

Characterization of Delayed Flowering in Soybean in Virginia

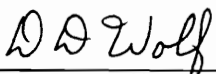
by

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(ABSTRACT)

Delayed flowering has the potential to overcome the problem of restricted vegetative growth, prior to flowering, that is often associated with double-cropped soybeans [*Glycine max* (L.) Merr.]. Objectives were to study delayed flowering in soybeans as influenced by date of planting, to estimate the lengths of the component vegetative periods in soybeans under short-day conditions, and to study the mode of inheritance of delayed flowering in soybeans. Date of planting experiments conducted in the field at two Virginia locations using 27 cultivars and breeding lines showed that genotypic differences exist for delayed flowering, especially between delayed and normal flowering isolines. Lengths of the juvenile and inductive periods were estimated for some selected early and late flowering genotypes. F85-8417 had a longer juvenile period, and F85-1226 had both longer juvenile and inductive periods than their respective early flowering isolines and cultivar Essex. The method of moving plants from inductive short-days to long-days, which has been used to estimate the length of inductive period, was adapted to estimate the length of the juvenile period as well. Delayed flowering in soybeans appeared to be controlled by two loci, each with two alleles, and delayed flowering appeared to be recessive. Any one of the genes in the homozygous recessive state delayed flowering. F85-1226 may be segregating for both genes while F85-8417 appeared to contain only one.

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# **CHAPTER I**

## **INTRODUCTION AND LITERATURE REVIEW**

## INTRODUCTION

Soybean [*Glycine max* (L.) Merr.] cultivation in Virginia was established during the early part of this century and most of the crop at that time was planted for use as hay or green manure. Presently soybean is mostly planted for bean production. Apart from full-season planting, double-cropping of soybeans after small grains has become a common practice in recent years accounting for one-third to one-half of the total crop.

Photoperiod and temperature are the main environmental factors that affect time of flowering in soybeans. In Virginia, soybeans must be planted early in the season, no later than June 15, for maximum productivity. When soybeans are planted after wheat harvest (late June through early July) in Virginia, the shortening days and warm temperatures often promote flowering before the attainment of adequate vegetative growth for maximum productivity. Thus, premature flowering is a major factor in low soybean yields when planted late in the season.

Three different approaches have been suggested to overcome the problem of low yields following suboptimal planting dates;

1. Utilization of higher plant populations and narrower row spacing compared to full season planting (Lawn and Byth, 1974),
2. Utilization of day-neutral or photoperiod insensitive cultivars (Criswell and Hume, 1972; Polson, 1972; Nissly, et al., 1981),
3. Utilization of photoperiod sensitive cultivars with a long vegetative period under short days (Board and Hall, 1985; Kiihl and Garcia, 1989).

The utilization of high plant populations and narrow row spacing seems to be the immediate and the simplest solution to compensate for the reduced plant growth. However, some cultivars are better adapted for high plant populations than others. Cultivar X row spacing, row spacing X planting date, and cultivar X row spacing X planting date interactions have been shown to exist (Boquest, et al., 1982). Cooper (1977) has suggested that short stature cultivars have the best potential for producing high yields under the high plant populations which often produce severe

lodging in taller cultivars. Maximization of seed yield will necessitate an optimum compromise between the degree of vegetative development and biological efficiency of seed production (Lawn and Byth, 1974). Thus, there is a limit to how much yield can be increased by increasing population density.

Although day-neutral cultivars have been identified, the available genotypes mature too early to produce economic yields at lower latitudes (Kiihl and Garcia, 1989) and are not adapted to Virginia. Some genotypes with a long vegetative period have been identified (Miyasaka et al., 1970; Hartwig and Kiihl, 1979). The long vegetative period is caused by a long juvenile trait which delays the onset of sensitivity to short photoperiods which induce flowering. 'Crockett', a cultivar expressing this trait, has been released for use in early planting in southern U.S.A. This trait might also hold promise for solving the problem of soybean yield losses caused by premature flowering when planted late in the season in Virginia. However, in this context, it is important that such cultivars mature before the average frost date in fall. Hopefully, by cross breeding, populations may be developed from which genotypes with a longer vegetative period independent of maturity date may be selected.

The overall objective of this research was to study modifications to photoperiod response that might improve yields of late planted soybeans. The specific objectives were to:

1. Study the delayed flowering trait in soybeans as influenced by date of planting in Virginia,
2. Estimate the lengths of component phases of the period from seedling emergence to first flowering of some selected lines utilizing controlled photoperiod studies, and
3. Study the mode of inheritance of the delayed flowering trait in soybeans under short-day conditions.

## REVIEW OF LITERATURE

### *Environmental Regulation of Flowering in Soybean*

The two main environmental factors that influence time of flowering in soybean are photoperiod and temperature (Huxley and Summerfield, 1974). Genotypic response to these environmental factors influences adaptation to specific latitudes and seasons.

#### **Response to Photoperiod**

Garner and Allard (1920) first reported the influence of photoperiod on soybean reproductive development. They recognized soybeans as a short day plant which requires days shorter than a certain critical daylength for normal floral development. Borthwick and Parker (1938a, 1938b, and 1939) found that the dark period was the critical portion of the 24 hour cycle to which the plant is responsive. Interruption of the dark period briefly near the middle by a small amount of radiation prevented floral initiation whereas interruption of the light period with short periods of darkness has no effect on floral initiation. In 'Biloxi' soybean, at least two short photoperiod cycles were required for floral induction (Garner and Allard, 1923; Borthwick and Parker, 1938b). Short days before and after first flowering are required for maximal flower production during the flowering period (Board and Settimi, 1988). Flowering is greatly delayed if the plant is returned to a long photoperiod after a few inductive short days (Borthwick and Parker, 1938b). Even under continuous daylengths longer than the critical photoperiod, soybean can still flower, but flowering is greatly delayed (Guthrie, 1972). Thus, soybean is usually considered a quantitative short day plant. However, though infrequent, there are soybean genotypes that respond to photoperiod qualitatively (Summerfield and Roberts, 1985). These qualitative types do not flower until they are exposed to photoperiods shorter than the critical daylength whereas quantitative types only delay flowering when exposed to photoperiods longer than the critical daylength (Summerfield and Roberts, 1985).

Photoperiod-sensitive plants must discriminate between day and night or measure the duration of one or both (Salisbury, 1963). The critical light intensities that control photoperiodic reactions in plants are considerably lower than levels occurring during the hours of sunlight (Francis, 1970). A "threshold illuminance" between 5 and 11 lux is needed to delay flowering in the cultivar Biloxi (Borthwick and Parker, 1938b). Modern cultivars respond to illuminance over the range of 2 to 100 lux in a quantitative manner (Major and Johnson, 1974; Takimota and Ikeda, 1961). The morning and evening twilight periods are important in determining the effective daylength for photoperiodic response in plants. Thus, Wang et al. (1987) calculated soybean responsive photoperiods as the time that the sun was higher than four degrees of arc below the horizon.

The trifoliolate leaves of soybeans are the organs that respond to photoperiod (Garner and Allard, 1925; Borthwick and Parker, 1938c). While different leaves of the same plant appear to be photoinduced independently, the most recent fully expanded leaf is the most sensitive to photoperiod (Borthwick and Parker, 1940). (Exposure of even one leaf to inductive daylength is sufficient to induce flowering in the whole plant.) Although grafting leaves of photoperiod insensitive cultivars onto noninduced plants of photoperiod sensitive Biloxi could induce flowering, grafts of previously photoinduced Biloxi leaves could not induce flowering in noninduced Biloxi plants (Heinze et al., 1949).

Shanmugasundaram and Tsou (1978), using a photoperiod insensitive soybean line and a photoperiod sensitive line, showed that photoperiod sensitive soybeans do not respond to short day induction during the first several days after emergence and the insensitive line required the same number of days to flower regardless of the daylength. The photoperiod insensitive phase of the photoperiod sensitive line was referred to as the juvenile phase. They also found that the juvenile phase was followed first by a photoperiod sensitive phase called the critical induction period and then by another photoperiod insensitive phase of several days. Huxley et al. (1974) suggested that soybeans have four successive phases of development from emergence: i) juvenile phase during which the flowering is not induced by short days, ii) inductive phase during which flowering is induced by a minimum number of short days, iii) regulation phase during which the number of flowers increases if inductive conditions continue, and iv) post regulation phase which is insensitive

to daylength. Board and Settimi (1988) reported that the cultivar Tracy-M, and a delayed flowering line, D77-12480, appeared to become responsive to short-day induction between 8 to 12 and 8 to 16 days after emergence, respectively. Cultivar differences for the length of the juvenile period exist and genotypes with a long juvenile period have been reported (Miyasaka et al., 1970; Hartwig and Kiihl, 1979; Kiihl and Garcia, 1989). The term "long juvenile" has been used to describe plants that exhibit delayed flowering under short day conditions (Hinson, 1989). However, this may be misleading because a longer inductive period or a longer floral development period could contribute to delayed flowering under short days in addition to a longer juvenile period.

Photosensitive soybeans begin to respond to photoperiod with the appearance of the trifoliolate leaves (Garner and Allard, 1925; Borthwick and Parker, 1938b). It takes at least nine days from emergence for seedlings to produce the first trifoliolate leaf (Fehr and Caviness, 1977). The inability of photoperiod sensitive lines to flower without the presence of trifoliolate leaves may explain the juvenile phase of about nine days from emergence (Shanmugasundaram and Lee, 1981). However, Shanmugasundaram (1981) reported that the day-neutral soybean has the ability to flower without trifoliolate leaves. He also found that the day-neutral soybean produced the flower-inducing substance regardless of photoperiod, not only flowers but also pods and seeds were produced when only cotyledonary and unifoliolate leaves alone were present.

Cultivars differ in their response to daylength. This differential response of cultivars to daylength has been measured in terms of days to flowering, days to maturity, number of nodes at flowering and maturity, plant height at flowering and maturity, duration of flowering, total number of flowers produced per plant, grain yield per plant, and others (Whigham and Minor, 1978; Shanmugasundaram, 1979). Nissly et al. (1981) found a wide range of photoperiod sensitivity, under both natural and artificial photoperiods among a large number of soybean strains of MG III. Several hundred soybean strains were tested and a wide range of strain differences for delayed flowering under extended photoperiods, compared to natural photoperiods, was observed. Among the strains tested, only PI317334B was found to be nearly 'day-neutral'. Shanmugasundaram (1981) studied the delay in flowering of soybean cultivars under artificially created long-photoperiods compared to natural short-photoperiod. Because different degrees of delay were ob-

served, he classified the photoperiod sensitivity of cultivars by the degree of delay in flowering. A sensitivity score of 0 to 1 (up to 8 days delay) was considered insensitive, whereas scores of 8 and 9 (beyond 57 days delay) were considered the most sensitive.

Johnson et al. (1960) studied the effects of photoperiod at various stages of soybean development and suggested that characterization of the photoperiodic requirements of a variety should also include the stages of development after flowering. Lawn and Byth (1973) reported that the pre-flowering, the flowering, and post-flowering phases of later maturing cultivars were considerably extended under long daylengths. However, early maturing cultivars were found to show only a slight response to daylength during each phase of development. These results agree with those of Nagata (1958) who observed differential responses of soybean cultivars to daylength at each growth stage.

### **Response to temperature**

Temperature is one of the main environmental factors that influences plant growth and development. Differences in temperature and relative sensitivity of different genotypes to temperature influence the rate and duration of phenological development in soybean (Shanmugasundaram et al. 1980).

When the development of the soybean plant is considered, the time required from planting through emergence (Hesketh et al., 1973) and the length of the juvenile stage (Borthwick and Parker, 1938a) are dependent on temperature under adequate moisture levels. Thereafter, both temperature and photoperiod affect time of floral induction (Major et al., 1975a) and development of the floral primordia (Borthwick and Parker, 1938a). However, in modeling of soybean phenological development, it is considered that only temperature and water stress affect the development of the first floral bud after initiation (Jones and Laing, 1978; Hodges and French, 1985). This is because the effect of photoperiod on floral development has been considered minor when compared to the effects of temperature and water stress in normal field conditions. After first bloom, progress of the first flower through pod and bean growth to maturity, duration of the flowering period, and progress of the last pod to maturity were modeled simultaneously as functions

of temperature, daylength, and water stress. Wang et al. (1987) emphasized the need for further information on the effect of the environment on the duration of flower bud growth in modeling soybean phenology.

Influence of temperature on days to flowering has been studied. Steinberg and Garner (1936) showed that increasing temperatures hastened flowering up to an optimum temperature of 28 C, above which flowering was delayed. Inouye and Shanmugasundaram (1985) reported that, with most of the less photosensitive cultivars, days to flowering was shortest at 30 C, followed by an increase in days to flowering at 25 C, 35 C, and 20 C. At 20 C, all plants showed cleistogamy whereas at 35 C, most cultivars aborted their flowers. Shibles et al. (1975) reported that days to flowering from emergence for adapted cultivars were mainly a function of accumulated temperature and were little influenced by natural photoperiod when soybeans were planted during a cold spring at latitudes greater than 40°. Garner and Allard (1930) indicated that year-to-year variation in the days from planting to flowering at any one planting date could be attributed to variation in temperature during the pre-flowering phase.

Lawn and Byth (1973) observed that temperature effects were apparent only in the absence of a strong photoperiodic response. Early plantings of early maturing cultivars had longer pre-flowering phases due to lower daily temperatures early in the season. Similarly, delayed maturity for late planting of late-maturing cultivars due to extended post-flowering periods were associated with lower daily temperatures late in the season. Major et al. (1975a) stated that prediction of flowering based on temperature was more accurate for early cultivars than for late maturing cultivars. Furthermore, Whigham and Minor (1978) reported that early maturing cultivars responded more to change in temperature than to daylength whereas late maturing cultivars responded more to daylength. ✓

Warrington et al. (1977) found that soybean plants did not differ greatly in growth rate when they were exposed to different day-night temperatures having the same mean. Roberts and Struckmeyer (1938) reported that flowering of two soybean cultivars was inhibited by low temperature. Low temperature suppressed the formation of flower buds on Biloxi soybean plants that had received photoperiodic induction treatment (Borthwick et al., 1941). This suppressing influence



of low temperature on floral initiation was later attributed to the effect of low temperature on the photoperiodic reactions occurring in the leaf blade during the dark period (Parker and Borthwick, 1943). When a single leaf was held at 10 C or lower and 32.2 C or higher during a five day induction period, floral initiation was greatly inhibited compared to that of 21 C. A single leaf was used in the experiment to show that the low temperature inhibition of flowering was due to the inhibitory effects on photoperiodic reactions in the leaves, rather than on translocation of any photoinduced stimulus produced in the leaf, or on differentiation of floral primordia at the terminal meristem.

