Photoperiodism and Genetic Control of the Long Juvenile Period in Soybean: A Review

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ABSTRACT

Soybean (*Glycine max* (L.) Merrill)is a short day plant that flowers when days are shorter than the maximum critical value, and this period is specific for each genotype. Soybean sensitivity to photoperiodism determines the limits of the sowing period for a latitude and hinders adaptation to wider ranges of latitude. The long juvenile period (LJP), which delays flowering under short day condictions, has been identified in soybean cultivars. The introduction of the LJP characteristic in soybean has made its cultivation possible in regions with latitudes lower than 15º. Knowledge of the controlling genetic mechanisms of this characteristic can help in the development of soybean genotypes for lower latitudes with greater adaptation to sowing periods within the same latitude. Some conclusions about the genetic LJP control in soybean were reached from the present review: a) plants with LJP have a lower development rate for flowering, resulting in the lengthening of the vegetative period; b) the LJP characteristic has a direct influence on plant photoreceptivity and flowering induction; c) the genetic control of flowering time in short days is determined by a different and independent genetic system from that which determines long day flowering time; d) late flowering under short day condictions is a quantitative characteristic controlled by recessive genes, and it is believed that one to five main genes control flowering. Genotypes with a single pair of recessive alleles did not have LJP.

KEY WORDS: Long juvenile period, Breeding for low latitudes, *Glycine max*.

INTRODUCTION

Many soybean development processes are related to daylight which has two important functions: soybean photosynthesis and photoperiodism. Photosynthesis is influenced by daylight intensity while photoperiodism is associated with daylight length. Photoperiodism deals with the effect of daylight on flowering induction. The photoperiod refers to the number of daylight hours per day. When not exposed to daylight for a determined number of days, flowering and fructification bearing are affected in many species.

Soybean plants flower when days are shorter than the maximum critical value, and this period is specific for each genotype. Consequently, soybean is a short day plant. Soybean sensitivity to photoperiod determines sowing period limits for a latitude and hinders adaptation to wider ranges of latitude.

According to Hymowitz (1970), the soybean originated and was domesticated in China, in regions between 30º and 45º North latitude. Commercial soybean cultivation was limited by photoperiod barriers until the end of the 1960s and it was restricted to regions with latitudes greater than 22º. The photoperiod barrier was broken only in the late 1970s, with the introduction of the long juvenile period trait, and mechanized soybean cultivation could finally be carried out in regions with less than 15º latitude (Neumaier and James, 1993).

Soybean breeding programs for low latitudes opened the way for commercial soybean cultivation in the fallow (dry period or winter). Nowadays it

is possible to cultivate soybean in the Savannah region where there are no frosts with irrigation in the fallow (Spehar et al. 1993).

The "cerrados" of Brazil are typical low-latitude tropical savannah areas in which agriculture is limited by low soil fertility, pH and high concentrations of aluminium. The introduction of soybean into these areas has depended on the selection of cultivars carrying strategic alleles which determine few key characteristics such as late maturity, high aluminium tolerance and calcium-use efficiency. Identification of the LJP and selection of genotypes in which this stage is prolonged are recognized as key components in the systematic exploitation of plant yield potential. New screening techniques have revealed that these savannah-adapted genotypes also carry alleles for high-Al and low-Ca tolerances, which allow deep rooting in plants and, consequently, drought tolerance. The combination of these favourable characters is essencial to the development of sustainable agriculture in the "cerrados" (Spehar, 1995).

Brazil is a pioneer in soybean cultivation in regions with latitude less than 20º. The participation of the Central-Western Region, including the state of Bahia, in the Brazilian cultivated area increased from 5.54% in the 1973/74 harvest to 39.00% in the 1992/93. The participation of this region in the Brazilian total production increased from 5.15% to 40.00% in these 19 years (Roessing and Guedes, 1993).
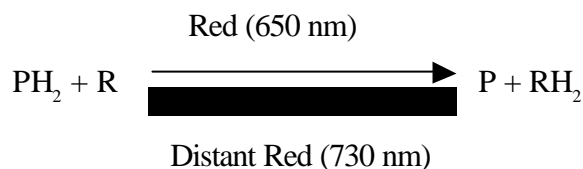
The long juvenile trait (LJP) is extremely convenient to use in breeding programs and has been used intensively in Brazil and in other countries. Greater knowledge of the controlling genetic mechanisms of this characteristic can help the development of soybean genotypes for low latitudes and for more flexible sowing periods.

This revision was carried out to help soybean breeding programs which deal with photoperiodism and genetic control of the long juvenile period.

SOYBEAN PHOTOPERIOD RESPONSES

The soybean is considered a Short Day Plant (SDP) of the quantitative photoperiod response type. However, there is a large variation in the photoperiod demands among existent cultivars. The dark period length is the factor that controls flowering induction. This stimulus originates in the leaf and moves rapidly towards the meristems via phloem (Hicks, 1978). Besides growth, the photoperiod affects maturity, plant height, seed weight, and number of pods, branches, nodes, etc...

The photoreaction involved in the photoperiodic induction can be outlined as follows (Vince-Prue, 1975 apud Gandolfi and Müller, 1981):

$$PH_2 + R \quad \xrightarrow{\text{Red (650 nm)}}_{\text{Distant Red (730 nm)}} \quad P + RH_2$$

The leaf pigment that absorbs radiation is of the phytochromatic type and it is indicated in the outline as PH_2. Under a red light, it reacts with another R component, a hydrogene receptor, changing into a P pigment. However, under distant red radiation, the opposite occurs with the equation. Therefore, at the end of a clear day, great part of the pigment is under the active P form. During the dark period (night period), this active form starts to revert to pigment PH_2 by a thermal reaction. As the two wavelengths are responsible for opposite responses, the quality of the light used on the plants is of extreme importance. Thus the use of fluorescent tubes, practically without the distant red component, normally asks for incandescent light complementation.

A short exposition to the distant red radiation at the end of the day increases stem and leaf stalk/petiole elongation. Working with the Ramsom cultivar, Thomas and Raper Jr (1985), observed that the elongation of the internodes and main stem was significantly greater when plants had been

exposed to incandescent lighting (high quantity of infra-red radiation) for 0,5 hrs at the end of the day than when they had been exposed to fluorescent lighting (high quantity of red radiation).

Critical day lenght or critical photoperiod is the duration of the lighting period under which the plant is induced to flower. Critical photoperiod determines plant change from vegetative to reproductive periods (flowering). Cultivar critical photoperiod decreases progressively from high to low latitudes (Fehr, 1987). The interaction between the photomorphogenic effects and those effects due to photosynthesis is a complex one. For instance, plants that flower early due to short photoperiods seldom develop normal height and foliage areas. Maturation can be delayed and grain production can be affected due to reduction in photosynthesis.

