

Planting Date Effect on After-Flowering Partition on Different Soybeans Maturity Groups and Stem-Termination

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Abstract: To predict effects of environment and genotype on soybean (*Glycine max* (L.) Merr.) yields under field conditions, a full understanding of photoperiod effects on growth and development throughout the soybean life cycle, especially after flowering, is needed. Two field experiments were conducted by using different planting dates to investigate effects of photoperiod on soybean growth during and after flowering for the 1992 and 1993 growing seasons. Growth stages of 10 soybean strains differing in maturity dates that included determinate and indeterminate genotypes were recorded throughout growing seasons. Results indicated that photoperiod affected all stages of soybean growth and development and in some genotypes, this included pod set and seed filling. Longer photoperiods induced more vegetative growth and delayed the maturing process. Later plantings (after mid-June) resulted in significantly fewer flowers, pods and seeds per plant and in significantly lower yields. The mechanism of photoperiod effects on soybean growth before and after flowering was similar in a quantitative way. This effect was realized through the alteration of the photosynthate partitioning processes between vegetative and reproductive growth. Due to accelerated reproductive processes under short photoperiods and high temperatures, the accumulation of dry matter slowed down or even reversed during the late reproductive stages for early maturing strains or other strains planted late. The vegetative status of and late MGs (IV₊ or later) at R1 stage was strongly correlated with final yields in both determinate and indeterminate strains. Information gathered from this study will prove valuable in building a better simulation model for soybean production.

Key words: Soybean, flowering, maturity groups, photoperiod, phenology, stem-termination

INTRODUCTION

The processes of soybean growth and development are controlled by genetic natures and environmental factors, such as temperature, photoperiod, water, soil and their interactions. Plant breeders and agronomists have tried to select for optimum combination of these factors to maximize sustainable yields using field plot techniques. However, fluctuations of the climate have complicated the process.

Soybean is generally sensitive to photoperiod. This photoperiod sensitivity was a major problem when soybean was first introduced into the U.S., due to its relatively narrow adaptation latitude^[1]. Photoperiod effects on soybean flowering have been studied extensively^[3-12]. However, the knowledge about photoperiod effect on the partitioning of photosynthates after flowering in soybeans under field conditions is very limited, while this information is crucial for people to understand many production questions, such as planting date, irrigation, row-space, planting density, weed control etc. Interactions between environment (especially photoperiod and temperatures) and soybean (*Glycine*

max (L.) Merr.) genotypes are very complicated^[13-16]. This interaction directly influences soybean yields. Studies indicated that photoperiod not only affects floral initiation, floral bud growth and development^[12,17,18], but also affects pod set^[19-21] and seed filling^[22]. These studies indicated that all stages, from floral induction to physiological maturity, were sensitive to photoperiod^[23,24]. Photoperiod and temperature effects on vegetative growth in soybeans have also been reported in many cases^[1,13,20,21,25]. Generally, short-days inhibit vegetative growth in favor of reproductive growth. Under long-day photoperiods, vegetative growth (such as number and length of inter-nodes on the main stems, the number of branches, leaf area and total dry weight) increased^[25]. However, the mechanisms and degree of these effects at various growth stages after flowering were not well understood. At present, there is still a limited understanding about the mechanisms involved in photoperiod effects on different stages of soybean growth. Therefore, a further understanding of photoperiod effects on soybean and development growth throughout its life cycle is needed.

In a previous study^[12], photoperiod effects on soybean floral bud initiation, floral bud growth and

development rates to open flowers were discussed. The objectives of this study are: 1) to discuss the effects of photoperiod on photosynthates partitioning further to soybean growth and development after flowering; 2) to study variations in photoperiod effects among strains differing in maturity and in stem termination behavior (determinate and indeterminate); and 3) to discuss the role of vegetative growth in determining how photoperiod effects are expressed as yield or maturity.