### **Interaction of temperature with photoperiod response**

Temperature greatly influences photoperiodic response (Hillman, 1962; Salisbury, 1963). However, researchers have been criticized for concentrating too much on photoperiodic effects rather than on the combined effects of photoperiod and temperature which really determine the rate of reproductive ontogeny (Summerfield and Wien, 1980). Controlled environmental facilities have been used successfully to break the natural association between daylength and temperature (Summerfield and Minchin, 1976), facilitating studies on the photoperiod X temperature interaction effect in phenological development of crop plants. Summerfield (1976) indicated that longer photoperiods delayed flowering and warmer nights hastened it, therefore, various combinations may produce similar results in the flowering response of a cultivar. Summerfield (1976) and Summerfield and Minchin (1976) emphasized the importance of greenhouse experiments under controlled conditions for better understanding of temperature and photoperiod interactions.

Temperature during the night, when the photoperiodic reactions are occurring in the leaf blade, affects the response of soybean to photoperiod (Parker and Borthwick, 1943). For certain cultivars of soybean, an increase in night temperature decreased the time to flowering (Summerfield et al., 1975). Huxly et al. (1974) reported that night temperature differences of the tropics, when coupled with photoperiodic effects, can profoundly affect the reproductive ontogeny of soybean. They observed that many cultivars selected for adaptation to wet tropics flowered earlier during the shorter

daylengths than during longer daylengths. However, photoperiod sensitive cultivars (MG VIII) flowered about 20 days earlier during warmer nights (24 C) than during cooler nights (19 C).

Cool temperatures and long daylengths delayed flowering whereas warm temperatures and short daylengths promoted early flowering in soybeans (Huxley and Summerfield, 1974; Board and Hall, 1985). Low temperatures are known to increase the critical photoperiod for flowering in short-day plants (Lang and Melchers, 1943; Kimura, 1966). In contrast, Summerfield et al. (1985) reported that, in general, the critical photoperiod in soybeans increased by some 100 to 120 min. over the 18 C to 27 C range of mean temperature. Thus, soybeans tend to be more sensitive to photoperiod under cool temperatures than under warm temperatures or photoperiod insensitive soybeans under warm temperatures may become photoperiod sensitive under cool temperatures. Both these situations result in delay in flowering in soybeans under cool temperatures when compared to that of under warm temperatures for a given daylength. As a result temperature effects would be more apparent under short-days than under long-days so that a greater difference in time of flowering between cool and warm temperatures under short-day conditions is expected compared to long-day conditions. A significant interaction between photoperiod and temperature was reported by Board and Hall (1965). This interaction was due to the greater effect of warm temperature in shortening the vegetative period under short days compared to long days. The effect of warm temperature in hastening the time to first flowering under short photoperiods was greater in the Maturity Group VI and VII cultivars than that of Maturity Group V cultivars and the delayed flowering genotypes (Group VI, VII and VIII) that are supposed to have a longer juvenile period.

### **Adaptational influence**

Soybeans are adaptable to a wide range of environments. They are grown from the tropics to about 55°N or S latitudes and from below sea level to about 2000m (Whigham, 1983) and are adaptable to growing seasons ranging from 90 to 180 days. For adaptation to such a remarkable range of environments, dissemination of the crop must have involved the exploitation of genetic differences and responsiveness to environment (Bunting, 1975).

Genetic variation in photoperiod sensitivity has played a significant role in adaptational ability of soybean (Shibles, 1980). The response of a soybean cultivar to photoperiod determines the range of latitudes over which it will be adapted. There is a close relationship between photoperiod response and maturity date in soybean (Garner and Allard, 1920; Criswell and Hume, 1972; Shanmugasunderam, 1979). Thus, soybean cultivars have been classified into 13 maturity groups, MG 000 to MG X, based on their photoperiodic response. Genotypes classified into MG 000 are those which have a critical photoperiod of about 16h, mature early, and are adapted to higher latitudes (45 - 50°) whereas late maturing (MG X) genotypes are grown in low latitudes (Weber, 1968). When the cultivars are moved away from their area of adaptation in the U.S., plants either mature too early in the South or fail to mature before the first frost in the North (Major et al., 1975).

In addition to the effect on flowering and maturity, photoperiod sensitivity may alter plant morphology. This may also provide adaptational value to the plant. Byth (1968) reported that plant height and node number increased with increasing number of days to flowering as photoperiod increased. This is in agreement with Inouye and Shanmugasundaram (1985) who observed that the number of days to flowering and resulting number of nodes in short-day cultivars were greater under long-day conditions than under short-day conditions. Increased days to flowering as day length increases were associated with maturity delays, increases in plant height and node number at flowering and maturity, longer flowering duration, greater number of flowers and pods per plant, and higher yield in photoperiod-sensitive soybean cultivars (Shanmugasundaram, 1979).

In the tropics, the time to first flower is determined by response to both photoperiod and night temperature whereas the rate of vegetative growth appears heavily dependent upon night temperature (Huxley and Summerfield, 1974). A lower rate of vegetative growth caused by low night temperatures lengthened the vegetative period and increased the physiological potential for seed production. However, they also indicated that these vegetative components may not utilize their full physiological potential for seed production because of adverse effects of warm day temperatures on flower and pod abortion. This is one of the main factors that affect the adaptational value of soybean in the tropics. In some tropically adapted soybeans, a 5 C change in night temperature is

even more effective than a 100 min. change in daylength in influencing time to the first open flower (Summerfield et al., 1975) indicating that not the photoperiod but the night temperature is the main factor that influences the adaptation of these cultivars in the tropics.

Temperature also plays a critical role in controlling plant morphology as well as pod to flower ratios (Raper and Thomas, 1978; Thomas and Raper, 1976, 1977) which in turn provides an adaptational value to the plant. Thomas and Raper (1978) also reported the influence of day and night temperature during floral induction on morphology of soybean. They saw a direct effect of temperature on pod appearance rate, pod number, and pod dry weight. They also showed that main stem trifoliolate leaf production was reduced by cool day and night temperatures. The impact of this is that more main stem trifoliate leaves means more main stem nodes, and thus, more sites for initiation of branches that usually results in higher pod yields.

#### *Seasonal Adaptation as Influenced by Date of Planting*

Adaptation of soybean to growing seasons and cropping systems is dependent upon its photothermal regulation of flowering. Timely flowering or the time taken from planting to flower is of considerable agricultural interest since it regulates when crops reach maturity and whether or not they have the potential to yield well under different situations (Summerfield and Lawn, 1987).

Previous research in Virginia (Camper and Smith, 1958) has shown that late June and early July seedlings gave lower seed yields than early June or May seedlings. Wolf (1924) reported progressively lower yields in Virginia for later seedings of two cultivars from May 11 to June 30. Yield reduction of soybean when planted late in the season has also been reported in Mississippi, Florida (Hartwig, 1954), Louisiana, and other Gulf Coast locations (Graves et al., 1978; Beatty et al., 1982; Board and Hall, 1983). Premature flowering has been reported to be a major factor in soybean yield losses at nonoptimal planting dates (Hartwig and Kiihl, 1979). Planting soybean late in the season has been found to result in more rapid flowering and restricted development during the vegetative period from emergence to first flowering (Borst and Thatcher, 1931; Hartwig, 1954; Osler and Cartter, 1954; Abel, 1961).

Hartwig (1954) obtained taller plants from May and early June seedlings than from earlier or later plantings. Weiss et al. (1950) showed that delayed planting produced shorter plants, reduced lodging, and smaller seed size. Carter (1974) reported that yield losses at nonoptimal planting dates were mainly caused by reduced fruit set. Also reduction in fertile node number (Carter, 1974; Carter and Boerma, 1979) and pods per plant (Beatty et al., 1982; Carter, 1974) has been reported at nonoptimal planting dates. A period of 42-58 days, depending on prevailing temperatures, from emergence to first flowering was necessary to attain a leaf area index (LAI) of three which is required for maximum yield (Constable, 1977). After formation of closed canopies, vegetative growth did not increase seed yield and, in some cases, seed yields were actually reduced, probably due to excessive vegetative dry matter accumulation particularly in stem materials, increased lodging, and the senescence of lower shaded leaves and branches (Lawn and Byth, 1974).

Date of planting, depending on genetic differences and responsiveness of genotypes, dictates whether the crop duration is completely contained within those portions of the year which are favorable for growth. Leffel (1961) reported that the flowering and post-flowering phases in soybean were shortened by delayed planting and attributed this response to shorter day lengths. This is in agreement with the results of Abel (1961) who reported that delayed planting, i.e. planting when the photoperiod was decreasing, reduced the time from 50% flowering to maturity in early cultivars whereas the pre-flowering phase was shortened in late-maturing cultivars and both pre- and post-flowering phases were shortened in medium-maturing cultivars. Lawn and Byth (1973), in agreement with Abel (1961), reported that the pre-flowering and post-flowering phases of later cultivars were considerably extended when those phases occurred during the period of longest daylengths. In addition to pre- and post-flowering phases, Lawn and Byth (1973) also found that the flowering phase increased in response to long daylengths. In the earliest maturing day neutral cultivars, the flowering phase was the only phase that increased in response to daylength.

## *Genetic Control of Flowering in Soybean*

Incorporation of the delayed flowering trait in soybean cultivars may be beneficial for reducing yield losses caused by premature flowering at suboptimal planting dates. Time of flowering in soybean has been shown to be highly heritable (Johnson and Bernard, 1962). However, Kiihl (1976), studying the cross between 'D72-7842', a normal line, and 'Santa Maria', a long juvenile line, reported that the genetic control of flowering under short-day conditions (long juvenile) and under long-day conditions was different. This is because under long-day conditions, genes for photosensitivity interact with genes for long juvenility, while under short-day conditions, only the long juvenile genes have an effect.

As early as 1927, Owen reported that the time of maturity, as measured by the time of flowering, was controlled by one major gene pair at one locus where the gene for late flowering is dominant. Byth (1968) observed that the  $F_2$  mean of the cross between 'Manloxi' and 'Avoyelles' for days to flowering was consistently smaller than the midparent value and thus concluded that early flowering exhibited dominance. Furthermore, he concluded that inheritance of flowering time was complex. Bernard (1971) reported two independent gene loci ( $E_1$  and  $E_2$ ) with two alleles at each locus that affected the time of flowering and maturity in soybean. Lateness was found to be partially dominant in both loci and the loci were found to be additive in effect. A third locus with two alleles ( $E_3e_3$ ) has been described by Buzzell (1971) and Kilen and Hartwig (1971). The recessive allele,  $e_3$ , which showed earlier field maturity did not respond to fluorescent daylength treatment that was used to extend photoperiod whereas  $E_3$  gave a fluorescent-sensitive response of delayed flowering and resulted in late field maturity. The genes  $E_2$  and  $E_3$  are not linked, they do not have an equal effect in delaying maturity, and when combined, have less than an additive effect (Buzzell and Bernard, 1975). A fourth locus with two alleles ( $E_4e_4$ ) affecting time of flowering similar to previous  $E$  genes was described by Buzzell and Voldeng (1980) in PI 297550. Although Shanmugasunderam (1977) reported that photoperiod insensitivity was controlled by a single recessive gene, a gene symbol was not assigned.

Genetic control of delayed flowering under short-day conditions has also been studied. Kiihl (1976) reported that the delayed flowering trait in Santa Maria, under short-day conditions, was controlled by recessive genes, but the number of genes involved was not determined. Using Santa Maria and PI159925 as sources, Hartwig and Kiihl (1979) concluded that the delayed flowering trait under short-day conditions was controlled by as many as three recessive genes. Although Azlan (1981) suggested that the delayed flowering trait was controlled by a single recessive gene, flowering date classes in the  $F_2$  populations he studied often were not discrete. Thus, the possibility of a second major gene controlling flowering date was not excluded. Malo (1986), using PI 159925 as the source of delayed flowering also suggested that delayed flowering was controlled by a single recessive gene since most  $F_2$  progenies she studied produced ratios of 3 early : 1 late flowering plants. However, three out of 26 progenies appeared to segregate for more than one gene. Hinson (1989), using PI 159925 as the source of delayed flowering, reported that long juvenility (delayed flowering under short-day conditions) was controlled by one recessive gene. However, presence of more than two flowering date and maturity date classes in a few late-generation segregating rows indicated that inheritance may be more complex. Furthermore, long juvenility was found to be strongly influenced by the genetic background since the same gene for long juvenility gave different juvenile lengths in different genetic backgrounds. Bidja Mankono (1988) observed segregating populations under three planting dates from June to August in Florida and concluded that the delayed flowering trait from PI 159925 was controlled by a single recessive gene. He also found evidence for a dominant gene that delayed flowering since some of his  $F_2$  populations segregated in a 3 late: 1 early ratio. However, the source of this gene was unknown and no evidence was found to relate it to the long juvenility of PI 159925.

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## **CHAPTER II**

### **DELAYED FLOWERING IN SOYBEANS AS INFLUENCED BY DATE OF PLANTING IN VIRGINIA**



## ABSTRACT

Double-cropping of soybeans [*Glycine max* (L.) Merr.], especially after wheat harvest, results in later than optimal planting dates for the soybeans. Soybeans planted later than 15 June usually have lower yields due to early flowering and restricted vegetative growth. This study was undertaken to determine whether the delayed flowering trait in soybeans might be useful in increasing yields of double cropped soybeans. Two field experiments, one in Blacksburg and the other in Warsaw, Virginia were conducted using 27 soybean genotypes representing a wide range of genetic backgrounds. Genotypes were planted from 3 May to 12 July at two week intervals. Genotype X date of planting X location interaction was significant. Days to flowering of all the genotypes decreased linearly as the date of planting progressed from 3 May to 28 June. In general photoperiod-insensitive genotypes did not exhibit the delayed flowering trait consistently over all planting dates in both locations. F85-8417, F85-1099, and F85-1226 flowered 7 to 23 days later than their respective isolines and Essex, a commercial cultivar. But they were comparable to Centennial and Ransom, late maturing commercial cultivars, in their flowering response across all the planting dates at both locations. Some lines selected for insensitivity to photoperiod also showed some promise in delayed flowering compared to Essex in late plantings. Although the delayed flowering trait may be useful in overcoming the problem of restricted vegetative growth at flowering, it may be useful in increasing yields only if it is not associated with excessively late maturity.