Based on their adaptation and maturation responses to the environment, cultivars have been classified in the USA into thirteen maturity groups (OOO to X). Cultivars from the same group have different development rates and can mature in different periods. The amplitude of the number of days for maturity within the same group but in different environments can reach up to three weeks. Early maturity cultivars belong to the OOO group which has longer critical photoperiods adapted to temperate regions. The X group comprises late maturity cultivars which are more sensitive to photoperiodism and better adapted to tropical regions (Fehr, 1987).

The latitude effect

Whenever a cultivar is sowed in the Northern Hemisphere, to the South of its adaptation area, it flowers and matures earlier due to the fact that the length of the critical night period for the flowering onset occurs earlier as well. Whenever sowed in the North, flowering and maturing are delayed; however, the opposite happens in the Southern Hemisphere. Thus the classification by maturation groups is not valid when region latitute is not mentioned.

In Figure 1, daylight length is represented with greater brightness than that of a candle-foot (10.7 lux) for 10°, 20° and 30° South latitude, and they are related to the months of the year (Berlato, 1981). Whenever sowed at 20°, a cultivar under a 14,0 hrs critical photoperiod will flower after December 22. However, if sown at 30°, flowering will occur in early February when the photoperiod reaches a critical value below that in which flowering induction can occur. If sowed at 10°, induction days occurs since the beginning of its cycle. The figure 2 is similar to Figure 1 since it shows Northern Hemisphere and Southern Hemisphere locations correspondence (Myasaka et al., 1981).

Whigham (1976) worked with 20 soybean cultivars sowed in twelve areas representing four latitude zones. The results of his experience are summarized in Table 1. These results led to the conclusion that the number of days to flowering and maturation increases as latitude increases while yield decreases.
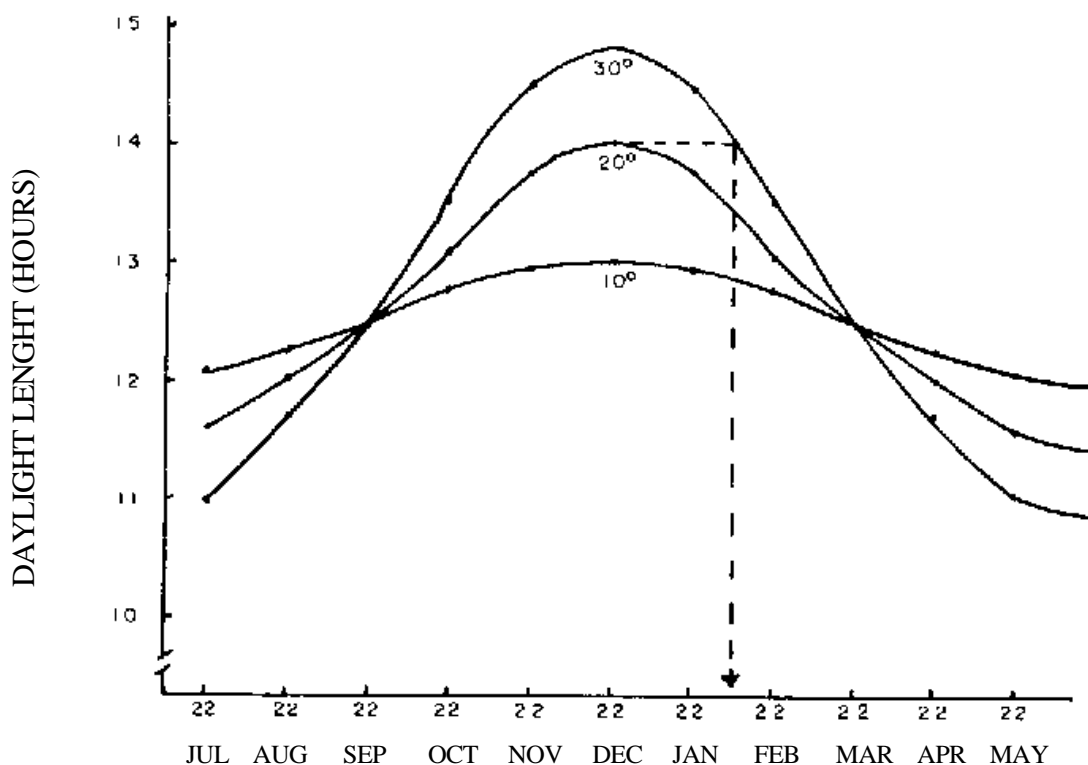
Figure 1 - Relationship between latitude and daylight length (light intensity > 10,7 lux) during the Southern Hemisphere soybean growth season (Berlato, 1981).
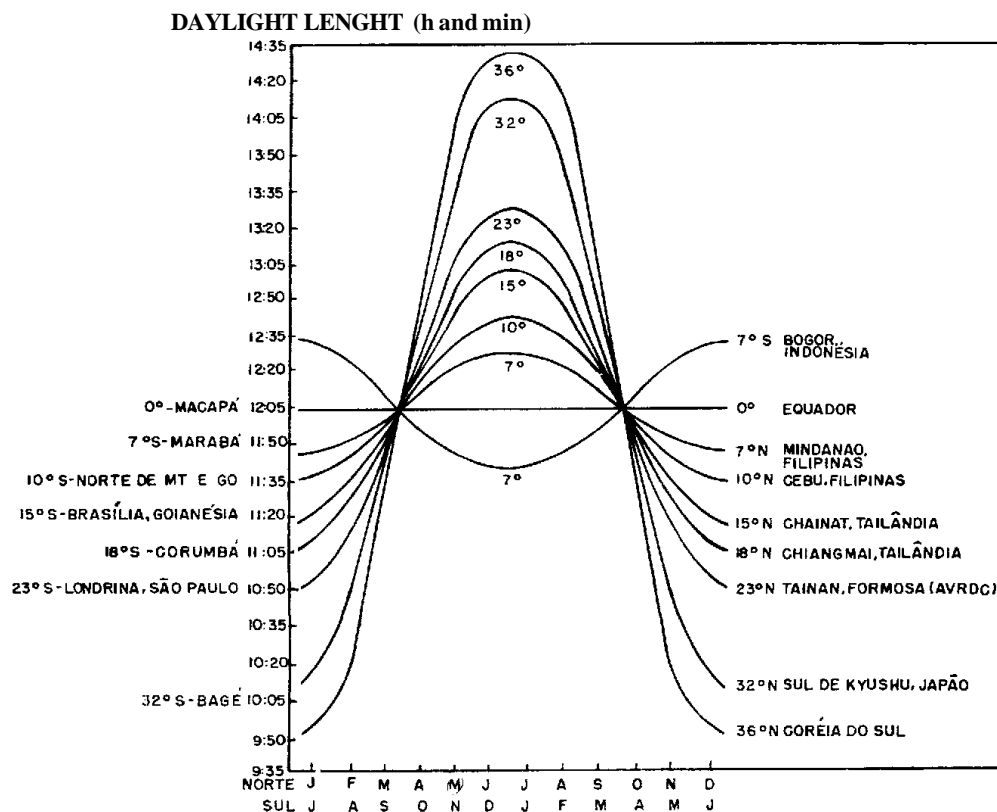

Figure 2 - Daylight length amplitude in different Asian locations in the Northern Hemisphere and locations with latitude correspondent to that found in Brazil (Miyasaka et al., 1981).