MATERIALS AND METHODS

Experiment 1: The experiments were conducted in a Flanagan silt loam (fine montmorillonitic, mesic Aquic Arguidoll) soil at the University of Illinois Crop Science South Farm at Urbana (latitude at about 40°), Illinois in 1992 and 1993. Eighteen strains with different maturity groups, ranging from MG 00 to MG VIII were used. However, this study will only focus on MG I to MG V soybean strains with both determinate and indeterminate strains. Soybean seeds of each strain were sowed with a plot configuration of 8 m (plot length) x 0.76 m (plant space). Photoperiod effect on natural field conditions was created by using five planting dates, ranging from early May to late July, with an approximate interval of two to three weeks between the plantings. Detailed planting dates and related information were the same as previously reported^[12]. Correspondent plantings for the two years are categorized as follows: mid-May, early-June, late-June, early-July, late-July. However, due to late maturity, yields and yield components were not collected from late-July plantings in both years. Therefore, data of yield and yield components from these plantings are not included in results and discussion. Vegetative and reproductive stages^[26] were determined every week from emergence of the first planting in late May to late September. Yield components (number of pods and seeds per plant) and nodal distributions were also recorded at R6 stage by randomly selecting 10 sample plants from each plot. Seed dry weight was also recorded at R8 stage of the first four plantings. Other production practices followed the recommended procedures for maximum yields in the Mid-west area.

Experiment 2

Soybean strains and culture practices: Two early maturity strains of 'Clark' backcross near-isoline, L71-920 (MG-I, indeterminate) and L63-778 (MG-II, determinate) and two late maturity strains of Clark near-isolines, L65-441 (MG-IV, indeterminate) and L65-546 (MG-IV, determinate) were used in this experiment. Both strains were sown on the June 20, 1993. The plots were 3.5 m long and 0.76 m apart, with 0.05 m between plants. Each

strain was replicated three times. Control plots were sown on the same date with the same design, but planted far enough away to avoid photoperiod effects from artificial lighting after dark. The other practices followed standard procedures.

Light conditions and photoperiod treatment: High-pressure sodium lamps (60 W), with five bulbs per row, were placed 0.75 m above the surface of the crop canopy. Forty minutes of light period were applied after the end of the normal daylight time. The natural photoperiod at that time was about 14.5 hrs. Light intensity was 40 $\mu\text{mol}/\text{m}^2/\text{s}$ (PAR, measured by LI-6200, LICOR, Inc. and), which was below the photosynthesis compensation point for soybean. Therefore, extra photosynthesis activity should not have occurred. Photoperiod treatments were applied on 11 August when plants of early MGs were at the R3 stage (pod beginning to set) and plants of late MGs had just shown visible floral buds. Growth stages of all control plants were the same as the treated plants for both the early and late MG comparisons before the photoperiod treatment had been imposed.

Other procedures: To separate temperature from photoperiod effects, Growing-Degree-Days unit (GDD) was used. In this study, GDDs were calculated as the follows:

$$\text{GDD} = \Sigma[(T_{\min} - T_b) + (T_{\max} - T_b)]/2$$

Where T_{\min} = minimum daily temperature (if less than 10°C, set to 10°C),

T_{\max} = maximum daily temperature (if greater than 30°C, set to 30°C),

T_b = base temperature (10°C).

Experiment design and data analysis: Under field conditions, soybeans grow under different photoperiods when they are planted in different dates. Therefore, photoperiod treatments in the first experiment were realized by growing those soybeans with different planting dates.

Both experiments were completely randomized design with three replications. Data from Experiment 1 was analyzed by one-way analysis of variance (ANOVA), with mean separation by Fishers Protected LSD (SAS Institute, 1989). Since no significant year effect was found in the data between 1992 and 1993, data of two years were pulled together for comparison wherever possible. Only LDS values are listed in the result tables. Regression analysis was also performed (at $\alpha=0.01$ and 0.05 levels) between yield components and final yields at R1 and R6 stages. T-test was performed in Experiment 2 at $\alpha=0.05$ level, to compare the difference between treatments and controls.

RESULTS

Experiment 1: Table 1 shows the effects of first four planting dates on various vegetative parameters at R6 for six indeterminate Clark near-isoline strains with maturity groups ranging from I to V. Among most parameters recorded, early plantings (early-June or before) resulted in greater values compared to that of later planting. These larger values were a consequence of longer periods of time for vegetative growth before flowering began.