## INTRODUCTION

Double-cropping of soybeans after wheat has become a common practice in Virginia. This practice results in later than optimal planting dates for the soybean. Soybeans planted later than 15 June usually have lower yields than earlier planted soybeans (Wolf, 1924; Camper and Smith, 1958). Other studies in the southern USA have also indicated that May to early June is the optimum planting period for adapted soybean cultivars (Henson and Carr, 1946; Hartwig, 1954; Smith, 1968; Graves et al., 1978; Beatty et al., 1982; Board and Hall, 1983). Planting late in the season has been reported to result in early flowering and restricted vegetative development (Hartwig, 1954; Osler and Cartter, 1954; Abel, 1961), which is the major reason for yield losses at nonoptimal planting dates (Hartwig and Kühn, 1979).

Photoperiod and temperature are the two main environmental factors that affect flowering in soybean (Huxley and Summerfield, 1974). However, temperature effects are apparent only in the absence of strong photoperiodic response (Lawn and Byth, 1973). Cool temperatures and long daylengths delay flowering while warm temperatures and short daylengths promote early flowering (Huxley and Summerfield, 1974; Board and Hall, 1985). Seasonal changes affect photoperiod (Whigham and Minor, 1978) and temperature. Therefore, at a given location, planting date determines the photoperiod and temperature under which the crop will be developing. When soybeans are planted late in the season (after 15 June) in Virginia, shortening days and warm temperatures promote early flowering before the attainment of adequate vegetative growth.

Delayed flowering soybean genotypes with a long vegetative period under short days have the potential to attain maximum productivity by avoiding premature flowering in late plantings (Board and Hall, 1985; Kühn and Garcia, 1989). No evaluation of delayed flowering soybean genotypes has been done in Virginia. The objective of this research was to study the delayed flowering in some selected soybean genotypes as influenced by the date of planting in the field in Virginia.

## MATERIALS AND METHODS

Planting date studies were conducted in the field at Blacksburg and Eastern Virginia Agricultural Experiment Station, Warsaw. Change in photoperiodically active daylength at Blacksburg during the growing season is shown in Fig. 1. Blacksburg is at latitude 37° 15' N and 630 m above sea level. Warsaw is at a slightly higher latitude (37° 58') than Blacksburg so growing season daylengths are slightly shorter than Blacksburg before 21 June and slightly longer thereafter. Although Warsaw is north of Blacksburg it has a much lower elevation (approximately 16 m above sea level) and thus has a longer growing season.

Twenty-seven genotypes were used in the study and are listed in Table 1 with their pedigrees and brief descriptions. The 12 lines with "F" designation are six pairs of isolines which were selected from advanced generation lines which were segregating for delayed vs. normal flowering in Florida (K. Hinson, personal communication). All Virginia (V) lines and Asian Vegetable Research and Development Center (AVRDC) lines were selected for photoperiod insensitivity. PI 317334B was identified by Nissly et al. (1981) as being photoperiod-insensitive and Delta (D) lines were selected in Mississippi for delayed flowering. Williams, Avery, Essex, Forrest, Centennial, and Ransom were included as standard cultivars representing maturity groups III, IV, V, V, VI, and VII, respectively.

Experiments were conducted during the 1989 growing season. All 27 genotypes were scheduled to be planted in both locations at two week intervals on 3 May, 17 May, 31 May, 14 June, 28 June, and 12 July. However, due to unfavorable weather conditions, some plantings were either delayed or advanced one or two days over the scheduled date in both locations.

A randomized complete block design with two replications was used at each planting date at each location. A plot consisted of a single row 90 cm long with a spacing of 30 cm between rows. Rows were seeded by hand with 25 seeds per entry. Flowering date was recorded as the day when half the plants in the row were blooming.

All data were summarized and analyzed using SAS GLM and REG. The number of days from planting to 50% flowering were calculated for each entry. A combined analysis over dates and locations was performed and the interaction of genotypes X blocks within location and planting date combination was used as the error term in the analysis. Days to flowering of each genotype was regressed on the first five planting dates (3 May through 28 June). In the regression analysis, date of planting, the independent variable, was represented as the number of days after 3 May. Thus, the successive planting dates in Blacksburg were represented by 0, 13, 27, 42, 56, and 72 days and in Warsaw by 0, 13, 28, 42, 56, and 71 days.

## RESULTS AND DISCUSSION

The daylength increased from about 14.5 h on 3 May, the first date of planting, to 15.5 h on 6 June and then decreased to about 15.25 h at the last date of planting in Blacksburg (Fig. 1). Average temperatures are increasing throughout this period at both locations and normal temperatures average 2-3 C higher in Warsaw than in Blacksburg.

Days to flowering from planting for each genotype at each planting date in Blacksburg and Warsaw are presented in Tables 2 and 3. On the average, days to flowering decreased as the planting dates progressed from 3 May to 12 July. This is opposite of the expected effect from the increasing daylength, so may be attributed mainly to the increase in temperatures. The three-way interaction effect of genotype X planting date X location as well as the two-way interaction effects of genotype X planting date, genotype X location, and planting date X location were significant at the 0.05 level in the combined analysis. Thus, response of each genotype at each location was studied separately using regression analysis. All the genotypes, except F85-1107, F85-8310, and Williams at Warsaw, showed a good linear relationship between days to flowering and planting date for the first five plantings at both locations (Tables 4 and 5). In general, days to flowering of all the genotypes decreased linearly as date of planting progressed at both locations. However, from inspection of the data, it appears that the linear decrease in days to flower was not continuing

through the last planting date (7/12). A comparison of the observed days to flower with that predicted for the last planting date by the linear regression might provide a means for identifying different responses to late plantings among the genotypes. Actual and predicted values for days to flowering for the 12 July planting date for each genotype at each location are presented in Table 6. One might expect that late flowering types might be distinguished from early flowering ones by a significant delay compared to the predicted days to flowering. A number of the observed values were significantly above the predicted, but there seems to be no consistent pattern so this technique does not appear to be helpful in detecting long juvenile types. A general increase in actual days to flower compared to the predicted value for the last planting date may be a response to decreasing temperatures in the late summer.

In general, earliest maturing cultivars had least response to date of planting (lowest regression coefficients) and late genotypes had the greatest response (Tables 4 and 5). None of the regression values for experimental lines were drastically different from cultivars of comparable maturity. Thus, regression analysis is not very helpful in identifying lines that have different flowering responses from standard cultivars. Therefore, visual inspection of the data is probably the best method for locating lines with delayed flowering at plantings that also mature about the same as Essex and Forrest which mature at an appropriate date for double-cropping. Maturity data were not obtained in this study, but there is a close relationship between flowering date and maturity date so date of flowering at the last planting date should provide comparison of relative maturity among entries.

Most of the photoperiod-insensitive lines did not appear to differ much from the standard cultivars in flowering response, but V82-571 seemed to be somewhat different. On the last planting it bloomed at about the same time as Essex, but in the early plantings it bloomed several days before Essex, indicating a somewhat decreased response to planting dates.

D82-2897, D82-2896, and D82-2976, which were selected as delayed flowering types in Mississippi did not differ in flowering response from Forrest or the other cultivars at either location. The reason for their not exhibiting delayed flowering is not clear, but it might be related to the differences in daylength during the growing season in Mississippi vs. Virginia.

In all the isoline pairs except in F85-8310 and F85-8311 the delayed flowering isoline flowered 7 - 23 days later than the respective early flowering isoline in both locations. Delayed flowering isolines F85-8417, F85-1226, F85-1099 and F85-8552 flowered much later than Essex at the last planting date in both locations, but their early flowering counterparts had flowering dates very similar to Essex. In the early planting dates, the delayed flowering isolines were generally later blooming than Essex, but the early flowering ones were similar to Essex or earlier. Thus, it appears that incorporating the delayed flowering trait into a line with similar maturity genes as Essex would result in a greater delay in maturity than is desirable. On the other hand, the F85-1107 and F85-1108 pair show what might happen if the delayed flowering trait is incorporated into germplasm with earlier maturity. The normal line, F85-1107, had a flowering response very similar to Williams, a group III cultivar, but the delayed flowering isoline, F85-1108, flowered earlier than Essex at early plantings but similar to Essex at late plantings at both locations. Similarly F85-8417 and F85-1226 flowered on about the same date as Centennial in early plantings but a few days later at late planting. F85-8552 flowered similar to Ransom at early plantings but later in late plantings at Blacksburg and earlier than Ransom at early plantings but similar to Ransom at late plantings in Warsaw.

Although the delayed flowering trait in soybean can be used to overcome the problem of premature flowering when planted late in the season as in double-cropping, it may be useful in increasing grain yield only if the delayed flowering does not delay maturity until very late in the season. Five of the isoline pairs and four cultivars were planted at Warsaw in a full season yield test on 1 June 1988 and in a double-cropping yield test on 7 July 1989. Data from these experiments are presented in Tables 7 and 8 (data obtained from G. R. Buss). Days to flower data in the full season yield test were comparable to days to flower in mid to late May planting dates in the planting date study and the flowering data for the double-crop test were similar to the last date of planting. In general, the delayed flowering isolines flowered and matured later than their normal isolines in both experiments. However, the yield trends were quite different for the tests. In the full season test, the delayed flowering isolines tended to have equal to slightly higher yields, compared to their early flowering isolines, but in the double-cropping test the delayed flowering isolines tended

to have lower yields than their earlier counterparts. Inspection of the data in Table 7 shows that in the full season test, F85-8417 delayed flowering by about 13 days but delayed maturity only about seven days and showed a  $0.20 \text{ Mg ha}^{-1}$  yield increase over its early flowering isoline, F85-8416. F85-1108 delayed flowering by about eight days but matured at the same time as F85-1107 and showed a significant yield increase over its early flowering isoline.

The double-crop yield test showed that, in general, grain yields of delayed flowering lines were lower than their respective early flowering isolines due to excessive lateness in maturity. For example, delayed flowering isoline F85-1226 delayed flowering by about 12 days resulting in delay in maturity of about 25 days and reduced yield of about  $0.98 \text{ Mg ha}^{-1}$  over its early flowering isoline F85-1221. Similar results were obtained with isoline pairs of F85-1096 /F85-1099 and F85-8416/ F85-8417 in the same yield test indicating the unsuitability of these delayed flowering lines for late planting. However, the opposite result was exhibited by F85-1108 in comparison to its early flowering isoline because it had a more reasonable maturity. The yield of F85-1108 was very similar to Essex, while in the full season planting it was significantly lower than Essex. This could be an indication that delayed flowering lines of an appropriate maturity for double-cropping might not be adapted for full season planting. More extensive testing is needed to determine the long term effect of the delayed flowering trait. However, it is clear that if the delayed flowering trait is utilized to improve cultivars for double-cropping, careful attention must be paid to selecting lines that have maturity appropriate for the intended area of use.

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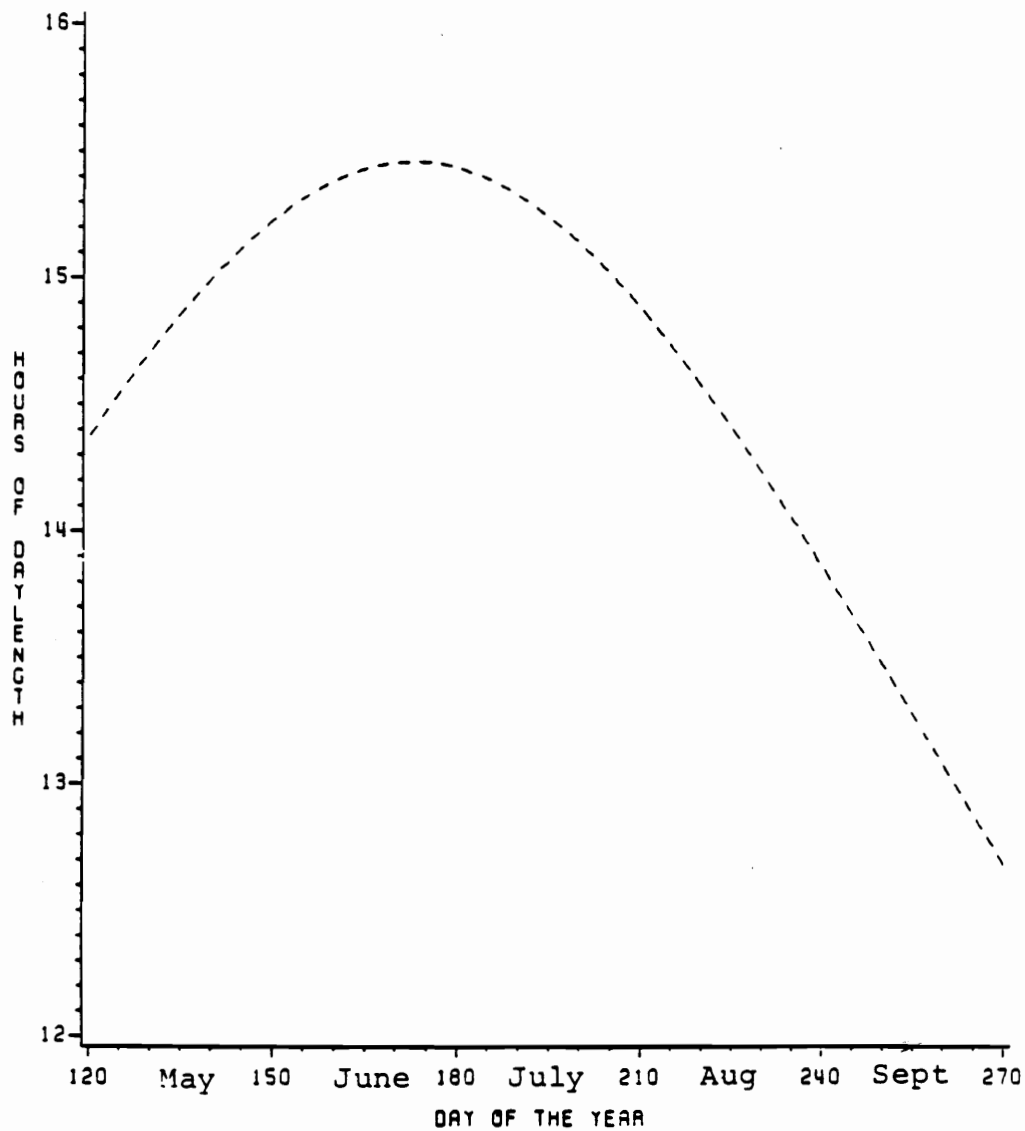


Fig. 1. Change in photoperiodically active daylength during the growing season at Blacksburg, Virginia.