Table 1 - The behavior of six soybean cultivars in different latitudes with altitude lower or equal to 500 meters (based on Whigham, 1976).

Cultivar	Maturation Group	Latitude ≤ 10º59'			Latitude from 11º to 20º59'			Latitude from 21º to 30º59'		
		Days to Flowering	Days to Maturing	Yield (kg/ha)	Days to Flowering	Days to Maturing	Yield (kg/ha)	Days to Flowering	Days to Maturing	Yield (kg/ha)
Willians	III	29,1	86,8	1965	32,5	94,1	1726	32,6	97,2	1538
Hill	V	32,1	86,1	1646	38,2	98,0	1532	40,3	98,3	1310
Davis	VI	32,1	92,1	1950	38,0	103,3	1712	38,9	103,9	1329
Bragg	VII	30,7	89,7	1851	34,5	100,2	1511	35,5	101,6	1483
Hardee	VIII	33,1	93,4	2047	40,1	104,4	1928	37,5	95,9	1490
Jupiter	IX	37,3	102,9	1512	43,2	116,1	1552	–	–	1583
Average		32,4	91,8	1828	37,8	102,7	1660	37,0	99,4	1456

Photoperiodism variations within the same location increase as latitude increases (Table 2). Thus, the greatest photoperiodism amplitude to 10º latitude is of 1 h and 10m. However, it changes to 6 hs and 55 m at 45º latitude.

Table 2 - Relationships between Latitude and Effective Photoperiod by calendar date in several latitudes (modified from Whigham and Minor, 1978).

Degrees Latitude	Effective Photoperiod							
	20 Dec[1] / 20 Jun[2]		20 Sep[1] and [2] Or 20 Mar		20 Jun[1] / 20 Dec[2]		Maximum Difference	
	hr	min	hr	min	hr	min	hr	min
10	12	20	12	52	13	30	1	10
15	12	00	12	55	13	50	1	50
20	11	42	12	58	14	10	2	28
25	11	28	13	00	14	30	3	02
30	11	10	13	00	15	00	3	50
35	10	52	13	08	15	40	4	48
40	10	30	13	12	16	15	5	45
45	10	08	13	12	17	03	6	55

[1] Northern Hemisphere
[2] Southern Hemisphere

THE SOWING PERIOD EFFECT

There are seasonal variations in each particular location; therefore, plants are submitted to different sowing periods with different photoperiods. Consequently, the sowing period is the most important cultural factor in the production of soybean (Saccol, 1975). Among the many effects the sowing period has on soybean development, its effect on the cultivar total cycle is the most significant. In Rio Grande do Sul State, both long cycle cultivars and medium/early early cycle cultivars present, in general, maximun length cycles when sowed in the first half of October. From then on, a delay in sowing will reduce the total cycle due to the decrease in the length of the several development sub-periods, mainly between emergenge and flowering, sub-period responsible for the greatest cycle reduction .This reduction is more intense in late and medium cycle cultivars.

Plant height and the first pod insertion are also affected by the sowing period. They are reduced whenever sowing is anticipated or delayed. The effect is stronger on late cultivars. Long cycle cultivars sowed too early but under favorable conditions have intense growth; however, they are subject to shattering. Quality, size and seed composition are also affected. High temperatures and humidity during seed development affect quality and promote fungi growth. As for the maturation period, they affect seed quality sometimes causing pod germination. High temperatures under dry conditions may interrupt maturation producing small, greenish and wrinkled seeds. In general, sowing done prior or after the best sowing period results in production decrease in all cultivars. There is greater grain yield reduction in the early cultivars when sowed late (Saccol, 1975).

In the "cerrados", the Santa Rosa (semi-late) and Paraná (early) cultivars have behaved better when sown in the second half of October. Late October up to the first half of Nov is the best sowing period for IAC-2 when plant height is satisfactory for mechanical harvesting besides the reduction in yield (Table 3) (Spehar et al., 1981).

Table 3 - Grain yield, plant height and cycle of three cultivars sowed in different periods at CPAC-DF 1976/77. Approximate latitude: 16°S (Spehar et al., 1981).

Sowing Date	Grain Yield (kg/ha)			Height of the Plant (cm)			Cycle (days)		
	IAC-2	Santa Rosa	Parana	IAC-2	Santa Rosa	Parana	IAC-2	Santa Rosa	Parana
15 October	2727	3210	2146	82	50	35	131	122	107
29 October	1884	2700	3184	85	60	60	126	120	98
12 November	2365	2460	2512	65	55	55	118	113	109
26 November	1441	2011	1790	70	45	40	149	121	98
10 December	1149	1166	1051	65	50	37	149	141	94
24 December	1160	1151	646	25	25	30	126	133	115
07 January	641	989	546	20	20	20	114	119	92

Tomkins and Shipe (1997) conducted a field study using two LJP cultivars and four elite LJP Florida strains at Blackville and Pendleton, South Carolina, to examine the performance of LJP genotypes at different sowing dates. Sowing dates were early (late April), normal (late May), and late (late June) in 1993 and 1994. The LJP genotypes showed neither genotype x sowing dates nor genotype x location interactions for seed yield or seed quality, indicating consistency of genotype performance across environments. In general, LJP genotypes showed superior photoperiodic adaptation to different sowing date environments.

FACTORS INFLUENCING SOYBEAN RESPONSE TO PHOTOPERIOD

Several factors influence response to photoperiodism and they are discussed next.