Many other studies have indicated that early plantings result in higher yields under normal conditions, as reported here (Table 2). Moreover, with the delayed plantings, drastic reductions in yield resulted. The patterns between determinate and indeterminate strain were similar. However, determinate strains generally had lower yields and the yield differences among the first three plantings in determinate strains were not as great as those of indeterminate strains. Stem terminate characters may have a role in this phenomenon since indeterminate strains can still continue vegetative growth and also produce more nodes after flowering under relative longer daylength (with earlier planting). Abundant vegetative growth and more internodes can result in greater yields. Determinate strains do not have these advantages. Therefore, row space of determinate strains planted late should be narrower.

From field observations, it was noticed that branching stopped at nodes directly below that of the first flower on the main stem. In late plantings, plants that flowered earlier at lower nodes, produced fewer branches. Branches can contribute considerably to final yield^[27]. Early plantings of the later maturity groups produced more branch pods because the plants flowered late at higher nodes on the main stem. Seed to pod ratios were relatively constant among genotypes and treatments, with a slight decrease at the fourth planting or later.

Dry matter was recorded for each strain at R6 and R8 stages, which provided information about dry matter change during the maturity. Figure 1 shows dry matter change during this period. During the maturation period, dry matter accumulation increased considerably in strains of early maturity groups (I to III) with early planting (early June or before). The accumulation process was reversed in late MGs and in strains planted late.

Pod number is one of the most important yield components associated with final yields. The distribution of pods on each node at R6 was recorded with maturity groups (Fig. 2). Early plantings had more pods at all node positions. This indicated that either early-planted soybeans have more flowers, or more flowers developed into pods. All flowers were recorded for four of the strains (determinate and indeterminate combined with early and late MG) in all five plantings (Table 3). Data indicated that soybeans planted late did have significantly fewer

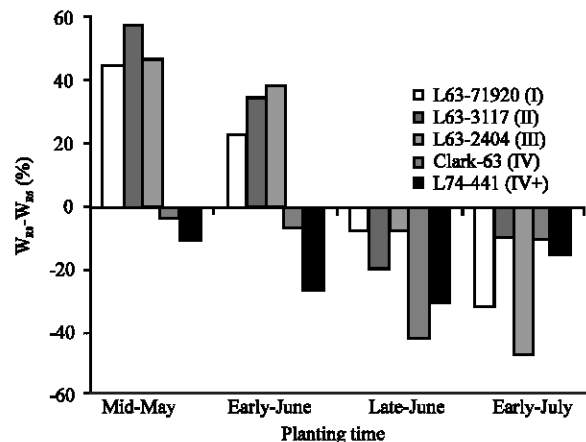


Fig. 1: Effect of photoperiod (indicated by planting date) on changes of dry matter (%) from R6 to R8 for different maturity groups (MGs). Roman letters indicate the MG.

flowers, indicating that photoperiod affected flower number. Also, node numbers on the main stem were less in late plantings (Table 2). In early MGs, most pods were on the main stem and branch nodes 3 to 11; in later MGs (IV+ and V), most pods were distributed between nodes 6 to 14. Late maturity group (IV+ and V) had more pods per plant, compared with early maturity groups, due to more nodes and branches. However, this did not translate into higher yields, due to a longer period of vegetative growth and a shorter seed filling period. When later maturity groups were planted early under long daylengths, excessive vegetative growth resulted.

Some of the yield components at R1 stage and R6 had significant correlations with final yields (Table 4). However, overall, the correlations were much less significant, except for the two late MG strains (L74-441 and L66-546). Stem dry weight and total dry weight at R6 were significantly and positively correlated with final yields in most strains, except in very early indeterminate and late determinate strains (Table 4).

