitted the 3:1 expected ratio for a single locus controlling flowering (Table III). Since for LJP to be expressed two recessive loci (*aabb)* must be present, no such gene differences were apparently present in the F_2 population of Paraná x Bragg. Transgressive segregation in the F_2 population in Experiment III may have resulted from modifying genes which possibly recombined with the *aa* gene from the Paraná cultivar and only acted when the photoperiod and temperature conditions were not critical or limiting to the manifestation of the transgressive late flowering trait. There was a good agreement in the observed 12:25:8 ratio with the expected genetic ratio of 1:2:1. Thus, the differences in the time to flowering between the two parents were attributable to the action of a single major gene (Table IV).

The Bragg cultivar is considered to behave classically for photoperiod, flowering early when cultivated under short-day conditions. The Paraná cultivar has a major gene in its genotype which, when combined with other genes, may manifest a LJP in early sowings (Kiihl and Garcia, 1989 and Miranda *et al.*, 1990).

The F_2 plants of the Bragg x Bossier cross of Experiments I and II followed a typically bimodal model with no transgressive segregation for late flowering (Bossier cultivar). In Experiment III, there was a multimodal distribution with visible transgressive segregation for late flowering. This trend may reflect the expression of the Bossier LJP gene, together with modifying genes that manifest themselves under certain photoperiod and temperature conditions in mid-October planting. The observed in Experiments I, II and III, fitted the Mendelian single locus hypothesis (Table III). Analysis of the F_3 segregation (Table IV) confirmed the segregation results obtained in the F_2 population. The frequency ratio fitted the expected ratio 1:2:1 ratio, showing that the two parents diverged in flowering at an allele of a single major locus. There was a certain coincidence in the parents flowering in all of the experiments for of the Paraná x Davis cross, as well as a normal frequency distribution for flowering (Tables I and II). This made categorizing the data difficult and it was not possible to identify a splitting point. The results indicate that the Paraná and Davis cultivars have a major gene in common for late flowering under short-day conditions. The F_2 segregation ranged observed in Experiment III may be the result of modifier genes. This hypothesis was confirmed when the data from crosses in which Davis and Paraná were combined with other genotypes and were compared and showed a fairly similar frequency distribution and segregation.

Toledo *et al* (1993, 1994) studied the genetic control of flowering in soybean genotypes under three photoperiods. Four soybean parents, including three with conventional type of response to photoperiod (BR85-29009, FT-2 and BR-13) and one long juvenile trait carrier (Oc-8), were crossed in all combinations, including reciprocals. Significant dominance, epistasis and genotype x enviromental effects were detected. Genes controlling classical and long juvenility combined freely. Intermediate responses between the typical classical and typical long juveniles were also observed in all cases. Such responses are only possible through the recombination of various genes of a single system.

The flowering frequency distributions of the F_2 plants of the crosses between Bossier x Davis, and Paraná x Bossier were very similar (Tables II and III) indicating that the genetic control of LJP may be conditioned by the recombination of pairs of recessive alleles (Table III). This hypothesis was confirmed by the F_2 progeny test (78 F_3 families). The ratio fitted the expected model for segregation of two loci (9:6:1) (Table IV). The results showed that the Davis cultivar had the same LJP gene in its genetic constitution as the Paraná cultivar (*aa),* but may differ in modifying genes. The inheritance of LJP, conditioned by two recessive genes, is a typical case of duplicate recessive epistasis.

The distribution of the F_2 plants was very similar to that of the corresponding generation in the Bragg x Paraná cross (Tables I and II). The relatively low chi-square values (Table III) confirmed the high probability of a pair of genes determining the flowering differences between the Bragg and Davis parents. This hypothesis was confirmed by the results of the progeny test of the F_2 population (Table IV). The ratio observed fitted the expected genetic model for single locus segregation (1:2:1).

Bragg is considered to respond classically to photoperiod, flowering early when planted under short-day conditions. Tisseli (1981) reported the presence of a major gene in the Davis cultivar, which, when recombined with other genes, may express the LJP characteristic. The results described above support the hypothesis that the Davis cultivar has the same major gene for LJP as the Paraná cultivar.

The F_1 populations from all the crosses studied had a mean time to flowering similar to the early parent, indicating that early flowering is dominant over late flowering. The LJP characteristic is conditioned by the effect of two recessive gene loci. Genotypes with a single pair of recessive alleles do not show the LJP characteristic in early sowings. The Paraná cultivar has one pair of recessive alleles, and its genotypic constitution is *aaBB.* The Davis cultivar has the same genetic constitution for the control of flowering as the Paraná cultivar. The Bossier cultivar contributes a pair of recessive alleles different from those of Paraná, and its genotypic constitution is *AAbb*. The LJP characteristic in MG/BR-22 (Garimpo) is controlled by the combination of two recessive genes, a case of a double recessive epistatic gene action. Its genotypic constitution is aabb. The Bragg cultivar did not have LJP genes and is represented as *AABB.* Maternal effects did not influence the genetic expression of flowering for these crosses. The small range of flowering in the greenhouse F_2 population indicated that this environment was not suitable for the expressing of genetic variability in the population. Early sowing in the field from the end of September to the middle of October was an effective strategy to allow selection of plants with LJP.

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