Table 1. Genotypes used in the planting date studies and their pedigrees and descriptions.

Genotype	Pedigree	Description
F85-1096	C† X Will	Early flowering isoline of 1099
F85-1099 ✓	C X Will	— Delayed flowering isoline of 1096
F85-1108	C X Will	Early flowering isoline of 1107
F85-1107 ✓	C X Will	— Delayed flowering isoline of 1108
F85-1221	C X Will	Early flowering isoline of 1226
F85-1226 ✓	C X Will	— Delayed flowering isoline of 1221
F85-8311	C X Will	Early flowering isoline of 8310
F85-8310 ✓	C X Will	— Delayed flowering isoline of 8311
F85-8416	C X Will	Early flowering isoline of 8417
F85-8417 ✓	C X Will	— Delayed flowering isoline of 8416
F85-8553	C X PI417,450A	Early flowering isoline of 8552
F85-8552 ✓	C X PI417,450A	— Delayed flowering isoline of 8553
D82-2896	Forrest X D78-5089	Delayed flowering
D82-2897	Forrest X D78-5089	Delayed flowering
D82-2976	Forrest X D78-5089	Delayed flowering
PI317334B	-	Photoperiod insensitive
V81-544B	V68-920 X Fiskeby V	Photoperiod insensitive
V82-571	Essex X Fiskeby V	Photoperiod insensitive
V85-5166	Essex X V81-544B	Photoperiod insensitive
AVRDC 8025	-	Photoperiod insensitive
AVRDC 8082	-	Photoperiod insensitive
Williams	Wayne X L57-0034	Maturity group III
Avery	Bedford X Crawford	Maturity group IV
Essex	Lee X S5-7075	Maturity group V
Forrest	Dyer X Bragg	Maturity group V
Centennial	Pickett 71 X D64-4636	Maturity group VI
Ransom	(N55-5931 X N55-3818) X D56-1185	Maturity group VII

† Indicates Kirby X [(Forrest (3) X D77-12480)] where D77-12480 was a selection from the cross Tracy X (Hill X PI 159925).

Table 2. Days to flower from planting for 27 soybean genotypes at six dates of planting in Blacksburg.

Genotype	Dates of planting					
	May			June		July
	3	16	30	14	28	14
----- d -----						
F85-1096	70	66	64	55	50	49
F85-1099	98	89	82	75	68	67
F85-1108	80	68	64	56	49	49
F85-1107	70	64	56	47	44	38
F85-1221	92	82	73	62	55	50
F85-1226	101	93	88	79	77	78
F85-8311	84	64	63	55	50	48
F85-8310	87	71	68	56	48	42
F85-8416	80	78	69	58	51	49
F85-8417	100	86	80	71	66	67
F85-8553	88	76	66	59	54	51
F85-8552	94	77	77	65	60	61
D82-2896	94	80	77	66	56	55
D82-2897	88	80	70	60	53	48
D82-2976	76	69	64	55	50	44
PI317334B	66	60	54	46	42	39
V81-544B	66	55	56	44	42	38
V85-571	80	72	68	56	50	48
V85-5166	87	73	68	60	52	49
AVRDC-8025	92	82	75	64	58	54
AVRDC-8082	85	75	66	58	50	46
Williams	71	64	59	53	45	42
Avery	80	72	65	57	50	49
Essex	89	78	68	62	53	51
Forrest	93	81	73	63	57	54
Centennial	100	87	82	71	64	62
Ransom	94	84	78	68	59	54
Mean	85a*	75b	69c	60d	54e	51f

\* Indicates planting date means followed by different letters differ at the 0.05 level based on DNMR test.

Table 3. Days to flower from planting for 27 soybean genotypes at six dates of planting in Warsaw.

Genotype	Dates of planting					
	May			June		July
	3	14	31	14	28	13
	----- d -----					
F85-1096	62	56	55	46	42	41
F85-1099	84	78	69	61	55	53
F85-1108	62	56	55	47	42	40
F85-1107	49	48	50	46	38	33
F85-1221	72	71	60	55	48	47
F85-1226	89	80	70	64	62	51
F85-8311	62	56	55	48	42	41
F85-8310	61	65	56	46	43	41
F85-8416	70	65	57	49	43	44
F85-8417	81	71	69	61	55	53
F85-8553	70	65	55	49	42	41
F85-8552	75	67	62	57	52	49
D82-2896	76	71	61	55	47	48
D82-2897	72	68	59	54	47	42
D82-2976	70	64	54	47	42	39
PI317334B	54	49	46	41	34	33
V81-544B	49	49	46	40	34	33
V82-571	69	64	54	48	42	41
V85-5166	73	66	57	49	43	42
AVRDC-8025	77	71	61	54	43	42
AVRDC-8082	72	65	59	50	42	37
Williams	49	49	48	43	36	33
Avery	62	62	55	50	41	39
Essex	73	66	54	51	43	41
Forrest	77	71	61	56	47	47
Centennial	88	71	68	61	52	48
Ransom	86	81	71	62	54	48
Mean	69a	64b	58c	51d	45e	42f

\* Indicates planting date means followed by different letters differ at the 0.05 level based on DNMR test.

Table 4. Coefficients (coef.) and their standard errors (SE) of linear regression analyses for days to flower of 27 genotypes at five planting dates in the field at Blacksburg.

Genotype	Coefficients and SE's of the linear regression				
	Intercept		Regression		Correlation coef.(r)
	Coef.	SE	Coef.	SE	
d					
F85-1096	71	1.1	-0.36	0.03	0.96**
F85-1099	97	2.4	-0.52	0.07	0.93*
F85-1108	78	1.0	-0.52	0.03	0.98**
F85-1107	70	2.0	-0.49	0.06	0.94*
F85-1221	91	0.9	-0.66	0.02	0.99**
F85-1226	100	1.0	-0.45	0.03	0.97**
F85-8311	78	2.8	-0.55	0.08	0.92*
F85-8310	84	2.6	-0.65	0.08	0.94*
F85-8416	85	1.0	-0.62	0.03	0.98**
F85-8417	97	1.8	-0.60	0.05	0.96**
F85-8553	85	1.6	-0.60	0.05	0.97**
F85-8552	90	2.0	-0.57	0.06	0.95**
D82-2896	92	1.9	-0.64	0.06	0.97**
D82-2897	88	0.9	-0.64	0.03	0.98**
D82-2976	75	2.6	-0.47	0.08	0.90*
PI317334B	65	1.6	-0.44	0.05	0.95**
V81-544B	64	1.5	-0.41	0.04	0.95**
V82-571	80	0.8	-0.55	0.02	0.98**
V85-5166	85	0.9	-0.62	0.03	0.98**
AVRDC-8025	90	1.0	-0.61	0.03	0.98**
AVRDC-8082	83	1.6	-0.62	0.05	0.97**
Williams	70	1.6	-0.44	0.05	0.96**
Avery	79	0.3	-0.54	0.01	0.99**
Essex	87	1.7	-0.62	0.05	0.95**
Forrest	91	1.2	-0.64	0.04	0.98**
Centennial	97	1.6	-0.62	0.05	0.97**
Ransom	93	1.4	-0.61	0.04	0.98**

\*, \*\* significant at the 0.05 and 0.01 level, respectively.

Table 5. Coefficients (coef.) and their standard errors (SE) of linear regression analyses for days to flower of 27 genotypes at five planting dates in the field at Warsaw.

Genotype	Coefficients and SE's of the linear regression				
	Intercept		Regression		Correlation coef.(r)
	Coef.	SE	Coef.	SE	
d					
F85-1096	62	1.03	-0.37	0.03	0.97**
F85-1099	84	0.65	-0.53	0.02	0.98**
F85-1108	62	0.78	-0.36	0.02	0.97**
F85-1107	51	2.67	-0.18	0.08	0.62
F85-1221	74	2.06	-0.47	0.06	0.93*
F85-1226	87	1.25	-0.51	0.03	0.97**
F85-8311	62	0.67	-0.34	0.02	0.98**
F85-8310	65	3.23	-0.39	0.09	0.82
F85-8416	71	0.56	-0.50	0.02	0.99**
F85-8417	80	2.53	-0.44	0.07	0.90*
F85-8553	71	0.75	-0.51	0.02	0.98**
F85-8552	74	1.26	-0.41	0.04	0.96**
D82-2896	77	1.23	-0.53	0.03	0.97**
D82-2897	73	0.95	-0.46	0.03	0.98**
D82-2976	70	0.74	-0.52	0.02	0.98**
PI317334B	54	1.26	-0.34	0.04	0.95**
V81-544B	51	1.70	-0.28	0.05	0.88**
V82-571	69	0.63	-0.49	0.02	0.98**
V85-5166	73	0.12	-0.55	0.02	0.98**
AVRDC-8025	78	0.78	-0.61	0.02	0.98**
AVRDC-8082	72	0.78	-0.53	0.02	0.98**
Williams	51	1.96	-0.23	0.06	0.81
Avery	65	1.74	-0.39	0.05	0.93*
Essex	72	1.57	-0.53	0.04	0.96**
Forrest	77	0.67	-0.54	0.02	0.98**
Centennial	84	2.9	-0.58	0.08	0.92*
Ransom	87	0.74	-0.58	0.02	0.98**

\*, \*\* Significant at the 0.05 and 0.01 levels, respectively.

Table 6. Predicted and actual days to flower (DF) for the last planting for 27 genotypes grown at Blacksburg and Warsaw.

Genotype	Blacksburg			Warsaw		
	Predicted DF		Actual DF	Predicted DF		Actual DF
	Value	CI†		Value	CI	
	----- d -----					
F85-1096	45	41-48	49*	36	33-39	41*
F85-1099	59	51-67	67	46	44-48	53*
F85-1108	40	37-43	49*	37	34-39	40*
F85-1107	34	27-40	38	38	30-47	33
F85-1221	43	40-46	50*	41	34-47	47
F85-1226	68	64-71	78*	51	47-55	51
F85-8311	38	30-48	48	38	36-40	41*
F85-8310	37	28-45	42	37	27-47	41
F85-8416	40	37-44	49*	35	33-37	44*
F85-8417	54	48-60	67*	48	40-57	53
F85-8553	42	36-47	51*	34	32-36	41*
F85-8552	49	42-56	61*	45	40-49	49
D82-2896	46	40-52	55*	39	35-43	48*
D82-2897	42	38-45	48*	40	37-43	42
D82-2976	41	33-50	44	33	30-35	37*
PI317334B	33	29-39	39	30	26-34	33
V81-544B	34	29-39	38	32	26-37	33
V82-571	42	38-43	48*	34	32-36	41*
V85-5166	44	38-44	49*	34	31-36	42*
AVRDC-8025	46	43-50	54*	35	32-37	42*
AVRDC-8082	38	34-44	46*	35	32-37	37
Avery	40	39-41	49*	37	31-43	39
Centennial	53	48-59	62*	43	33-52	48
Essex	42	37-48	51*	34	29-39	41*
Forrest	45	41-49	54*	39	37-41	47*
Ransom	50	45-54	54	46	43-48	48
Williams	38	33-44	42	35	29-41	33

\* Indicates an observed value significantly above the predicted value.

† 95% Confidence interval.



Table 7. Days to flower and maturity from planting and grain yield of 15 genotypes in full season yield test in 1988 at Warsaw.†

Genotype	Days to flower	Days to maturity	Grain yield
	----- d -----		Mg ha <sup>-1</sup>
F85-1096	50	126	1.27
F85-1099	70	150	1.49
F85-1107	42	126	0.95
F85-1108	50	126	1.39
F85-1221	63	133	1.57
F85-1226	72	153	1.61
F85-8416	57	134	1.34
F85-8417	70	141	1.54
F85-8553	55	128	1.23
F85-8552	62	136	1.28
Essex	60	133	2.67
Forrest	61	134	1.62
Centennial	70	150	1.22
Ransom	70	150	1.44
<i>LSD</i> <sub>0.05</sub>		3	0.22

† Personal communication, G. R. Buss, CSES Dept., VPI&SU, Blacksburg, Virginia.

Table 8. Days to flower and maturity from planting and grain yield of 15 genotypes in double cropping yield test in 1989 at Warsaw.†

Genotype	Days to flowering	Days to maturity	Grain yield
	----- d -----		Mg ha <sup>-1</sup>
F85-1096	43	124	2.51
F85-1099	56	140	1.56
F85-1107	30	103	1.43
F85-1108	43	123	2.55
F85-1221	45	114	2.54
F85-1226	57	139	1.56
F85-8416	44	117	2.20
F85-8417	56	138	1.35
F85-8553	46	106	2.26
F85-8552	56	134	2.18
Essex	45	117	2.65
Forrest	48	124	2.35
Centennial	45	123	2.13
Ransom	46	128	2.64
<i>LSD</i> <sub>0.05</sub>		1	0.29

† Personal communication, G. R. Buss, CSES Dept., VPI&SU, Blacksburg, Virginia.