Juvenile period
The period between emergence and flowering may be divided into at least three phases for the majority of species: 1) the pre-inductive phase when the plant is insensitive to the photoperiod, that is, its development is not affected by the photoperiod; 2) the inductive phase, when the plant is sensitive to the photoperiod, that is the development rate is influenced by the photoperiod; and 3) the post-inductive phase, where the plant is again insensitive to the photoperiod (Roberts and Summerfield, 1987; Wilkerson et al., 1989; Ellis et al., 1992). The pre-inductive phase is also known as youth or the juvenile period. As the juvenile phase is insensitive to the photoperiod, soybean genotypes with a long juvenile period characteristic have late flowering even under short photoperiod conditions and low latitudes.

According to Kiihl et al. (1983), in the initial studies on the long juvenile period under short day conditions carried out in Brazil , breeders, looking for materials with a long juvenile period, used alleles from the PI 240664 line, introduced from the Philippines. The program coordinated by Kiihl and collaborators was to develop cultivars for sowing in 15° of latitude with flowering from 45 to 55 days after emergence and maturity at 110 to 140 days .

Nogueira and Miranda (1989) studying the flowering behavior differences in the UFV-1, IAC-8, D77-11244 and Santa Maria soybean cultivars, which have a similar cycle, concluded that, with the exception of the UFV-1, they had a long juvenile period. The authors concluded that the cultivars had different flowering behavior and that winter sowing clearly defined their behavior.

Miranda et al. (1990), who were developing soybean cultivars with greater yield capacity and better adaptation to São Paulo State, carried out hybridization among genetic material with genes for long juvenile period, including Paraná, Davis, Hardee, Hill and Santa Rosa cultivars. As a result, the IAC-15 cultivar was released. This cultivar carried the LJP alleles from Paraná and Davis, and exceeded the other genotypes in plant height and yield.

It is necessary to determine precisely how many days there are in the vegetative growth phase before the inductive period is reached and flowering begins to identify cultivars with a long juvenile period (Collinson et al., 1993). Therefore, experiments were carried out using inductive and non-inductive photoperiods. Plants which germinated under one of the photoperiods were transferred to the other at regular intervals and vice-versa. Thus it was possible to determine the duration of the juvenile period, named the pre-inductive phase, and the inductive period, for four genotypes: UFV-1 (responsive to photoperiod and early), G2120 (responsive to photoperiod and late), Biloxi (early flowering under short days) and CPI 104521 (previously considered as a carrier of the long juvenile period). The results were 11.2, 32.7, 11.9 and 18.6 days for the juvenile period, respectively. Besides the longer juvenile period, G2120 and CPI 104521 also flowered later under the inductive photoperiod.

Among the recommended cultivars for low latitude regions (less than 12° South latitude), which includes the Northern and Northeastern Brazilian states, the Tropical, BR-11 (Carajás) and the BR-10 (Teresina) cultivars have been the most sowed.

The Tropical cultivar has a total cycle of 115 to 125 days in areas between zero and 15° of latitude. The yield is approximately 2,200 kg/ha, where there is good soil fertility and rainfall distribution (Kiihl et al., 1981).

The BR-10 (Teresina) and BR-11 (Carajás) cultivars are both F_6 offsprings from the cross UFV-1 x IAC73-2736-10, carried out in 1974. The breeding line IAC 73-2736-10 is a selection which corresponds to a natural mutation in Hardee cultivar, and has late flowering under short day conditions. The yield of the BR-10 (Teresina) cultivar is on average 19% greater than that of the'Tropical', and, under favorable environments, may yield more than 3,000 kg/ha. With a 130 days of total cycle, it was a new option for the Brazilian low latitudes, as it flowers ten days later than the 'Tropical'. The 'BR-11 (Carajás)' has about 140 days of total cycle and was a new option for Brazilian low latitudes, as it flowers ten days later than the 'BR-10 (Teresina)' and 20 days later than the 'Tropical' (Almeida et al., 1984; Bays et al., 1984).

Farias Neto (1987) studied soybean genotype behavior and variability in summer and winter sowing periods. The author concluded that the incorporation of alleles for long juvenile period in the cultivars became a promising strategy to neutralize sowing period and /or low latitudes effects on soybean genotype behavior.

According to Neumaier and James (1993), the photoperiod barrier was broken only at the end of the 1970's with the introduction of the long juvenile period characteristic. Afterwards, mechanized soybean could finally be sowed in the equatorial region. They presented examples of soybean cultivars released in tropical and subtropical regions and their respective adaptation latitude: FT-Cristalina (15°-20°); Tropical (less than 15°); Doko (15°-20°); Paranagoiana (less than 20°); BR-9 (Savana) (15°-20°); BR-10 (Teresina)(less than 15°); BR-11 (Carajás) (less than 15°); EMGOPA 303 (less than 20°); BR-15 (Mato Grosso) (15°-20°); BR-27 (Cariri) (less

than 15°); BR-28 (Seridó) (less than 15°) and EMBRAPA 9 (Bays) (less than 15°). These authors further report that when exposed to short days, soybean cultivars with a long juvenile period remain vegetating for a longer period than traditional cultivars, and may flower earlier than traditional cultivars under long days. Brazilian cultivar values for the juvenile period and number of days to flowering, respectively, are as follows: Paraná: 10.4 and 37.5; OCEPAR 8: 8.7 and 35.8; OCEPAR 9: 23.3 and 48.5; Paranagoiana: 25.1 and 58.0; IAS-5: 9.0 and 34.0; Bragg: 9.7 and 34.3; BR-27 (Cariri): 26.5 and 56.0; BR-15 (Mato Grosso): 12.5 and 37.0.

Although the long juvenile period has been widely used in Brazil after countries such as Australia and the USA, its physiological mechanism remains little understood. Sinclair and Hinson (1992) have suggested that the juvenile characteristic is given by a lower development rate to flowering. It is not clear whether the characteristic establishes a true juvenile phase or if it simplifies conditions, reducing the sensitivity to the photoperiod so that a longer photothermal period occurs before flowering is induced. It is not understood how temperature adjusts (models) the expression of this characteristic and how the genetic background influences these relationships. Such information could help clarify and make the use of the juvenile period more effective in soybean breeding (Neumaier and James, 1993).

Sinclair and Hinson (1992) studied the effect of the quantity of light, temperature and photoperiod length on isogenic lines with and without LJP derived from the PI 159925 genotype. They concluded that the lines with LJP have greater critical photoperiods than the normal ones. The lines with LPJ developed less under a 15 hour photoperiod. The LJP characteristic has a direct influence on photoreception and floral induction. These authors suggest that either the allele for LJP determines the reduction of photoreceptive activity or the production of an inhibitor which delays the quantity of photoreceptors.

Flowering time genetics and the juvenile period:
In studies under long day conditions, the days-to-flowering trait in soybean has been considered a quantitative inherited trait (Shanmugasundaram, 1978b). However, under short day conditions, the late flowering trait is controlled by a few recessive alleles, and may be transferred to a breeding program under short day conditions, using a moderate sized plant population (Kiihl, 1976; Shanmugasundram, 1978a).