Experiment 2: In early MGs, when the long-day conditions were applied abruptly at a relatively late stage (R3), vegetative growth was not greatly affected, but pod number and mass were significantly changed from that of the control in the indeterminate isoline L71-920 (Table 5). Longer photoperiods resulted in fewer pods and less pod mass per plants. Longer photoperiods did not have a significant effect on numbers of new nodes and leaves formed after first flower for both determinate and indeterminate strains, in either early or late maturity groups (Table 6). Total plant dry mass did not differ for treated and control plants in both determinate and indeterminate strains (Table 6). Longer photoperiods resulted in greater dry mass values of stems and leaves,

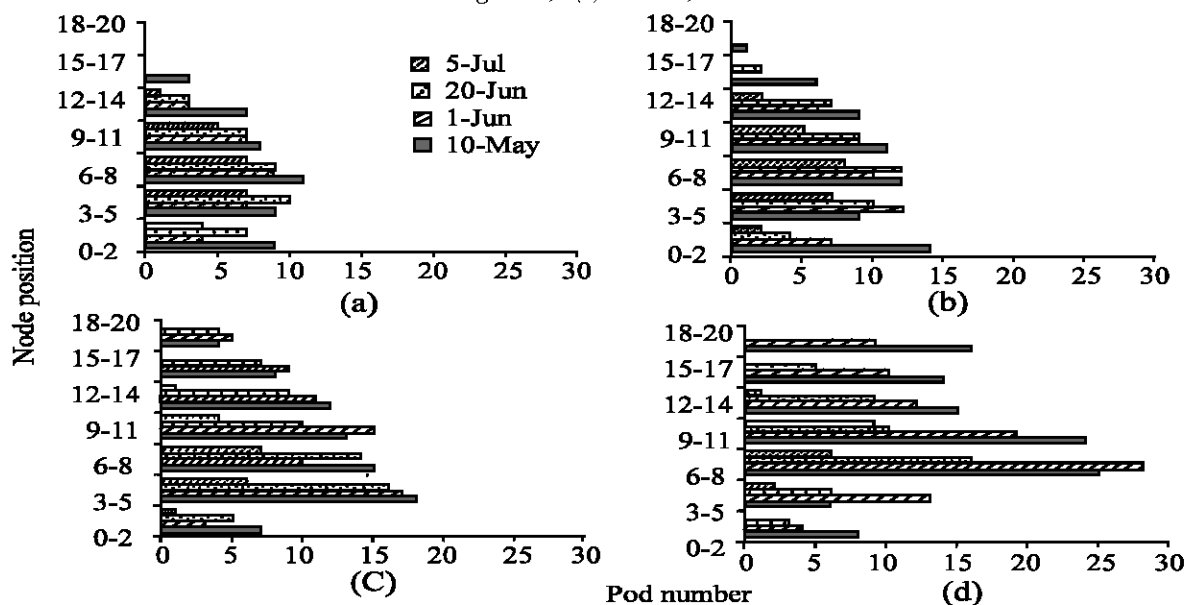


Fig. 2: The effect of planting time on main stem nodes for strains differing in maturity. Roman letters represent maturity groups

leaf areas and Specific Leaf Weights (SLW), but lower pod mass in treated plants. A greater understanding could be obtained from a study including longer photoperiod treatments using a greater number of strains.

DISCUSSION

Mechanism of planting date effect on soybean plant growth and development: Results from these experiments showed that vegetative growth after flowering was affected by photoperiod, which here was expressed as different planting dates under field conditions. The sensitivity of photoperiod response may have varied with the stage of growth. Although this phenomenon was reported earlier^[23,24], the mechanism was not well discussed. The hypothesis is that much of the photoperiod effect after flowering may be a consequence of effects before flowering. Vegetative growth in indeterminate strains continues up to the beginning of pod filling; whereas it stops in determinate strains with the beginning of flowering. Therefore, little vegetative growth in response to photoperiod after flowering in determinate strains was observed (Table 5 and 6). The vegetative growth of indeterminate strains was affected by photoperiod treatment after flowering more than that of determinate strains, suggesting that the stem termination habit interacts with photoperiod in controlling plant growth and development after flowering.

There is evidence that changes in plant hormones, such as gibberellins and cytokinins, may affect flowering processes^[2]. The mechanism responsible for photoperiod

effects seen in this experiment may be that longer photoperiods induced more hormones in leaves and stems, which allowed the vegetative growth to continue to be a strong sink, competing with that of reproductive growth processes after flowering, inhibiting the partitioning of photosynthates to pods. This hypothesis can be supported by responses observed in determinate strain L63-778, where long photoperiods slowed vegetative growth more than in L71-920, an indeterminate strain of similar maturity. In the former strain, longer photoperiods did not re-induce vegetative activity and partitioning still favored pod set and seed filling.