# **CHAPTER III**

**LENGTHS OF COMPONENT VEGETATIVE**

**PHASES IN SOYBEANS**

## ABSTRACT

A longer vegetative period has been suggested as a way to overcome premature flowering at nonoptimal planting dates in soybeans [*Glycine max* (L.) Merr.]. Length of the vegetative period depends on the individual lengths of the successive component juvenile, inductive, and floral development phases. Thus, a study was undertaken to estimate the lengths of juvenile and inductive phases of some selected early and late flowering soybean genotypes under inductive short-day conditions. Juvenile and inductive lengths differed among genotypes. Late flowering F85-8417 appeared to have a longer juvenile period, but similar inductive period, compared to its early flowering isoline F85-8416 and 'Essex', a commercial cultivar. Late flowering F85-1226 appeared to have longer juvenile and inductive periods than its early flowering isoline, F85-1221, and Essex. Absolute lengths of these phases varied among experiments, probably due to temperature differences, but relative lengths between genotypes were consistent. Published methods for estimating the lengths of juvenile and inductive phases involve moving plants from long to short-days and short to long-days, respectively. The method of moving plants from long to short-days appeared to be not effective in estimating the length of the juvenile period in soybeans. The modified technique of fitting quadratic curves of number of short-days to flower on number of long-days preceding short-days to estimate the juvenile length under the above method did not appear promising for soybean since soybean is not an obligate short-day plant. The method of moving plants from short to long-days was adapted by moving plants as early as two days after emergence to estimate the lengths of both juvenile and inductive phases. The method appeared promising in estimating the length of the juvenile period in soybean when compared to the above methods.

## INTRODUCTION

Cool temperatures and long daylengths delay flowering while warm, short-days promote early flowering in soybean (Huxley and Summerfield, 1974; Board and Hall, 1985). When soybeans are planted late in the season, shortening days and warm temperatures promote early flowering which results in restricted vegetative development (Borst and Thatcher, 1931; Hartwig, 1954; Osler and Cartter, 1954; Abel, 1961). Hartwig and Kiihl (1979) reported that premature flowering in response to nonoptimal planting dates was a major factor in soybean yield losses. A promising way to overcome the consequences of premature flowering is to utilize photoperiod sensitive genotypes characterized by a long vegetative period (Board and Hall, 1985; Kiihl and Garcia, 1989). Shanmugasunderam and Tsou (1978) subdivided the period from emergence to first flowering of soybean into three successive component phases: a juvenile phase when plants are insensitive to photoperiod, a critical inductive phase when plants are sensitive to photoperiod, and a final phase when plants are again insensitive to photoperiod. Huxley et al. (1974) suggested that soybeans have an additional regulatory phase, in between the inductive and final photoperiod insensitive phases, when the number of flowers increases if inductive conditions continue. Howell (1960) found that floral primordia become microscopically visible after three inductive cycles, but require an additional 10 days to be conspicuous. Development of floral primordia was hastened as the number of short photoperiods after floral initiation was increased (Borthwick and Parker, 1938).

The increased length of one or any combination of the component vegetative phases may result in a comparatively longer vegetative period and thus later flowering. Study of the length of the vegetative period as it is divided into component phases may be more informative than studying it as a single trait. This would be particularly useful in genetic studies on the delayed flowering trait under short-day conditions. The objective of this study was to estimate the lengths of the component phases of the vegetative period of some selected delayed and early flowering genotypes of soybeans using different methods.

## MATERIALS AND METHODS

Two greenhouse experiments were conducted at Blacksburg, Virginia. The lines and standard cultivars (genotypes) used in these experiments are presented in Table 9. Treatments included continuous long-days (LD), continuous short-days (SD), moving plants initially grown under SD to LD, and vice versa. Moving plants from LD to SD (LD-SD) can detect the length of the juvenile phase, while moving plants from SD to LD (SD-LD) can detect the time of the completion of induction (Shanmugasundaram and Tsou, 1978).

Soybean genotypes were planted in 10 cm plastic pots containing a medium of soil, peat, and sand in approximately equal proportions. Six to eight seeds of each genotype were planted per pot, the number of pots depended on the number of replicates and the number of photoperiod transfers per genotype. One pot per replication was always used. About five days after emergence, seedlings were thinned to three plants per pot.

### *First experiment*

Three replications were planted in a randomized complete block design on 18 June, 1989. Based on previous information on delayed flowering and photoperiod-sensitivity, 'Essex', V82-571, F85-8417, F85-8416, F85-1226, and F85-1221 were chosen for this experiment to represent different types of reactions. F85-8417 and F85-1226 have the delayed flowering trait and are isolines of the earlier flowering F85-8416 and F85-1221, respectively. V82-571 was selected for being relatively insensitive to photoperiod and Essex is a normal flowering cultivar. Three pots of each genotype were initially kept under SD and subsequently moved to LD at 8, 12, 16, 20, 24, 28, 32, 36, and 40 d after emergence. Similarly, three pots were initially kept under LD and subsequently moved

to SD at 4, 8, 12, 16, 20, and 24 d after emergence. Three pots of each genotype also remained under SD and LD until flowering.

A 9 h photoperiod was simulated by covering pots on a bench with a 100% light exclusion black cotton cloth from 5 pm to 8 am every day until the last plant finished flowering. A 16 h photoperiod was simulated with incandescent and fluorescent lighting prior to dawn and after dusk since natural daylength was less than 16 h. Greenhouse temperatures were about 28 C and 23 C during the day and night, respectively.

Dates of first and last flowering were recorded for each plant in all the treatments. The number of nodes at flowering, total number of flowers, and the number of nodes bearing pods per plant were recorded only in the treatments where plants were moved from SD to LD. Average date of emergence was recorded and days from emergence to first flowering was calculated for each plant. Duration of flowering (days from first flowering to the end of flowering) for each plant under the SD-LD treatment was also calculated.

### *Second experiment*

This experiment was planted on 12 July, 1990 using a completely randomized design with two replications. The same genotypes were used as in experiment 1, except for V81-571, due to its response similarity to Essex. Two pots of each genotype initially kept under SD were moved to LD at 2, 4, 6, 8, 12, 16, 20, and 24 d after emergence. Two pots of each genotype remained under both SD and LD until flowering.

The SD and LD greenhouse environments were established as described in the first experiment. Greenhouse temperatures were about 32 C and 27 C during the day and night, respectively. The time lapse from seedling emergence to first flowering was recorded for each plant.

### *Data analysis*

The method adapted by Shanmugasundaram and Tsou (1978), hereafter referred to as method 1, was used to estimate the successive lengths of juvenile and photoperiod sensitive, or inductive, phases. Plants moved from non-inductive LD to inductive SD at any time during the juvenile period would all be expected to bloom at the same time, but plants moved after they had become sensitive to photoperiod would show delays in flowering corresponding to the number of LD after their juvenile period had ended. Whether flowering is delayed or not is determined by the use of normal analysis of variance. The end of the inductive period is determined by successively moving plants from inductive SD to non-inductive LD. Days to flower will decrease with increased exposure to SD until induction is complete and should plateau after that point. Whether days to flower decreases or plateaus is determined by a normal analysis of variance. Length of the inductive period can be estimated by subtracting the length of the juvenile phase from the length of the period taken for completion of induction.

The quadratic method, hereafter referred to as method 2, adapted by Lyons and Booze-Daniels (1986) was modified and used to estimate the length of the juvenile phase for comparative purposes. The use of leaf number as the independent variable in the original method was replaced by the number of LD preceding SD in the modified method. In this method, blooming data obtained from plants moved from LD to SD was used. The number of short days to flower is calculated by subtracting the number of LD from the number of days from emergence to first flowering. Then a quadratic regression is calculated using the number of short days to first flowering as the dependent variable and the number of LD preceding the transfer to SD as the independent variable. If the quadratic relationship is significant, the length of the juvenile phase is estimated by calculating the parabolic vertex, i.e. the prior exposure to LD corresponding to the least number of SD to first flower.



The data from each entry under the LD-SD treatments were analyzed separately by both methods. Each entry under the SD-LD treatment was analyzed separately to estimate the time of the completion of photoperiod induction by method 1. Correlation coefficients between days to flowering and duration of flowering from the 0 to 16 and 0 to 24 SD-LD treatments for short and long juveniles, respectively were estimated in the first experiment. Pot averages were used in all the analyses.

## RESULTS AND DISCUSSION

### *LD-SD treatments*

The number of days from emergence to flowering for each LD-SD treatment for each genotype in experiment 1 is presented in Table 10; anthesis occurred in all plants.

The 4-day treatment for all genotypes exhibited delayed flowering when compared to continuous SD. This indicates, based on method 1, that the length of the juvenile period was between 0 and 4 days for all the genotypes. Thus, no differences in the length of the juvenile phase were observed. However, F85-1226 and F85-8417 should to be long juveniles (personal communication, K. Hinson) and flower comparatively late under continuous short-days than the other genotypes (Table 10).

Method 2 examines a quadratic relationship between the number of non-inductive LD preceding inductive SD and the number of SD to flower. As prior exposure to LD increases, the number of subsequent SD to flower should decrease first, then inverse after the juvenile period is passed due to aging. If the quadratic relationship exists, then the number of LD that corresponds to the minimum number of short-days for first flowering is the length of the juvenile period. This method has not been applied to a quantitative photoperiodic plant like soybean.

Application of method 2 to soybeans is shown by taking delayed flowering F85-8417 and Essex as examples. Although, F85-8417 had the shape of the quadratic curve as expected with significant linear and quadratic terms (Fig. 2), its length of the juvenile period was estimated to be 23 days. This is an unrealistic value since F85-8417 took only 32 days to flower under continuous short-days. The curve for Essex (Fig. 3) had significant linear and quadratic terms but with the reverse shape of the expected curve. The delayed flowering line, F85-1226, behaved similar to F85-8417. Furthermore, all the other genotypes had significant reverse quadratic fits over the expected indicating the inapplicability of method 2 to soybean. This may be mainly attributed to the fact that the method has the basic assumption that long-days have no effect on flower induction, but that does not appear to be the case in soybeans (Guthrie, 1972).

### ***SD-LD treatments***

This treatment was used to estimate the length of the inductive phase. The number of days from emergence to flowering and the flowering duration for each genotype in each SD-LD treatment are presented in Tables 11 and 12, respectively. All plants of Essex, F85-1221, and F85-8416 that were moved to LD from 16 to 40 days after emergence flowered at the same time and in fewer days than the 12 day treatment. This indicates that the induction of these genotypes was complete between 12 and 16 days after emergence under relatively high temperatures during summer. Similarly, the induction of V82-571 was complete between 8 and 12 days after emergence. F85-1226 exhibited progressively fewer days to flower from the 0 to 24 day treatment, indicating that its induction was completed between 20 and 24 days after emergence. Similarly, the induction of F85-8417 was complete between 16 and 20 days.

Interestingly, F85-1226 and F85-8417 flowered at the same time under continuous LD as when moved from SD to LD after eight days from emergence indicating that exposure to short-days during the eight days of early growth had no effect on flowering. Thus the length of the juvenile

phase for both lines appeared to be between 8 and 12 days under the conditions of this experiment. Both F85-1226 and F85-8417 are long juveniles (personal communication, K. Hinson) and both possess the delayed flowering trait under short-day conditions. They were clearly different from their isolines in days to flowering in all treatments except continuous LD. However, the fact that the maximum reduction in days to flower of these two lines occurred during the 4-day period immediately following the end of the juvenile period indicates that maximum induction in soybeans takes place during the first few days of the inductive period. This procedure could be used to accurately estimate the juvenile and inductive periods if treatment intervals are closely spaced.

The duration of flowering varied among photoperiod treatments within each genotype (Table 12). Flowering duration under continuous LD appears to be the same as that under 40 (continuous) SD for Essex and V82-571. However, flowering duration under continuous LD appears to be significantly longer compared to continuous SD for the other four genotypes. All of the genotypes showed some extension of the flowering period for several transfer treatments before they had attained minimum days to flowering. The maximum flowering duration coincided fairly closely with the point at which minimum days to flowering was reached.

Soybean appears to drastically extend the duration of flowering if moved to LD after a few days of induction by SD. In F85-8417 and F85-1226, exposure to eight SD after emergence did not extend the duration of flowering longer than that of under continuous LD. This indicates that these genotypes were insensitive to photoperiod during the first eight days after emergence. However, if these genotypes were moved from SD to LD 12 days after emergence, they flowered longer, indicating that photosensitivity had commenced. Thus, the flowering duration data provide a similar estimate of the juvenile period as did the days to flower data. The correlation coefficients between days to flowering and duration of flowering using 0 to 16 SD-LD treatments for Essex, V82-571, F85-1221, F85-8416, and 0 to 24 SD-LD treatments for F85-1226 and F85-8417 were -0.87, -0.85, -0.86, -0.95, -0.94, and -0.83, respectively. These correlation coefficients were highly significant ( $P < 0.01$ ) and indicate that duration of flowering increases as the number of days to flower decreases

before the complete floral induction has occurred in soybeans. Only the 0 to 16 and 0 to 24 SD-LD treatments for short and long juveniles, respectively, were used in these correlation studies because neither days to flowering nor the duration of flowering were variable after the completion of induction and early and late flowering genotypes had just completed induction at 16 and 24 days after emergence, respectively.

Number of nodes at flowering, total number of flowers, and the number of nodes bearing pods per plant at each SD-LD treatment for each genotype are presented in Tables 13, 14, and 15 respectively.

The number of nodes and the total number of flowers of genotypes exposed to SD-LD treatments showed a trend similar to that of duration of flowering, but the ends of the juvenile and inductive periods were not clearly defined.

The response of the number of nodes bearing pods to SD-LD treatments did not show any appreciable variation among any of the treatments or genotypes. There seemed to be little relationship to total number of nodes or number of flowers.

In the greenhouse experiment conducted during summer 1990 (Table 16) moving plants from SD to LD started two days after emergence so that juvenile lengths as short as two days could be detected. In F85-1226 and F85-8417, the plants under continuous LD and the plants moved to LD up to six days post emergence flowered at the same time. However, the plants moved eight days after emergence had drastically reduced days to flowering. This indicates that the juvenile lengths of these genotypes were between six and eight days under the prevailing temperature conditions (32 C ). Similarly, the lengths of juvenile phases of Essex, F85-1221, and F85-8416 were estimated to be between two and four days.

The lengths of the juvenile and juvenile plus inductive periods for each genotype, as determined during summer 1989 and 1990, are presented in Table 17. Lack of agreement in the lengths of the periods in different tests within a genotype may be attributed to the temperature effects. Temperatures are known to affect the juvenile length in soybean (Borthwick and Parker, 1938; Shibles et

al., 1975). Temperatures during the 1990 experiment were higher than in 1989 and that is reflected in the consistently shorter periods.