Woodworth (1923) carried out the first studies on the effect of main genes on the control of days to flowering in soybean. The author found that the number of days to flowering was intimately linked to plant size. The F_2 generation segregated at each three tall plants with late flowering to one short plant with early flowering .

Owen (1927) found that maturity in the cross between the Black Eyebrow and J-5 cultivars was affected by a simple main gene. He was unable, however, to show clearly the proportion 3:1, but even so he named the gene E/e. Further studies followed discussing other aspects of the time-to-flowering inheritance and maturity in soybean. Veatch (1930) found that time to flowering was closely linked to time to maturity and further showed that late flowering was dominant over early flowering.

The participation of a few main genes in the manifestation of flowering was also shown by Singh and Anderson (1949). These researchers studied maturity inheritance in the F_2 and F_3 generations from six crosses whose parents varied from 85 to 140 days to maturity. They managed to recuperate the parental types in the F_2 generation with a relatively small population.

Transgressive segregation for flowering and maturity was also observed by Weber and Moorthy (1952). The results from three crosses led them to conclude that few genes were involved, and that transgressive segregation, in both directions, was caused by the effects of modifying genes.

However, Bernard and Weiss (1973) were the first to detail the effect of main genes on the control of flowering time in soybean. These authors studied the genotypes of individual plants from the F_2 generation from crosses among isogenic lines in the Clark cultivar, to which the alleles that control maturity had been transferred. The genotype of each F_2 plant was confirmed by the study of the F_3 and, in some cases, F_4 progenies. They concluded that there were two pairs of independent genes affecting time to flowering and time to maturity, the E_1/e_1 and the E_2/e_2. Both dominant alleles determine late flowering. According to Bernard and Weiss (1973), the gene with which Haque (1964) was working was the E_1/e_1, and the L 6-2132 A14 line was practically identical to the Clark cultivar, as it came from the same F_4 line. The E_1 allele, according them, is present in the majority of the cultivars from the Southern United States, while the e_1 is common in cultivars from the North.

Buzzell (1971) clarified the genetic effect on time to flowering and on sensitivity to light quality. The author identified the E_3/e_3 gene while working with the Blackawk x Harosoy 63 cross, which, besides giving either sensitivity or insensitivity to artificial fluorescent light, affects the days to flowering and to maturity in the field. The dominant E_3 allele is responsible for the sensitivity to light and for late maturity. The recessive e_3 allele gives insensitivity to the fluorescent light and determines early maturity under field conditions. This recessive allele is more frequent than its dominant allele in cultivars from the 00, 0 and I maturity groups, while the contrary was found in the cultivars from the II to VIII groups. This indicates that the e_3 allele performed an important role in the development of extremely early soybean cultivars.

Kilen and Hartwig (1971) found that the Lee and Hill cultivars are insensitive to light quality, while the Dorman and the Arksoy are classified as sensitive. They observed that the time to flowering segregation for the F_2 generation from the Dorman X Hill and Arksoy X Lee crosses were in the

proportion of three late and insensitive to light quality plants to one early and light sensitive plant, when developed under fluorescent light. Tests for allelism carried out by Buzzell and Bernard (1975) showed that the E_3/e_3 gene is the same as that referred by Kilen and Hartwig (1971) and different from the E_2/e_2 gene.

In Japan, Thseng and Hosokawa (1972) identified two pairs of genes, symbolized by AABB, which control flowering in the Sangowase and Harosoy cultivars. The genes had intra and inter allelic interactions for days to flowering and additive effects for days to maturity.

Chaudhary and Singh (1974) assessed seventeen F_1 families involving eight promising soybean cultivars to find natural heterosis. All the hybrids were earlier than the parents, with the exception of the Bragg X Pickett and Bragg X Hood crosses, which did not differ significantly from the parents. The authors concluded that, in general, hybrids were intermediary from the parents, but there was no manifestation of heterosis in the days-to-flowering trait.

Buzzell and Voldeng (1980) found the presence of a fourth gene, named E_4/e_4, related to flowering in soybean when studying segregants involving the PI 297550, a genotype insensitive to the photoperiod. According to them, the recessive e_4 allele is responsible for insensitivity to day length.

McBlain (1985) and McBlain and Bernard (1987) described a fifth gene which controls flowering soybean. The authors used 'Harosoy' isogenic lines. The dominant allele E_5, like all the other genes identified under long day conditions, was transferred from PI 80 837 to the Harosoy isogenic line which determines late flowering. The E_5/e_5 gene is different from the E_1/e_1, E_2/e_2, E_3/e_3, and E_4/e_4 according to allelism tests.

In previous studies, Kiihl (1976), Hartwig and Kiihl (1979), Tisseli Junior (1981) and Toledo and Kiihl (1982a; 1982b) found that time to flowering and maturity genetic control in soybean under short day conditions is different from that under long day conditions. These researchers found that late flowering is controlled by recessive genes under short day conditions. The number of genes involved varies according to the genotypes studied, and the presence of one to five main genes controlling flowering time in soybean was considered.

Toledo et al.(1993; 1994) estudied 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 (OCEPAR 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 classicals and typical long juvenile type were also observed in all cases. Such responses are only possible through the recombination of various genes of a single system.

Gilioli (1979) studied the total cycle of natural soybean mutants and their original genotypes in photoperiods of 10h:56m and 13h:21m hours. The natural mutants were: UFV-1 (from Viçoja cultivar); IAC74-2736-10 (from Hardee cultivar); PR77-10001(from OC73-2338 breeding line) and Paranagoiana (from Paraná cultivar). The author concluded that all the LJP genotypes studied originated from a single gene mutation in their respective original genotypes. The days to flowering trait in the mutants Paranagoiana, PR77-10001 and IAC74-2736-10 are controlled by the recessive ta_1 allele, and the mutations probably occurred in the same locus. However, for the UFV-1 mutant, the mutation must have occurred in another locus or the action of the mutant allele was intensely affected by the interaction with other genes.

Kiihl (1988), in a personal communication with Destro (1991), refered to the genetic control of the long juvenile trait in natural soybean mutants obtained in Brazil. The genotypes and their respective gene pairs are: Paranagoiana (1 recessive gene); SS-1 (1 recessive gene); BR-23

(2 recessive genes); Tropical (n); Doko (n, not all the genes are from Tropical); BR 83-147 (unknown).