Effect of the timing of photoperiod treatments: The timing of a photoperiod treatment is also important. If longer photoperiods are applied at later stages of growth (such as pod filling) in late maturity strains, or in early maturity groups after flowering, there will be little effect on growth or partitioning. However, growth periods before and immediately after flowering were equally sensitive to the changes in photoperiod imposed. It is logical to assume that this similarity in response indicates that photoperiod responses in both vegetative and reproductive growth may be involved the same mechanism. Treatments later in the flowering period did not produce big differences in plant mass between treatment and controls. However, pod number and mass were reduced, indicating that the photoperiod treatment affected partitioning processes. The effect of time and length of photoperiod treatments should be a quantitative phenomenon. The extra photoperiod treatments had the greatest effect upon the Leaf Area Index (LAI) (Table 5 and 6).

Table 1: Effects of planting date on vegetative parameters at R6 stage for six indeterminate clark near-isoline strains in 1992 and 1993

Planting date	Leaf area cm ²	Pod weight gram	Stem gram	Leaf gram	Height cm	Node
L71-920 (I)						
Mid-May	1185	22.1	9.5	5.6	85	15.3
Early-June	841	16.3	5.6	3.5	73	12.9
Late-June	573	12.1	4.6	3.0	61	12.2
Early-July	462	6.3	3.1	2.4	45	12.0
Average	765.3	14.2	5.7	3.6	66	13.1
LSD	116	2.3	1.4	1.2	11	0.7
L63-3117 (II)						
Mid-May	1037	26.5	9.8	4.9	86	16.6
Early-June	1014	18.3	6.3	4.4	84	15.0
Late-June	761	15.1	6.3	3.5	74	14.2
Early-July	490	7.6	5.1	3.1	63	12.7
Average	826	16.9	6.9	4.0	76.8	14.6
LSD	153	3.2	1.7	1.0	13	0.9
L63-2404(III)						
Mid-May	1430	23.5	11.6	6.3	96	16.5
Early-June	1298	17.6	9.7	5.6	87	15.6
Late-June	812	14.6	6.5	3.9	73	14.4
Early-July	634	8.1	5.1	3.1	63	12.3
Average	1043.5	16.0	8.2	4.7	79.8	14.7
LSD	177	3.5	2.1	1.3	10	0.8
Clark 63 (IV)						
Mid-May	1786	38.6	11.6	11.5	102	19.5
Early-June	1356	26.7	10.2	7.5	105	19.7
Late-June	1102	19.4	10.7	5.5	93	13.4
Early-July	715	9.1	5.0	3.4	76	9.2
Average	1240.0	23.5	9.4	7.0	94	15.5
LSD	156	4.2	1.3	1.5	16	1.1
L74-441(IV+) (IV+)						
Mid-May	1233	26.3	15.6	7.3	102	21.5
Early-June	1147	17.8	14.1	5.6	106	20.4
Late-June	954	11.5	9.3	3.8	91	16.3
Early-July	458	5.5	5.4	2.2	66	13.1
Average	948	15.3	11.1	4.7	91.3	17.8
LSD	123	2.6	1.4	1.2	13	1.4
L65-3366 (V)						
Mid-May	1194	32.1	22.6	8.0	115	24.5
Early-June	967	26.5	22.1	8.2	109	23.1
Late-June	526	17.7	15.3	4.1	87	18.5
Early-July	431	6.7	6.1	3.1	69	13.9
Average	780.0	20.8	16.5	5.9	95	20
LSD	118	3.5	2.7	1.6	25	2.1

Table 2: Effect of planting date on final yield for some soybean strains/strains from different maturity groups in 1992 and 1993