Since the lengths of the juvenile periods could be determined only within a range of several days, accurate estimates of the lengths of the inductive periods cannot be made. However, it can be seen that the difference in length of the juvenile period between the long juvenile lines (F85-8417 and F85-1226) and their isolines is very consistent. In contrast, time from emergence to completion of induction appears to differ more between F85-1226 and its isoline than between F85-8417 and its isoline. Thus it appears that F85-1226 has a longer inductive period than the other long juvenile line, F85-8417.

The method of moving plants from SD to LD at regular intervals has the ability to clearly distinguish between the juvenile and inductive periods. It can also provide accurate estimates for the duration, in days, of each period if plants are moved at daily intervals during the transition between periods. This method assumes that the SD induction is not reversed by LD. This assumption is reasonable for quantitative short-day plants for which long-days are not completely non-inductive. The method involves only moving plants from SD to LD in estimating the length of both juvenile and inductive periods, thus saving time, space, and resources over the method 1 which involves moving plants from SD to LD in estimating inductive length and moving plants from LD to SD to estimate the juvenile length. The proposed method can also make use of the responses of duration of flowering and the number of nodes to SD-LD treatment in addition to the time of flowering in estimating the juvenile length.

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Table 9. Description of genotypes used in the experiment and the source of origin.

Genotype	Description	Source of origin
Essex	Commercial cultivar	
V82-571	Low sensitivity to photoperiod	G. R. Buss
F85-1221	Early flowering under short days	K. Hinson
F85-1226	Delayed flowering isoline of F85-1221	K. Hinson
F85-8416	Early flowering under short days	K. Hinson
F85-8417	Delayed flowering isoline of F85-8416	K. Hinson



Table 10. Number of days from emergence to flower for six genotypes when moved from long-days (LD) to short-days (SD) at six moving treatments in summer 1989.

Genotypes	Number of LD preceding SD						
	0	4	8	12	16	20	24
				d			
Essex	22 gB*	29 f <sup>25</sup>	33 e <sup>25</sup>	36 d <sup>24</sup>	40 c <sup>25</sup>	44 b <sup>24</sup>	47 a <sup>23</sup>
V82-571	24 gB	29 f <sup>25</sup>	33 e <sup>25</sup>	35 d <sup>25</sup>	39 c <sup>23</sup>	43 b <sup>23</sup>	45 a <sup>21</sup>
F85-1221	24 gB	30 f <sup>26</sup>	35 e <sup>27</sup>	37 d <sup>23</sup>	41 c <sup>25</sup>	44 b <sup>25</sup>	48 a <sup>21</sup>
F85-1226	33 gA	35 f <sup>31</sup>	37 e <sup>29</sup>	39 d <sup>27</sup>	43 c <sup>27</sup>	47 b <sup>27</sup>	51 a <sup>27</sup>
F85-8416	24 gB	29 f <sup>25</sup>	34 e <sup>26</sup>	36 d <sup>24</sup>	40 c <sup>24</sup>	44 b <sup>24</sup>	47 a <sup>23</sup>
F85-8417	32 gA	34 f <sup>25</sup>	35 e <sup>26</sup>	38 d <sup>24</sup>	42 c <sup>24</sup>	46 b <sup>24</sup>	48 a <sup>23</sup>
		30 <sup>20</sup>	32 <sup>27</sup>	33 <sup>22</sup>	36 <sup>26</sup>	38 <sup>26</sup>	40 <sup>24</sup>

\* Means within rows followed by the same lowercase letters and means within the first column followed by the same uppercase letters do not differ at the 0.05 level based on DNMR test.

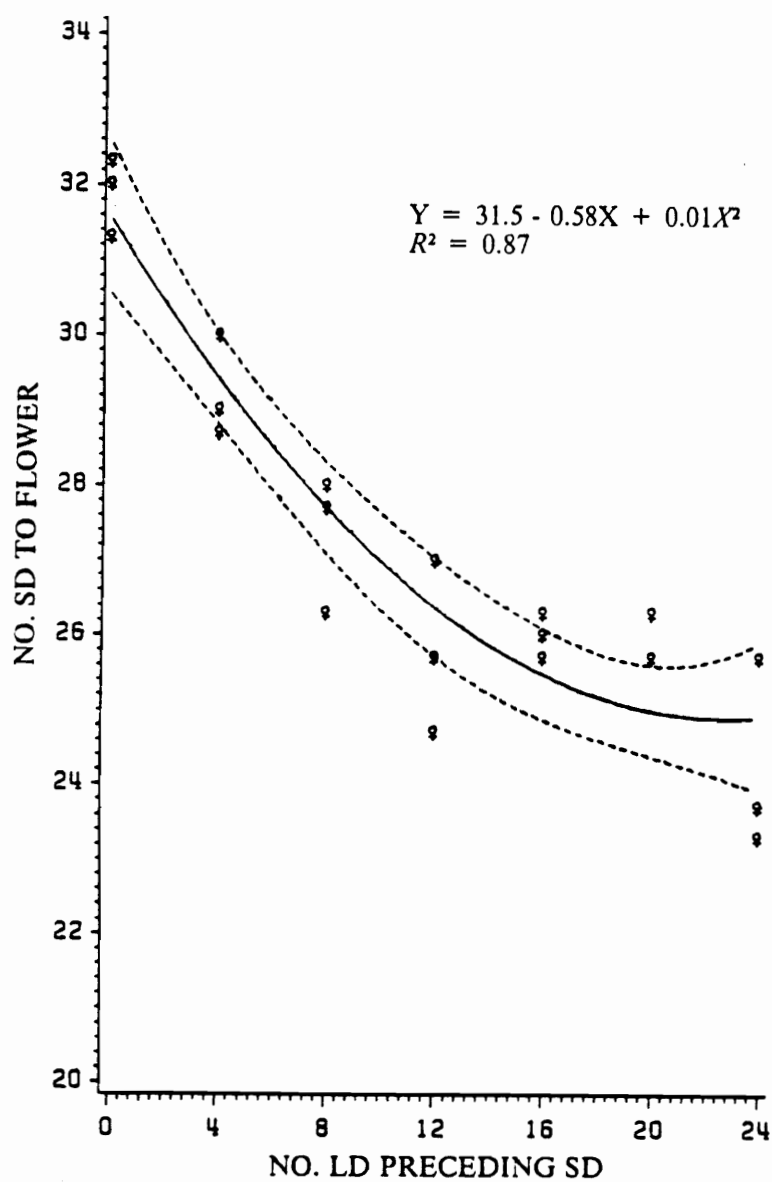


Fig. 2. The quadratic relationship of number of short-days (SD) to flower on number of long-days (LD) preceding short-days for F85-8417 in summer 1989. Dashed lines indicates confidence limits at  $P = 0.05$ .

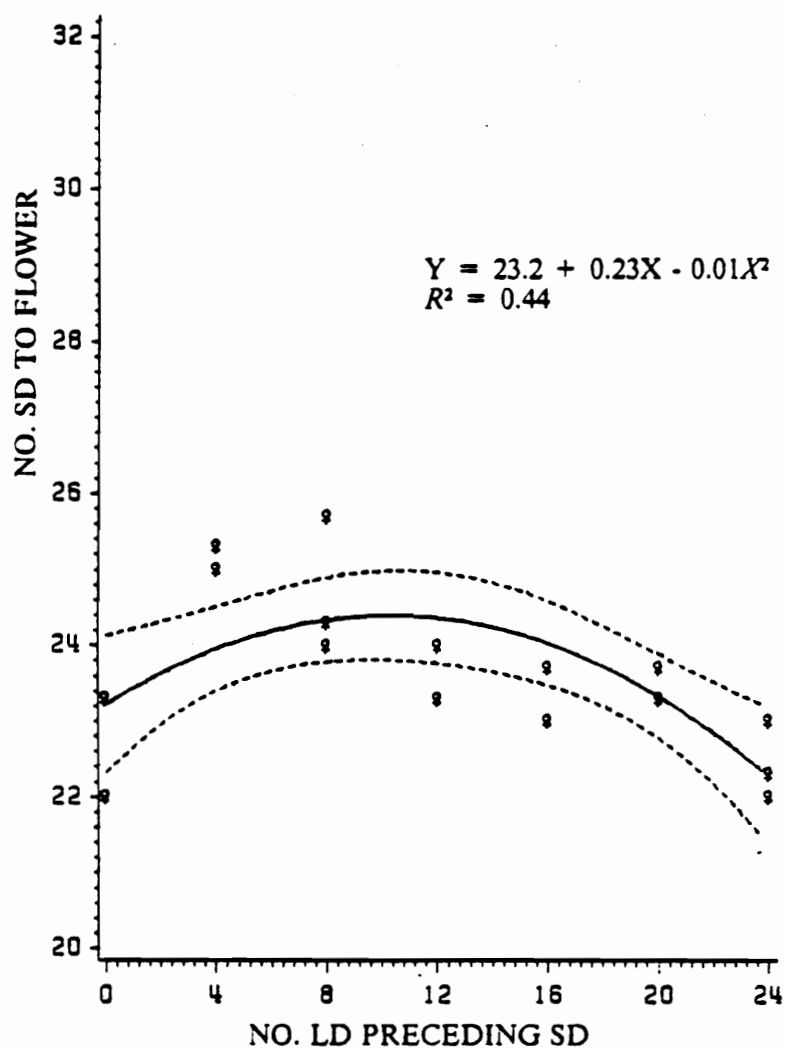


Fig. 3. The quadratic relationship of number of short-days (SD) to flower on number of long-days (LD) preceding short-days for Essex in summer 1989. Dashed lines indicate confidence limits at  $P = 0.05$ .

Table 11. Number of days from emergence to flower for six genotypes when moved from short-days (SD) to long-days (LD) at 10 moving treatments in summer 1989.

Genotype	Number of SD preceding LD									
	0	8	12	16	20	24	28	32	36	40
	----- d -----									
Essex	78a*	27b	25b	22c	22c	22c	22c	22c	22c	22c
V82-571	55a	26b	24c	24c	22c	24c	24c	23c	24c	23c
F85-1221	83a	56b	28c	24d	25d	24d	24d	24d	24d	24d
F85-1226	89a	88a	62b	58b	44c	33d	35d	35d	33d	33d
F85-8416	89a	36b	27c	25d	24d	24d	24d	24d	24d	24d
F85-8417	83a	83a	58b	56b	33c	32c	32c	32c	32c	31c

\* Means within rows followed by the same letters do not differ at the 0.05 level based on DNMR test.

Table 12. The duration of flowering for six genotypes when moved from short-days (SD) to long-days (LD) at 10 moving treatments in summer 1989.

Genotype	Number of SD preceding LD									
	0	8	12	16	20	24	28	32	36	40
	----- days from first to last flower -----									
Essex	7d*	31a	25b	23c	14c	9d	9d	9d	9d	9d
V82-571	9c	22a	18b	19ab	9c	8c	8c	8c	7c	9c
F85-1221	15c	23b	33a	27b	24b	14c	9d	8d	9d	8d
F85-1226	14b	13b	28a	27a	31a	31a	28a	28a	10bc	9c
F85-8416	15d	37a	37a	35b	27c	14d	9e	8e	9e	9e
F85-8417	18b	15bc	23a	25a	28a	26a	27a	14bc	8c	7c

\* Means within rows followed by the same letters do not differ at the 0.05 level based on DNMR test.

Table 13. Number of nodes at flowering for six genotypes when moved from short-days (SD) to long-days (LD) at six moving treatments in summer 1989.

Genotypes	Number of SD preceding LD					
	0	8	12	16	20	24
	----- number of nodes -----					
Essex	13a	4b	4b	4b	4b	4b
V82-571	10a	5b	5b	5b	5b	4b
F85-1221	14a*	7b	5c	4c	4c	4c
F85-1226	14a	14a	9b	9b	7c	6c
F85-8416	15a	6b	4c	4c	4c	4c
F85-8417	14a	14a	9b	8b	6c	6c

\* Means within rows followed by the same letters do not differ at the 0.05 level based on DNMR test.

Table 14. Total number of flowers for six genotypes when moved from short-days (SD) to long-days (LD) at six moving treatments in summer 1989.

Genotypes	Number of SD preceding LD					
	0	8	12	16	20	24
	----- number of flowers -----					
Essex	95a	52b	44b	37bc	34bc	17c
V82-571	154a	51b	42c	35c	17d	13d
F85-1221	269a*	110bc	83bc	58cd	50cd	40d
F85-1226	273a	186ab	172bc	134bc	120bc	82bc
F85-8416	144a	97b	88b	63b	52b	48b
F85-8417	166a	122ab	99ab	96ab	86ab	67b

\* Means within rows followed by the same letters do not differ at the 0.05 level based on DNMR test.

Table 15. Number of nodes bearing pods at maturity for six genotypes when moved from short-days (SD) to long-days (LD) at six moving treatments in summer 1989.

Genotypes	Number of SD preceding LD					
	0	8	12	16	20	24
	----- number of nodes bearing pods -----					
Essex	7a	5b	5b	4b	4b	4b
V82-571	7a	6b	6b	5c	5c	4d
F85-1221	7a*	5b	5b	5b	5b	5b
F85-1226	8a	8a	8a	7a	6a	6a
F85-8416	6a	5abc	5abc	5abc	5abc	4c
F85-8417	7a	6a	6a	5a	5a	5a

\* Means within rows followed by the same letters do not differ at the 0.05 level based on DNMR test.



Table 16. Number of days from emergence to flower for five genotypes when moved from short-days (SD) to long-days (LD) at 10 moving treatments in summer 1990.

Genotype	Number of SD preceding LD									
	0	2	4	6	8	12	16	20	24	CS†
	----- d -----									
Essex	67a*	69a	29bc	30b	28bc	22cd	20d	20d	20d	20d
F85-1221	78a	79a	35b	34b	26c	22d	22d	22d	22d	22d
F85-1226	97a	97a	96a	94a	55b	52b	52b	38c	32d	33d
F85-8416	69a	67a	35b	34b	27c	22d	22d	21d	21d	22d
F85-8417	83a	82a	83a	84a	39b	35b	29c	26c	27c	28c

\* Means within rows followed by the same letters do not differ at the 0.05 level based on DNMR test.