Bonato (1989) studied a diallel involving the original cultivar Paraná and the natural variants Pirapó 78, SS-1 and Paranagoiana to determine days-to-flowering inheritance. The author concluded that the additive action was more important than the dominance for the days-to-flowering characteristic. The mutations which form the Paranagoiana and the SS-1 cultivars were recessive and occurred at the same locus in the Paraná cultivar. The author proposed the designation Es_1 for the allele in this locus in the Paraná cultivar, es^a_1 for the allele in the Paranagoiana mutant and es^b_1 for the allele in the SS-1 mutant. The Pirapó-78 mutant differed from the others with a second gene known as Es_2, and the es_2 allele was present in the mutant Pirapó 78. The genotypes for time to flowering and maturity in the four cultivars are: Paraná *($Es_1Es_1Es_2Es_2$)*; Paranagoiana *($es^a_1es^a_1Es_2Es_2$)*; SS-1 *($es^b_1es^b_1Es^2Es^2$)* and Pirapó 78 *($Es_1Es_1es_2es_2$)*.

Derbyshire et al. (1990) studied the natural variants Paranagoiana, SS-1 and Pirapó-78, which are considered mutants of the soybean cultivar Paraná. The electrophoretic profiles of the total protein, acid phosphatase, alcohol dehydrogenase, esterase, malic dehydrogenase, peroxidase and urease of seed extracts of the four cultivars were determined. These did distinguished the natural variants Paranagoiana and SS-1 from the original cultivar Paraná. However peroxidase, esterase and malic dehydrogenase profiles of the natural variant Pirapó-78 were different from the respective profiles of the original cultivar Paraná. The data are consistent with the origin of the natural variants Paranagoiana and SS-1 by mutation, but suggest a different origin for Pirapó-78.

Bonato and Vello (1999) studied inheritance in natural variants from the Paraná soybean cultivar, developed under photoperiodic conditions ranging from 13 h 31 min daylight at sowing to 14 h 23 min, 59 days afterwards. Results indicated that early flowering and maturity are controlled by a single dominant gene. Natural mutations that originated the natural variants Paranagoiana and SS-1 occurred at the same locus in the Paraná cultivar. It was not possible to determine if the recessive alleles of these mutant cultivars are different. The disignation E_6 was proposed for the allele determining earliness in the Paraná cultivar, and e_6 for the allele determining late flowering and maturity in the Paranagoiana and SS-1 cultivars , until the individuality of the Paranagoiana and SS-1 alleles is confirmed.

Hinson (1989) considered "long juvenile period" a suitable term to describe plants which had late flowering under short day conditions. Studying the inheritance of this characteristic to select genotypes adapted to latitudes lower than 27° the author observed that juveniles were controlled by a recessive gene in the segregant generation. All the crosses among cultivars with a long juvenile period and traditional types had a three early flowering plants to one late flowering plant segregation ratio. The presence of another two classes for days to flowering indicated that inheritance may be more complex, although the population studied was small. Such an observation suggests that these differences may be caused by two genes with additive effects.

Based on information that juvenile period inheritance is simple (few genes involved), and that there is the possibility of selecting genotypes with a long juvenile period under short day conditions, the following plan is used in the breeding program at the National Soybean Research Center of EMBRAPA (Londrina-PR): a) genotypes used in crosses are sowed in vases in a greenhouse, to coincide with the flowering period in November and December; the crosses are carried out in January and February and the seeds are harvested in March or April; b) the F_1 are cultivated during the winter in greenhouses with supplementary light, for 20-30 days, to avoid early flowering; c) the F_2 populations are sowed early in the field, in the first half of October. One pod per plant is collected from plants with a long juvenile period and samples

are prepared for the "Single Pod Descent" (SPD); d) the F_3 population in the SPD is carried out in the winter, and one pod per plant is harvested; e) the F_4 population is sowed early in the field, in October, and the best plants with long juvenile period are harvested individually; f) F_5 offspring are sowed early in October , and the best lines are selected (Kiihl and Garcia, 1989).

Despite some overlapping of the phenotypes, the genes which control the duration of the juvenile period seem to be distinct from those which determine response to photoperiod in soybean. The control of the long juvenile period in the PI 159925, by only one recessive gene, which does not involve the quantitative heredity of days to flowering, was reported by Hinson (1989) . The PI 159925, PI 240664, IAC73-2736, Paranagoiana and PR77-10.001 genotypes are mentioned by Kiihl and Garcia (1989) as juvenility carriers. In the same work, SS-1, Pirapó-78 and Ocepar-8 are mentioned once they differ from the Paraná cultivar by one gene only ,which is responsible for the juvenility and from the BR80-6889 breeding line and BR-23 cultivar which have long juvenile period determined by two pairs of recessive alleles, one from the Paraná and the other from the Bossier. The gene present in Paraná is the same found in Davis, whose juvenile period lasted 18 days, as mentioned by Collinson et al. (1993).

Moro et al. (1993) studied dominance and degree of parental genetic divergence in the days-to-flowering trait by using four F_2 generation soybean crosses carried out in Viçosa, Minas Gerais State. The days to flowering trait had early dominance. The greater diversity among the parents for this trait was found in the FT-Cometa X IAC-8 cross and the least, in the Paraná X IAC-12 cross. The genetic diversity was greatest in the FT-Cometa X IAC-12 cross.

Working with lines derived from crosses among BR85-29009, FT-2, BR-14 and OCEPAR-8 parents, Toledo et al. (1993) concluded that "there was an easily established differentiation among the

two types of response to day length, given by plants with long juvenility or with classic quantitative responses and which the genes controlling the flowering in soybean, probably, were not divided into two independent systems, but are part of a single system controlled by many loci".

Angelo et al. (1994) and Angelo (1995) studied the segregation 10 F_3 offspring generation plants from a cross between Paranagoiana cultivar, with juvenile period, and lines without lipoxygenases 2 and 3, from the FT-Cristalina. The segregant offspring was analyzed by the BSA method (Bulked Segregant Analysis) to identify RAPD (Randomly Amplified Polymorphic DNA) molecular markers which segregated with the long juvenile period. It was concluded that there was more than one gene influencing flowering date, although the pleiotropic effect of a main gene that controls days to flowering was detected. A polymorphic marker, apparently co-dominant, was identified for one of the offsprings.

Ray et al. (1995) presented results of studies carried out from 1984 to 1991 on the genetic control of the LJP characteristic. The investigations were carried out on F_2 segregant populations developed from crosses among lines with classic flowering and PI 159925 (LJP source). The authors further analyzed isogenic lines differing only for the LJP characteristic and segregant F_5 populations for the LJP characteristic. The results presented provide consistent evidence that the LJP characteristic is controlled by a single recessive gene. The Soybean Genetic Committee approved the symbol *J/j* for LJP (*J*- for classic flowering and *jj* for LJP). Comparisons between homozygotic and heterozygotic plants indicated that the *J* allele is completely dominant to the *j* allele. The delay in flowering caused by the *j* allele is influenced by the genetic background in which it occurs and also by the non-photoperiod environmental effects.