Stem termination	Planting							LSD
	Strain	MG	Mid-May	Early-June	Late-June	Early- July	Mean	
Indeterminate	L71-920	I	3668	2260	1390	557	1969	239
	L63-3117	II	4910	2321	1347	624	2301	364
	L63-2404	III	3849	2454	1154	477	1984	312
	Clark-63	IV	4313	2622	1224	626	2196	269
	L74-441	IV ₊	2605	1436	939	405	1346	319
Determinate	L65-778	II-	1025	1452	1016	386	969	198
	Gnome	II	3315	2104	1112	651	1759	211
	Hobbit	III	2446	2225	1534	388	1648	188
	L63-3016	IV	1547	924	995	479	986	186
	L66-546	IV ₊	2387	1816	1138	435	1444	207

Effect on yield components and final yields: It was not surprising to see dramatic decreases in yield as plantings were delayed (Table 2). Decreased values in associated vegetative parameters at the R1 stage may have contributed to such yield decreases (Table 1). However, pod numbers and seed size are major components

contributing to higher yields. Compared with early plantings, pod numbers per plant in later plantings were greatly decreased, contributing to decreases in yield. This pod decrease in later plantings was associated with should be a quantitative phenomenon. The extra photoperiod treatments had the greatest effect upon the

Table 3: Effects of planting date on total number of flowers per plant for four strains (strains) in 1992 and 1993

Strain/Strain	L63-3117	Gnome	Clark-63	L63-3016
MG/Termination	II/Dt _i	II/dt _i	IV/Dt _i	IV/dt _i
Planting date				
Mid-May	82	84	116	64
Early-June	95	84	96	57
Late-June	69	68	54	48
Early-July	41	36	47	26
Late-July	20	19	34	19
Average	61	58	69	43
LSD	13	11	16	9

Table 4: Correlation coefficients between vegetative and phenology parameters at R1 and R6 and final yield for determinate and indeterminate strains (strains) in 1992 and 1993

Yield component	Total dry wt	Leaf dry wt	Stem dry wt	Leaf area	Leaf number	Height
		gram/plant		cm ² /plant		cm
R1 Stage						
Indeterminate (MG)						
L71-920 (I)	0.412	0.570	0.252	0.274	0.071	-0.624
L63-3117 (II)	-0.103	-0.180	-0.341	-0.350	-0.368	-0.697
L63-2402 (III)	0.358	0.385	0.372	0.240	-0.494	-0.781
Clark-63 (IV)	0.563	0.599	0.494	-0.208	-0.218	-0.885
L74-441 (V)	0.977x	0.978x	0.980x	0.983x	0.916y	0.877
Determinate (MG)						
L65-778 (II-)	0.423	0.545	0.205	0.408	0.062	-0.240
Gnome (II)	0.832	0.779	0.878	0.920y	0.812	0.279
Hobbit (III)	0.634	0.831	0.800	0.837	0.903y	0.332
L63-3016 (IV)	0.761	0.384	0.156	0.558	0.269	-0.622
L66-546 (V)	0.975x	0.951x	0.986x	0.963x	0.995x	0.956x
R6 Stage						
Indeterminate (MG)						
L71-920 (I)	0.216	0.022	0.376	0.495	-0.385	-0.295
L63-3117 (II)	0.962x	0.952x	0.976x	0.948x	0.988x	0.908y
L63-2402 (III)	0.914y	0.876	0.902y	0.837	0.790	0.409
Clark-63 (IV)	0.929y	0.948x	0.909y	0.948x	0.709	0.833
L74-441 (V)	0.990x	0.788	0.997x	0.887	0.993x	0.940x
Determinate (MG)						
L65-778 (II-)	0.943x	0.925y	0.950x	0.916y	0.826	0.989x
Gnome (II)	0.988x	0.465	0.910y	0.682	0.851	0.734
Hobbit (III)	0.994x	0.956x	0.999x	0.944x	0.918y	0.972x
L63-3016 (IV)	0.885	0.937x	0.937x	0.802	0.826	0.752
L66-546 (V)	0.880	0.762	0.762	0.813	0.883	0.858

*:Numbers with x and y are statistically significant at 0.01 and 0.05 level, respectively

Table 5: Effects of applying extra photoperiod after normal daylength at R3 stage on later vegetative growth and reproductive development in two early maturity soybean strains. Data in the Table are based on per plant and were taken at seven weeks after treatment