† Continuous short-days.

Table 17. Estimated lengths of the juvenile and juvenile plus inductive periods for six genotypes in summer 1989 and 1990.

Genotype	Juvenile length		Juvenile + inductive length	
	1989	1990	1989	1990
	----- Length (d) -----			
Essex	0-8	2-4	12-16	8-12
V82-571	0-8	-†	8-12	-
F85-1221	0-8	2-4	12-16	8-12
F85-1226	8-12	6-8	20-24	20-24
F85-8416	0-8	2-4	12-16	8-12
F85-8417	8-12	6-8	16-20	12-16

† Indicates V82-571 was not included in summer 1990.

# **CHAPTER IV**

## **INHERITANCE OF DELAYED FLOWERING IN SOYBEANS**

## ABSTRACT

The delayed flowering trait might have potential to overcome the restricted vegetative growth, prior to flowering, that is associated with double-cropped soybeans [*Glycine max* (L) Merr.]. Knowledge of the inheritance of delayed flowering would be useful for incorporating the trait into commercial cultivars. However, the available reports on the genetic control of delayed flowering are not consistent. Thus a study was undertaken to determine the genetic control of the delayed flowering trait in soybeans under short-day conditions. Essex, isoline pair F85-8417 and F85-8416, and isoline pair F85-1226 and F85-1221, were used as the parents of the crosses used in the study. The delayed flowering of F85-8417 and F85-1226 is due to a long juvenile phase. PI 159925, a plant introduction from Peru, is the original source of the delayed flowering trait. F85-1226 also has a longer inductive phase than its earlier flowering isoline, F85-1221, or F85-8417. Essex, an adapted commercial cultivar, flowers at about the same time as F85-8416 and F85-1221 in greenhouse and field experiments.  $F_2$  populations and parents of delayed flowering X normal and normal X normal crosses were grown under two photoperiod treatments; continuous short-days and eight short-days followed by long-days until flowering. The latter treatment was designed to separate plants with long and short inductive periods within groups of long and short juvenile plants. Both methods were successful in distinguishing long juvenile plants from short juvenile ones, but there was no distinct segregation for long vs. short inductive periods. Delayed flowering appeared to be controlled by two loci each with two alleles and delayed flowering appeared to be recessive. Any one of the genes in the homozygous recessive state delayed flowering. F85-1226 may be segregating for both of these genes whereas F85-8417 appeared to contain only one.

## INTRODUCTION

Premature flowering is a major factor in yield losses when soybeans are planted late in the season, as in double-cropping. Utilization of soybean genotypes with a long vegetative period under short-day conditions has been suggested to overcome the problem of premature flowering at non-optimal planting dates (Board and Hall, 1985; Kiihl and Garcia, 1989).

The period from seedling emergence to first flowering can be divided into three successive component phases, viz. juvenile phase, which is insensitive to photoperiod, an inductive phase, which is sensitive to photoperiod, and the end phase, which is again insensitive to photoperiod (Huxley and Summerfield, 1974; Shanmugasundaram and Tsou, 1978). Cultivar differences exist for the length of the juvenile phase (Miyasaka et al., 1970; Hartwig and Kiihl, 1979; Board and Settimi, 1988; Kiihl and Garcia, 1989) and for the length of the inductive phase as well (Table 17, Chapter iii). Thus, a longer vegetative period, or delayed flowering, under short-days could result from either a longer juvenile period, a longer inductive period or, both.

Inheritance of delayed flowering has been studied as a single trait. Kiihl (1976) reported that the delayed flowering under short-day conditions in 'Santa Maria' is controlled by recessive genes, but he did not indicate the number of genes involved. Hartwig and Kiihl (1979) using Santa Maria and 'PI 159925' as the sources of delayed flowering concluded that the trait was controlled by as many as three recessive genes. Azlon (1981), using PI 159925 as the source, first suggested that delayed flowering under short-day conditions was controlled by a single recessive gene. However, he could not exclude the possibility of a second major gene since flowering date classes in the populations he studied often were not discrete. That the delayed flowering trait is controlled by a single recessive gene was also supported by the data obtained by Malo (1986) who found that most  $F_2$  progenies from a cross of early X late flowering produced a 3 early : 1 late flowering ratio using PI 159925 as the delayed flowering source. However, three of the 26 progenies appeared to segregate for more than one major gene. Hinson (1989), describing delayed flowering under short-day

conditions as 'long juvenility' and using PI 159925, concluded that the trait was controlled by one recessive gene. However, he also indicated that the inheritance of delayed flowering may be more complex, due to the presence of more than two classes of flowering and maturity dates in a few late generation segregating rows. Furthermore, he found that long juvenility was strongly influenced by the genetic background since the different genotypes with the same delayed flowering source showed different degrees of delay in flowering. Bidja Mankono (1988) reported that delayed flowering of PI 159925 was controlled by a single recessive gene and found evidence also for a dominant gene of unknown source that delays flowering. He studied his segregating  $F_2$  and advanced populations at three planting dates in June, July, and August in the field in Florida. Therefore, the possibility of the influence of 'E' genes which regulate maturity date and are strongly influenced by photoperiod (Bernard, 1971; Buzzell, 1971; Kilen and Hartwig, 1971; Buzzell and Voldeng, 1980) cannot be excluded.

The available information on the genetic control of delayed flowering is inconsistent so that there is a need for further studies on this subject. The objective of this study was to determine the genetic control of the delayed flowering trait in soybeans under short-day conditions.

## MATERIALS AND METHODS

The parents used in the study included 'Essex' a popular commercial cultivar and two pairs of isolines obtained from Dr. Kuell Hinson at the University of Florida, Gainesville. F85-1226 and F85-8417 are the delayed flowering isolines of F85-1221 and F85-8416, respectively. Both pairs of isolines were selected for delayed flowering in the field in the  $F_8$  generation of the cross [Kirby X (Forrest (3) X D77-12480)] X Will. D77-12480, which has the delayed flowering trait, is from the cross between Tracy and (Hill X PI 159925). PI 159,925, a plant introduction from Peru, is the original source of the delayed flowering trait.

All the parents were planted at four planting dates (6/2, 6/12, 6/20, and 6/27) in single rows of 3 m length and 90 cm apart during the summer 1989 to synchronize flowering of early and delayed flowering lines. All crosses were made in the field at Blacksburg, Virginia, from late July through late August, 1989.

Three  $F_1$  plants per cross were grown in 20 cm diameter pots in the greenhouse at Blacksburg during winter and spring, 1990. Pots were filled with a medium of soil, peat, and sand in approximately equal proportions. Three seeds per pot were planted and seedlings were thinned to one plant per pot. Plants resulting from self-pollination were distinguished from  $F_1$ 's by hypocotyl color in appropriate crosses before thinning and verified at flowering time. Essex has purple flowers and hypocotyls and each of the isolines has white flowers and green hypocotyls. Both of these traits are controlled by a single gene and the purple color is dominant. Genetic markers were not available to distinguish hybrids from self-pollinations for the crosses between isolines.  $F_2$  segregation for flowering behavior or lack of it was the only marker for these crosses. In the crosses involving Essex, it was used as the male parent. In the crosses between isolines the delayed flowering parent was used as the female.

The hybrids and three plants of each parent were grown under 15 h photoperiod using supplemental lighting to extend the natural daylength for maximum seed production.

All the  $F_2$  populations were grown in 15 cm diameter pots in the greenhouse during summer 1990. Initially 6-8 seeds were planted in each pot and thinned to four seedlings seven days after emergence.

$F_2$  populations were grown under two photoperiod treatments; continuous short-days (treatment 1) and eight short-days preceding 16 h long days (treatment 2). In all the crosses that involved F85-1221 and F85-1226, about 20 plants from each of three  $F_1$  plants were grown in each treatment. About 12 plants from each of three  $F_1$ 's of the crosses that involved F85-8416 and F85-8417 were grown per treatment. Both photoperiod treatments were intended to distinguish delayed flowering plants from normal flowering plants. In treatment 1, the delayed flowering plants would be expected to flower only a few days later than normal ones (the difference between long juvenile and normal juvenile periods). Treatment 2 was designed with the expectation that eight short-days would induce plants with a short, or normal, juvenile period but would not induce long juveniles, thus greatly expanding the difference in flowering dates of the two types. It was also anticipated that treatment 2 might separate plants with long vs. short inductive periods within the long juvenile and short juvenile classes, providing length of inductive period is inherited qualitatively. Eight to 12 plants of each parent were grown under both treatments to serve as checks for classifying  $F_2$  plants.

For the short-day treatment, pots were kept under tall benches and were covered with light-excluding black cloths at 7 pm and uncovered at 9:30 am (9 <sup>long short</sup> 1/2 h photoperiod) until all the plants bloomed. Long-day treatment of 16 h photoperiod was simulated by extending natural daylength with artificial lighting. The maximum daytime temperatures in the greenhouse were about 32 C and night temperatures were about 5-7 C lower.

Dates of planting and emergence were recorded. Plants were inspected every day and flowering dates were recorded. Days from emergence to first flowering was calculated for each plant.  $F_1$  families of the same cross were tested for homogeneity (Little and Hills, 1978) and pooled if no significant differences at the 0.05 level were observed. Chi-square analyses (Little and Hills, 1978) were performed on  $F_2$  data to test goodness-of-fit to expected segregation ratios.



## RESULTS AND DISCUSSION

The mean and range of days to flower for  $P_1$ ,  $P_2$ , and  $F_1$  for all the crosses are presented in Table 18. The mean days to flower for all  $F_1$  plants, except one plant from the cross of F85-8416 X Essex exceeded the midparent value. All  $F_1$  plants of F85-1221 X Essex and F85-8417 X Essex exceeded the highest parent. This observation might lead to the conclusion that long juvenility is dominant which is not in agreement with Azlon (1981), Malo (1986), and Hinson (1989). However, these plants were grown under relatively long-days, in which the long juvenile trait is not expressed. It appears that the later flowering of most  $F_1$ 's is simply an expression of hybrid vigor or the effect of dominant late maturity genes at different loci in the parents acting in an additive fashion.

### Crosses involving F85-8417 and F85-8416 isoline pair

In the cross between F85-8417 and F85-8416, two out of three  $F_1$  plants were identified as self-pollinated since all  $F_2$  plants bloomed with the late parent (F85-8417); no segregation of flowering date classes was observed. The single hybrid plant did not produce enough  $F_2$  plants for an adequate sample.

The frequency distributions of days to flower of the parental and  $F_2$  plants of the cross between F85-8416 and Essex under photoperiod treatments 1 and 2 are presented in Tables 19 and 20, respectively. The  $F_2$  distribution of this cross had no discrete classes for flowering date under either treatment, as expected, since both F85-8416 and Essex are similar in the length of the juvenile phase. These results suggest that both F85-8416 and Essex contain the same gene for early flowering under short-days and are homozygous for the gene.

Frequency distributions of days to flower of the parental genotypes and the  $F_2$  progenies derived from the cross between F85-8417 and Essex under treatments 1 and 2 are presented in Tables 21 and 22, respectively. Both photoperiod treatments appeared to provide a good separation of long vs. normal juvenile plants as evidenced by the lack of overlap between the parents and the lack of very few intermediate plants. No segregation into sub-classes for long vs. short inductive periods

was evident under treatment 2, indicating that length of the inductive period probably is not simply inherited. Much of the variation in flowering date, especially within the delayed flowering checks, appeared to be due to a lack of uniformity in age or stage of development. A previous experiment (Tables 11 and 17, chapter iii) had estimated the juvenile length of F85-8417 at eight to twelve days. Thus, moving plants from short-days to long-days at eight days after emergence should have prevented long juveniles from being exposed to any short-days. However, a similar experiment run concurrently with this study estimated the juvenile period of F85-8417 to be six to eight days (Table 16, chapter iii). Apparently high temperatures caused the shortening of the juvenile period and most of the long juvenile plants were exposed to about two short-days, which is enough to greatly reduce the days to flower compared to what would be expected under continuous long-days. However, a few of the long juvenile plants, including some F85-8417 plants, were extremely delayed in flowering. Presumably, these plants were just a day or two later in their development and had not completed their juvenile period prior to being moved to long-days. Nevertheless, both treatments appeared to separate the long and short juveniles well, so the data were combined (Table 23).

All the  $F_2$  distributions had more plants in the early class than in the late one. Each  $F_2$  under each treatment and the pooled data provided a good fit to a 3 early : to 1 late ratio and the segregation of the families within and between treatments were homogeneous (Table 23). These results suggest that delayed flowering is controlled by one locus with two alleles with long juvenility being recessive. This is in basic agreement with Malo (1986), Bidja Mankono (1988), and Hinson (1989) who also reported that long juvenility is controlled by one recessive gene.

#### **Crosses involving F85-1226 and F85-1221 isoline pair**

The frequency distributions of parental and  $F_2$  plants of the cross between F85-1221 and Essex under treatment 1 and 2 are presented in Tables 24 and 25, respectively. Of three  $F_1$  families, only one flowered concurrently with the parent plants under both treatments as would be expected if both parents are short juvenile types. The other two families segregated into two discrete flowering

date classes, one class flowering with the parents and the other flowering later than both parents. It appears that F85-1221 was either segregating for the delayed flowering trait or contained mixtures in the rows used for crossing.

Chi-square analysis for each  $F_2$  distribution under each treatment showed that early and late types fit a 3:1 ratio only in the progeny of plant 3 (Table 26). The progeny of plant 2 did not fit a 3 early : 1 late ratio, but showed an acceptable fit to a 9 early : 7 late ratio which would be consistent for segregation of two recessive genes that control delayed flowering independently. It does not seem likely that the segregation is caused by the presence of any of the maturity genes such as  $E_1$  or  $E_2$ , since the dominant allele of each controls lateness, and these would produce a much larger proportion of late plants. It is possible that the original single plant from which F85-1221 was derived, was heterozygous for both loci and thus was selected as being early.