Aiming at selecting less sensitive soybean genotypes to photoperiodism to widen the sowing

period, Toledo et al. (1995) studied advanced lines derived from crosses involving cultivars with classic flowering (BR-13, FT-2 and BR85-29009) and cultivars with late flowering for short days (Ocepar-8) under different sowing times (September, October, November) in Londrina, PR, Brazil. It was possible to obtain lines with the most diverse responses to photosensitivity in the segregant generations, leading the authors to conclude that the genetic mechanism in the control of the days to flowering characteristic is quantitative and probably single for the three sowing periods.

Vargas (1996) studied LJP heredity in natural soybean variants selected from the Doko, BR-9, Davis, EMBRAPA-1 and BR-16 cultivars in Londrina-PR. Early flowering was dominant over late flowering. Doko 18-T and Doko Milionária are identical mutants and differ from Doko by a pair of recessive alleles which determines LJP. The São Carlos cultivar differs from the Davis 1 cultivar by one pair of recessive alleles. The E92-7 line differs from BR-16 by one pair of recessive alleles which controls the delay in flowering, and BR92-14638 differs from BR-16 by two pairs of recessive alleles which delay flowering by 25 days.

Pipolo (1996) studied the inheritance of the long juvenile period in the MG/BR-22 (Garimpo) cultivar and in the BR80-6778 line. Four classic flowering cultivars, Bragg, Paraná, Bossier and Davis were crossed among each other and with MG/BR-22 (Garimpo) and BR80-6778. Flowering was assessed daily in the F_1, F_2 and F_3 populations, under early sowing conditions (mid September and early-October). Early flowering was dominant over late flowering under short day conditions. The long juvenile period was conditioned by the effect of gene recombinations, doubly recessive in different loci and by the action of modifying genes. Genotypes with a single pair of recessive alleles did not show LJP under short day conditions. Genetic control of the studied characteristic is controlled by three pairs of genes. The LJP characteristic is controlled in the MG/BR-22 (Garimpo) cultivar by two pairs of recessive genes $j_2 j_2 j_3 J_4 J_4$. The BR 80-6778 line has a pair of alleles for long juvenile period in common with MG/BR-22(Garimpo) ($j_2 j_2$) and another pair of alleles, $j_4 j_4$, which delays flowering under short day conditions. The LJP inheritance for the BR80-6778 ($j_2 j_2 J_3 J_3 j_4 j_4$) soybean line was detailed by Carpentieri-Pípolo et al. (2000a) and for the MG/BR-22 (Garimpo) ($j_2 j_2 j_3 j_3 J_4 J_4$) was detailed by Carpentieri-Pípolo et al. (2000b).

SENSITIVITY TO PHOTOPERIOD

The use of insensitive cultivars to photoperiodism, within a large belt of adaptation and with no significant changes in behavior and cycle, simplifies the work of the breeder since it promotes better results in a great latitude belt. Neutral lines according to flowering days were mentioned by several authors (Criswell and Hume, 1972; Polson, 1972; Huxley et al., 1974; Gandolfi et al., 1977; Younes, 1982 ; Cregan and Hartwing, 1984). Data observed by Huxley et al. (1974), is found in Table 4. The ordering for cultivar flowering for the two photoperiods was the same; however, there was a progressive delay due to the duration of the longest day. The Fiskeby 5 cultivar presented the same number of days for flowering under the two photoperiods.

Table 4 - Number of days of the sowing to the emergence of the first soybean flower (four plant averages) (Huxley et al., 1974).

Cultivar	Length of the day		Delay in Flowering
	11h40min.	13h20min.	
Fiskeby 5	28	28	0
Hshi-Hshi	28	32	4
TK 5	30	38	8
Improved Pelican	32	52	20
CES 407	35	60	25

Cregam and Hartwig (1984) conducted flowering day regression on the duration of the photoperiod which varied from 11 to 20 hs in 10 soybean genotypes sown in 1980. Data indicated that the genotypes can be classified into three categories: genotype with no response, those with only linear responses and those with linear and quadratic responses. Fiskeby 5 cultivar was the only one among the genotypes that did not respond to photoperiodism, confirming the data obtained by Criswel and Hume (1972) and Huxley et al.(1974).

Not all genotypes neutral to the number of days for flowering in greenhouse condictions behave the same way in the field (Criswell and Hume, 1972; Gandolfi et al., 1977). Younes (1982) evaluated segregating crosses of genotypes adapted to short days and neutral lines for daylight length, and concluded that this response is under polygenic control and presents low inheritability.

TEMPERATURE

Studies on the interaction between photoperiodism and temperature showed that the outset of the first flowering was most affected by temperature variations during the dark period than during the light period, considering that the soybean never flowers under night temperature below 14°C (Parker and Borthwick, 1939 apud Gondolfi and Müller, 1981). Experiences involving leafless plants and cooling have indicated that flowering inhibition is the result of the influence of low temperatures on stimulus transportation (Borthwick et al., 1941 apud Gondolfi and Müller, 1981).

Garner and Allard (1930), apud Gondolfi and Müller (1981) studied four soybean cultivars for eight years and concluded that summer temperatures below 25°C delay flowering. A 1°C decrease in the average temperature delayed flowering for two to three days. Variations from one year to another regarding flowering of a determined soybean cultivar, sown at exactly the same day, are due mainly to temperature differences during development. However, differences among cultivars should be credited mainly to their responses to photoperiod.

Cultivars present great differences regarding their sensitivity to photoperiod, and the temperature affects the less sensitive ones significantly (Lawn and Byth,1973; Whigham and Minor, 1978). Therefore, early maturation cultivars respond better to temperature changes than to daylight length. This was confirmed by Major et al. (1975), only under low temperature conditions. These authors observed that daylight length was the dominant factor under high temperature conditions. Late maturation cultivars respond better to changes in daylight length than to temperature variations.

In temperate regions, cold temperatures and the length of the longest day add to flowering delay. Thus, short days are more important than cold temperatures in altering the number of days to maturation (Whigham and Minor, 1978).

Board and Hall (1984) studied the interaction between photoperid and temperature. They showed that, when compared to the cold temperature (21°C), the highest temperature (27°C) shortened the flowering period and had greater effect on short days rather than long days. The influence of temperature on flowering in soybean has been reported by others authors. Higher night temperatures have 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).