	L71-920 (MG-I, Dt _i)		L63-778 (MG-II, dt _i)	
	Treatment	Control	Treatment	Control
Node number	10.1(0.35*)	9 (0.35)	7.1 (0.2)	6.9 (0.3)
Height (cm)	66.3 (3.2)	61.4 (2.3)	41.2 (1.8)	40.3 (1.7)
Stem weight (g)	2.8 (0.18)	2.8 (0.17)	2.8 (0.23)	2.6 (0.13)
Leaf area (cm ²)	629 (49)	563 (35)	716 (52)	665 (22)
Pod number	14.8 (2.2)**	22.7(2.4)	26.3 (1.8)	23.2 (1.2)
Pod weight (g)	4.6 (0.35)**	7.1 (0.4)	7.2 (0.4)	7.0 (0.3)
Weight/pod	0.33 (0.02)	0.33 (0.02)	0.34 (0.02)	0.38 (0.03)
Total weight	11.5 (0.75)	3.5 (0.81)	14.9 (0.8)	14.0 (0.6)

Numbers in parenthesis are standard errors

**Number that has significant (t-test, and α level at 0.01 level) difference compared with the control

Leaf Area Index (LAI) (Table 5 and 6). Greater leaf areas, stem weights and total weights at R6 also impacted final yields and this was more significant for adapted maturity groups (such as MG II to MG III) at the Urbana latitude.

The ability of large plants to partition photosynthate to pods for a longer period may be obvious. Early plantings of strains adapted to Urbana, Illinois latitude

obviously resulted in larger plants, which in turn resulted in longer bean filling periods. However, the dry matter decrease between R6 and R8 in late plantings and late MGs had not been reported before. One of the reasons for this phenomenon may be due to the accelerated shortened photoperiod in late growing seasons, which speed up the senescence processes. Vegetative growth under short photoperiods did not provide enough

Table 6: Effects of applying extra photoperiod after normal daylength at R1 stage on later vegetative growth and reproductive stage in two late maturity soybean strains. Data in the Table are based on per plant and were taken at seven weeks after treatment

	L74-441 (MG-IV+, Dt ₁)		L66-546 (MG-IV+, dt ₁)	
	Treatment	Control	Treatment	Control
Node number	20.3(0.4)**	18.9 (0.4)	14.6(0.17)	14.6 (0.18)
Height (cm)	95.9 (2.3)	93.1 (2.3)	87.9 (2.2)**	82.8 (2.3)
Stem dry weight (g)	19.2 (1.0)**	15.4 (0.8)	13.4 (1.0)	13.1 (0.8)
Leaf area (cm ²)	2248 (149)**	1652 (161)	1670 (115)**	1188 (79)
Pod number	51.5 (3.4)	48.9(3.4)	31.6 (2.6)	43.8(3.3)**
Pod dry weight (g)	7.4 (0.79)	13.2 (0.82)**	3.3 (0.4)	8.12(0.85)**
Dry weight/pod	0.14 (0.01)	0.27	0.10 (0.01)	0.19(0.02)**
Total dry weight	37.2 (1.84)	37.0 (2.3)	27.1 (0.23)	29.3 (1.78)

*Numbers in parenthesis are standard errors

**Number that has significant (t-test, and α level at 0.01 level) difference compared with the control

photosynthate to overcome that lost from plant respiration. The vegetative and reproductive growths were not properly balanced to produce maximum yields. The combination of planting dates and MG at a specific geographical location (latitude) determines this balance.

CONCLUSION

Planting dates have been studied for many years and many geographic regions. A thorough understanding about the mechanism of photoperiod effects on soybean growth and development is crucial. Studies discussed in this paper indicate that photoperiod affects soybean growth and development through its lifecycle. Photoperiod, along with other environmental factors and all the interactivities involved, contributes to the control of the ratio of the crop's vegetative to reproductive components. In doing so, it controls the dynamics of the crop canopy architecture and photosynthetic surface (leaf behaviors). Though to define each individual critical response point will be a tremendous task, especially under field conditions, the understanding of basic principles would certainly add in building a better computer model for management in soybean production.

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