The frequency distribution of parental and  $F_2$  plants of the cross between F85-1226 and Essex under treatments 1 and 2 are presented in Tables 27 and 28, respectively. In each of the  $F_1$  families under both treatments, two discrete flowering date classes were evident. Two plants in one family under treatment 1 were somewhat intermediate, but they appeared to fit best with the early class. Two progenies under treatment 1 had more plants in the early class than in the late one. Segregation of these progenies fits a 3 early : 1 late ratio under both treatments (Table 29). Progenies were pooled after a homogeneity test indicated no significant difference at the 0.05 level. Pooled data had a strong fit to a 3 early : 1 late ratio. This suggests that delayed flowering in these two progenies of F85-1226 under short-days is controlled by one recessive gene. The remaining family had similar numbers of plants in the early and late flowering classes under treatment 1 and were tested against 9 early : 7 late and 3 early : 1 late ratios. The good fit to the 9 : 7 ratio indicates that delayed flowering under short-days is controlled by two recessive genes. The segregation pattern of the progeny under treatment 2 was an equally acceptable fit to the 3 early : 1 late or 9 early : 7 late ratios. The pooled data of the progeny over two treatments showed a good fit to the 9 early : 7 late ratio, but a poor fit to the 3 early : 1 late ratio.

The frequency distribution of parental and  $F_2$  plants of the cross between F85-1226 and F85-1221 under treatment 1 and 2 are presented in Tables 30 and 31, respectively. Both  $F_1$  families segregated for more than one flowering date class indicating that they were the progenies of hybrids. In these progenies, two flowering date classes were evident under both treatments. Chi-square analyses over progenies and over treatments showed that the early and late flowering classes were homogeneous and agreed with the 3:1 ratio (Table 32).

### *General discussion*

It appears clear that the isoline parents are not genetically pure since two different ratios, 9 : 7 and 3 : 1, were observed. It seems unlikely that the isolines of a pair would differ by other maturity genes since they were selected in a late generation. It would seem more logical that the original source, PI 159925, had two similar genes for long juvenility and they were distributed among the isolines.

The data suggest that delayed flowering is controlled by two loci with two alleles each. Delayed flowering is recessive and is expressed if either of the loci are homozygous recessive. This is mostly in agreement with Kiihl (1976) and Hartwig and Kiihl (1979) who reported that the delayed flowering under short-days may be controlled by more than one recessive gene.

Both of the photoperiod treatments used in this study can be used in distinguishing between long and short juvenile plants, but exposure to continuous short-days would seem to be the easiest to use and thus preferable in most cases.

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Table 18. Parental and hybrid parameters of the crosses made.

Cross	Population	Days to flower	
		Mean	Range
F85-1226 X Essex	$P_1$	65	62 - 68
	$P_2$	60	58 - 61
	$F_1$	67	66 - 68
F85-1226 X F85-1221	$P_1$	65	62 - 68
	$P_2$	60	59 - 62
	$F_1$	66	64 - 68
F85-1221 X Essex	$P_1$	60	59 - 62
	$P_2$	60	58 - 61
	$F_1$	65	63 - 67
F85-8417 X Essex	$P_1$	63	59 - 64
	$P_2$	60	58 - 61
	$F_1$	79	76 - 81
F85-8417 X F85-8416	$P_1$	63	59 - 64
	$P_2$	58	55 - 60
	$F_1$	62†	
F85-8416 X Essex	$P_1$	58	55 - 60
	$P_2$	60	58 - 61
	$F_1$	60‡	60 - 60

†, ‡ Values are based on one and two  $F_1$  plants, respectively.

Table 19. Frequency distributions of days to flower for F85-8416 ( $P_1$ ), Essex ( $P_2$ ), and their  $F_1$  families under continuous short-days.

Days from emergence to 1st flowering	$P_1$	$P_2$	$F_1$ family	
			<i>pro. 21/10/60</i>	
			1	2
			----- no. -----	
18		1		
19			2	
20	2	1	2	3
21	6	6	7	6
22	3	2	1	
23		3	1	1
24		1	1	



Table 20. Frequency distributions of days to flower for F85-8416 ( $P_1$ ), Essex ( $P_2$ ), and their  $F_1$  families under eight short-days preceding long-days.

Days from			$F_1$ family	
emergence to	$P_1$	$P_2$		
1st flowering			1	2
	----- no. -----			
23	2	2	2	4
24	1	1	3	1
25	1	2	1	4
26			3	2
27			2	2
28	2	1	1	2
29	1		1	
30	2		1	
31		2		
32	1			
33		2		

Table 21. Frequency distributions of days to flower for F85-8417 ( $P_1$ ), Essex ( $P_2$ ), and their  $F_1$  families under continuous short-days.

Days from emergence to 1st flowering	$P_1$	$P_2$	$F_1$ family		
			1	2	3
			----- no. -----		
20		1			
21		6	3	3	4
22		2	5	7	3
23		3	1		1
24			2		1
25					
26					
27			1		
28	5		1		
29	1			2	1
30	1			1	1
31			1		
32	1			1	

Table 22. Frequency distributions of days to flower for F85-8417 ( $P_1$ ), Essex ( $P_2$ ), and their  $F_1$  families under eight short-days preceding long-days.

Days from emergence to 1st flowering	$P_1$	$P_2$	$F_1$ family		
			1	2	3
			----- no. -----		
23		2	2	1	1
24		1	1		1
25		2	7	3	
26				1	1
27				3	2
28		1	1	1	1
29				1	1
30			1		
31		2	1		
32					
33		2			1
34		2			
.					
38	2			1	
.					
42					1
43	2			2	1
44					
45				1	1
46				1	
47	1				
48	1				
.					
65			1		
.					
70	1				
71	2				
.					
79	1				
80					
81	1				
.					
88	1				1
89			1		

Table 23. Number of plants in early and late flowering classes for  $F_1$  families (fam.) of F85-8417 X Essex under continuous short-days (trt. 1) and eight short-days preceding long-days (trt. 2) and chi-square tests for fit to expected  $F_2$  ratios.

Trt.	Fam.	Flowering class		df	Chi-square 3 : 1	
		Early	Late		Value	P†
		----- no. -----				
1	1	11	3	1	0.095	0.95-0.90
	2	10	4	1	0.095	0.95-0.90
	3	9	2	1	0.272	0.90-0.50
2	1	13	2	1	1.089	0.50-0.10
	2	10	5	1	0.556	0.50-0.10
	3	8	4	1	0.444	0.90-0.50
Total				6	2.551	
Pooled		61	20	1	0.004	0.95-0.90
Homogeneity				5	2.547	0.90-0.50

† Probability.

Table 24. Frequency distributions of days to flower for F85-1221 ( $P_1$ ), Essex ( $P_2$ ), and their  $F_1$  families under continuous short-days.

Days from emergence to 1st flowering	$P_1$	$P_2$	$F_1$ family		
			1	2	3
			----- no -----		
20		1	3	3	1
21		6	8	2	2
22	3	2	8	5	6
23	6	3	2	1	5
24	1	1			1
25					1
26					
27				1	
28				5	
29				2	3
30				2	2
31				1	

Table 25. Frequency distributions of days to flower for F85-1221 ( $P_1$ ), Essex ( $P_2$ ), and their  $F_1$  families under eight short-days preceding long-days.

Days from emergence to 1st flowering	$P_1$	$P_2$	$F_1$ family		
			1	2	3
			no. -----		
23		2	6		2
24	1	1	4		2
25	2	2	3	1	4
26	1		4		1
27	1			2	2
28		1			3
29				1	7
30	2			2	1
31	3	2		1	1
32					
33		2		1	1
34	2	1		1	2
.					
38				3	
.					
43				1	
44				1	1
45					1
.					
49				1	
.					
55				1	
56				1	1
.					
75				1	
.					
80				1	
81				2	

Table 26. Number of plants in early and late flowering classes for  $F_1$  families (fam.) of F85-1221 X Essex under continuous short-days (trt. 1) and eight short-days preceding long-days (trt. 2) and chi-square tests for fit to expected  $F_2$  ratios.

Fam.	Trt.	Flowering class			Chi-square			
					3 : 1		9 : 7	
		Early	Late	df	Value	P†	Value	P
		---- no. ----						
2	1	11	11	1			0.349	0.90-0.50
	2	9	12	1			1.534	0.50-0.10
Total				<u>2</u>			<u>1.883</u>	<u></u>
Pooled		20	23	1			1.667	0.50-0.10
Homogeneity				1			0.216	0.90-0.50
3	1	16	5	1	0.016	0.95-0.90		
	2	26	3	1	3.320	0.10-0.05		
Total				<u>2</u>	<u>3.336</u>	<u></u>		
Pooled		42	8	1	2.160	0.50-0.10		
Homogeneity				1	1.176	0.50-0.10		

† Probability.

Table 27. Frequency distributions of days to flower for F85-1226 ( $P_1$ ), Essex ( $P_2$ ), and their  $F_1$  families under continuous short-days.

Days from emergence to 1st flowering	$P_1$	$P_2$	$F_1$ family		
			1	2	3
			----- no. -----		
20		1	1	1	2
21		6	5	3	2
22		2	10	8	6
23		3	1	3	2
24		1			
25				2	
26					
27			1		2
28				1	2
29	3		2	1	4
30	1			1	1
31	1				1
32	2			1	1
33	2				
34	2				



Table 28. Frequency distributions of days to flower for F85-1226 ( $P_1$ ), Essex ( $P_2$ ), and their  $F_1$  families under eight short-days preceding long-days.

Days from emergence to 1st flowering	$P_1$	$P_2$	$F_1$ family		
			1	2	3
			----- no. -----		
23		2	1		1
24		1	5	1	
25		2	3	1	4
26		1	1		
27			2	3	1
28		1		1	
29			1	1	1
30				1	2
31		2	1	1	1
32				2	
33		2			1
34		1		1	1
.					
38	1		1		
.					
43	1				
44	1			1	
45	1				
47	1				
47	1				
.					
59	3				
.					
68	2		1		
.					
75			2		1
76	1			1	1
.					
79	1				1
80				1	
81				2	
82	2				
83			1		
84			1	1	
85	1				1
.					
89	2				1
.					
95	2		1	1	
96	1		1		

Table 29. Number of plants in early and late flowering classes for  $F_1$  families (fam.) of F85-1226 X Essex under continuous short-days (trt. 1) and eight short-days preceding long-days (trt. 2) and chi-square tests for fit to expected  $F_2$  ratios.

Trt.	Fam.	Flowering class			Chi-square			
					3 : 1		9 : 7	
		Early	Late	df	Value	P†	Value	P
---- no. ----								
1	1	17	3	1	1.067	0.50-0.10		
	2	17	4	1	0.396	0.90-0.50		
2	1	14	8	1	1.514	0.50-0.10		
	2	13	7	1	1.067	0.50-0.10		
Total				4	4.038			
Pooled		61	22	1	0.100	0.90-0.50		
Homogeneity				3	3.938	0.50-0.10		
1	3	12	11	1	6.391	0.02-0.01	0.155	0.90-0.50
2	3	12	6	1	0.667	0.50-0.10	0.793	0.50-0.10
Total				2	7.058		0.948	
Pooled		24	17	1	5.927	0.02-0.01	0.087	0.90-0.50
Homogeneity				1	1.131	0.50-0.10	0.861	0.50-0.10

† Probability.

Table 30. Frequency distributions of days to flower for F85-1226 ( $P_1$ ), F85-1221 ( $P_2$ ), and their  $F_1$  families under continuous short-days.

Days from emergence to 1st flowering	$P_1$	$P_2$	$F_1$ family	
			1	2
			----- no. -----	
21		1	1	
22		3	7	7
23		6	1	3
24		1	3	
25				2
26				2
27				
28				
29	3			
30	1			
31	1			1
32	2			1
33	2		1	
34	2			1

Table 31. Frequency distributions of days to flower for F85-1226 ( $P_1$ ), F85-1221 ( $P_2$ ), and their  $F_1$  families under eight short-days preceding long-days.

Days from emergence to 1st flowering	P1	P2	$F_1$ family	
			1	2
			----- no. -----	
24		1		
25		2		
26		1		
27		1	1	
28			3	
29				1
30		2		
31		3	3	3
32			3	2
33				1
34		2	4	2
.				
38	1		1	
39				1
43	1			
44	1		1	
45	1			
46				
47				1
.				
51			1	
.				
59	3			
.				
68	2			
.				
75				
76	1		1	
.				
79	1			
.				
81				1
82	2			1
83				
84			1	
85	1			
.				
88				1
89	2		1	
.				
95	2			
96	1			

Table 32. Number of plants in early and late flowering classes for  $F_1$  families (fam.) of F85-1226 X F85-1221 under continuous short-days (trt. 1) and eight short-days preceding long-days and chi-square tests to fit to expected  $F_2$  ratios.

Trt.	Fam.	Flowering class			Chi-square			
				df	3 : 1		9 : 7	
		Early	Late		Value	P†	Value	P
		---- no. ----						
1	1	12	1	1	2.076	0.50-0.10		
	2	14	3	1	0.489	0.50-0.10		
2	1	14	6	1	0.266	0.90-0.50	1.536	0.50-0.10
	2	9	5	1	0.857	0.50-0.10	0.371	0.90-0.50
Total				4	3.688			
Pooled		49	15	1	0.083	0.90-0.50		
Homogeneity				3	3.605	0.50-0.10		

† Probability.

## VITA

Demuni Sumith De Z. Abeysiriwardena was born in Sri Lanka on January 4, 1951, the first child and first son of Mr. and Mrs. Demuni Milton de Z. Abeysiriwardena. He lived with his parents and continued his high school education until the age of 21 years. In 1972 he entered the Faculty of Agriculture, University of Peradeniya, Sri Lanka and graduated in April, 1976 with a B. S. degree in Agriculture. Following graduation, he joined the faculty of his alma mater as an assistant lecturer from April, 1976 to December, 1977. Subsequently, in January 1978, he moved to the Department of Agriculture, Sri Lanka as a research officer in plant breeding and worked on rice until February, 1982. He entered the Virginia Polytechnic Institute and State University in February 1982 and completed the requirements for M. S. degree in Agronomy in March, 1984. Then he returned to his previous position in the Department of Agriculture, Sri Lanka and continued work on rice breeding until November, 1987. He returned to the Virginia Polytechnic Institute and State University in December, 1987 and completed the requirements for a Ph. D. degree in Agronomy in December, 1990.