Flowering delay due to low temperatures promote the cultivation of segregating material in regions where winter frosts do not occur. This situation is favorable especially when working with soybean breeding methods that demand few seeds as in the pod per plant (SPD) method, for instance. This can be very useful to soybean breeders in these regions.

NUTRITION

The N is an important nutrient in the beginning of the sexual reproduction phase and, although not determinant in the induction to flowering as photoperiod and temperature are, its availability can affect the neccessary period for the onset of the first flower buds. Scully et al. (1945) apud Gandolfi and Müller (1981), concluded that there is a relationship between photoperiod and nitrogen nutrition with flowering induction. These authors observed that changes in photoperiod showed differences in cultivar responses to nitrogen nutrition variation. Patterson and Raper Jr. (1985), observed that seeds developed under short day conditions contain more N concentration than those developed under long day conditions.

Raper and Kramer (1987), mention several authors when discussing that photoperiod has greater effect on the N accumulation rate than on the C seeds, and that the N concentration rate decreases with the increase of the photoperiod which is associated with the retention of greater N concentrations in the leaves. There is also a reduction in the senescence and the amount of leaf fall during maturation. The concentration of carbohydrates in the leaves during the reproductive period is greater during short photoperiods, which is apparently regulated by the SPS enzyme activity.

SOIL HUMIDITY

Water is one of the most important factors in plant development. According to Gandolfi and Müller (1981), the occurrence of hydric deficiency during flowering and maturation accelerates plant development. Before flowering, the development is delayed. Under excessive humidity before being harvested, especially under temperatures higher than 15°C, plants continue their vegetative phase without husking; seeds do not mature and diseases appear.

THE INFLUENCE OF PHOTOPERIOD ON THE SOYBEAN SUB-PERIOD DEVELOPMENT

Johnson et al. (1969) worked with six soybean cultivars and observed that the duration of the post flowering sub-periods is greater in plants submitted to long day treatments (LD). Lawn and Byth (1973) sowed 18 soybean cultivars in Australia (Lat. 27°37'S) and concluded that there is a high correlation coefficient between photoperiod and pre-flowering sub-period duration; the late cultivars were more sensitive and two early cultivars were unaffected by photoperiod. The flowering sub-period (beginning and end of flowering) showed a high correlation coefficient in all cultivars, the late ones being sensitive. The post-flowering phase was delayed until the occurrence of shorter days and it was influenced by both photoperiod and temperature.

Thomas and Raper (1984) worked with Ransom cultivar in the greenhouse, changing the photoperiod length (10 to 16 horas) after the V_1 and V_6 stages. They concluded that the duration of the pre-flowering period changed with the different photoperiods. However, the subsequent early flowering differentiation was faster in shorter days.

Guiamét and Nakayama (1984a) worked with the Williams cultivar in the greenhouse where they exposed plants to the long day treatment after flowering and kept other plants under the short day treatment. By using plants with two branches, they exposed one to the short day treatment and the other to the long day treatment. They concluded that long days expanded the grain-filling period, increased the number of pods and seeds and consequently grain yield, but maturation and senescence were delayed.

Guiamét and Nakayama (1984b) worked with the McCall, A-100, Williams, Forrest, Ransom and Alamo cultivars from the 00, I, III, V, VIII e IX maturity groups, respectively. The plants were exposed to the sun until flowering and later, some plants, submitted to an additional three hours of light during the dark period (LD). They concluded that long days increased the vegetative period (larger production of green mass), except for the A-100. There was also an increase in the reproductive period in all cultivars, greatly affecting the late ones. The number of pods and seeds increased in the 'MacCall', 'Williams', 'Forrest' and 'Ransom' cultivars; however, there was a reduction in seed size, except for McCall.

Gbikpi and Crookstom (1981) observed that the reduction of photoperiod during the grain filling phase increases filling rate. They also concluded that late development seeds found in the superior part of the plant showed higher protein and dry matter accumulation rates.

Fehr and Caviness (1977) described soybean development stages and mentioned the variation amplitude in number of days for each development stage. The variation amplitude of the same stage depends on temperature, daylight length, cultivar and other factors.

CONCLUSIONS

1) The physiological mechanism of the long juvenile period (LJP) is little understood. Plants with LJP have a lower rate of development for flowering which results in the lengthening of the juvenile phase.

2) The LJP characteristic has a direct influence on the photoreception of the plant and on floral induction. The alleles for LJP determine a decrease in the photoreceptive activity or the alleles for LJP determine the production of an inhibitor which retards the quantity of photoreceptors in the plant.

3) Genetic control of flowering time under short days is determined by a different and independent genetic system from that one which determines flowering under long days. Late flowering is controlled under short day conditions by recessive alleles, while late flowering is dominant over early flowering, in long days conditions.

4) Late flowering under short day conditions is determined by a single system controlled by many loci, therefore is a quantitative characteristic. The number of genes involved varies according to the genotype, taking into account the presence of one to five main genes controlling flowering. Genotypes with a single pair of recessive alleles do not show LJP.

RESUMO

Fotoperiodismo e Controle Genético do Período Juvenil Longo em Soja

A soja (Glycine Max (L.) Merrill) é uma planta de dias curtos e é induzida ao florescimento quando os dias são menores que um valor crítico máximo, sendo que esse período crítico é específico para cada genótipo. A sensibilidade da soja ao fotoperíodo determina os limites para a época de semeadura numa mesma latitude, como também

dificulta sua adaptação a faixas mais amplas de latitude. A característica período juvenil longo (PJL), que retarda o florescimento, tem sido identificada em cultivares de soja. Com a introdução de PJL, a soja pode ser explorada em regiões de latitude abaixo de 15º. O conhecimento mais amplo dos mecanismos genéticos controladores dessa característica auxiliaria o desenvolvimento de genótipos de soja para baixas latitudes e com maior adaptação quanto à época de semeadura numa mesma latitude. Através deste estudo de revisão pode-se estabelecer as seguintes conclusões para o controle genético do PJL em soja: a) plantas com PJL apresentam uma menor taxa de desenvolvimento em direção ao florescimento, resultando no alongamento do período vegetativo; b) a característica PJL tem uma influência direta sobre a fotorrecepção da planta e sobre a indução floral; c) o controle genético do tempo para o florescimento em dias curtos é determinado por um sistema genético diferente e independente daquele que determina o florescimento em dias longos; d) o florescimento tardio sob condições de dias curtos é uma característica quantitativa controlada por genes recessivos, sendo considerado a presença de um a cinco genes principais controlando o florescimento. Genótipos com um único par de alelos recessivos não manifestam PJL.

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