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EFFECT OF TEMPERATURE AND MATURITY GROUP ON PHENOLOGY OF FIELD GROWN NODULATING AND NONNODULATING SOYBEAN ISOLINES*

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GEORGE T., BARTHOLOMEW D. P. and SINGLETON P. W. *Effect of temperature and maturity group on phenology of field grown nodulating and nonnodulating soybean isolines.* BIOTRONICS 19, 49-59, 1990. Lack of sufficient field data on how temperature, photoperiod (latitude), or crop nutrition independently or interactively determines phenological development and yield limit our ability to predict the suitability of soybean (*Glycine max* (L.) Merrill) genotypes for cultivation in varied environments. The effect of temperature and N nutrition on phenology of soybean from four maturity groups was studied at field sites with elevations of 320, 660, and 1050 m on the island of Maui, HI. Four determinate nodulating soybean genotypes representing the maturity groups 00 ('Clay'), IV ('Clark'), VI (D68-0099), and VIII ('Hardee'); one indeterminate genotype of Group VI (N77-4262); and their nonnodulating isolines were planted at each site on the same day. Nonnodulating isolines were used to evaluate the effects of N nutrition on phenology. The mean maximum/minimum air temperatures at the three elevations during the experiment were 27/20, 25/17, and 23/14°C, respectively. Photoperiod decreased from 13 h at planting to 11 h at the last harvest. Soybean maturity was delayed with decreasing temperature mainly due to extended vegetative growth periods averaging 23 and 64% longer at the 660- and 1050-m sites, respectively, compared to the lowest site. Flowering (R1) and physiological maturity (R7) at the highest site were delayed on average by 22 and 25 days, respectively, relative to development at the lowest site. Within each site, duration of the vegetative phase increased with increasing maturity group number presumably due to photoperiodic effects. Higher maturity groups accumulated a greater number of growing degree days (GDD) before R1 at each site than did the lower maturity groups. The GDD requirement before R1 also increased with increasing elevation. The effect of elevation (temperature) on the duration of the seed-fill phase was minimal under similar N nutritional levels. The rate of seed dry matter accumulation ($\text{kg ha}^{-1} \text{ day}^{-1}$) decreased with increasing elevation, but increased with increasing maturity group number. Nonnodulating isolines flowered

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later and matured earlier than their nodulating counterparts due to nitrogen insufficiency. These results provide information to refine models predicting phenological development and yield of soybean genotypes for varied environments.

Key words: *Glycine max* (L.) Merrill; soybean; nonnodulating isolate; phenology; temperature; elevation; nitrogen nutrition.

INTRODUCTION

The suitability of soybean genotypes for cultivation in varied geographical locations depends in part on their phenological response to environment. Soybean phenology is primarily determined by temperature and photoperiod (10, 17, 18). Temperature is important during early development, floral initiation is primarily a photoperiodic response, floral growth is regulated mainly by temperature, and both temperature and photoperiod influence post-flowering development (13). However, other environmental variables such as mineral nutrition and water stress (13, 14, 22, 23) also influence soybean phenology. Nitrogen nutrition of soybean is of particular importance because insufficiency of this nutrient often has been linked to earlier senescence in soybean (6, 27). At least in one instance, flowering of soybean was delayed due to nitrogen insufficiency (15).

Most reports concerning the effects of temperature on soybean phenology either used planting date as a variable (17, 18, 31) or employed controlled environments (10, 29, 30). Because of the strong photoperiodic influence on flowering and reproductive development of soybean (10, 17), field studies often confound the effects of temperature and photoperiod because photoperiod changes with planting date or latitude. According to Lawn and Byth (17), low temperature effects on phasic development of soybean in the field were apparent only when photoperiodic effects were minimum. Where night temperatures were artificially elevated by enclosing plants in heated chambers in the field, Seddigh and Jolliff (25) found that warm night temperatures considerably hastened flowering and physiological maturity of a soybean maturity group (MG) 0 genotype. Similar results were reported by Seddigh *et al.* (26) with MG 000, 00, and 0 genotypes. They minimized the confounding of photoperiodic effects with temperature effects by using locations with a similar latitude. Basnet *et al.* (1) reported that high elevation lengthened intervals between growth stages in several soybean genotypes grown in a temperate environment. Major *et al.* (18) concluded that there were no differences in sensitivity to temperature of flowering among MG I through V at a constant photoperiod of 14 h, but later MG flowered after the early ones. Most controlled environment studies of soybean phenology have only examined the effects of environment on development up to the time of flowering (10, 16, 30) and rarely gathered data on entire plant life cycle and yield (12).

Phenological events in soybean generally have been predicted using temperature and photoperiod (2, 10, 16, 18, 31). However, as noted above, other factors such as nitrogen nutrition are also likely to influence phenological development.

There is need to examine further the interactions between temperature, photoperiod, and nitrogen nutrition on the phenology of soybean without the confounding effects of other variables. Also, limited data have been collected for the broad range of soybean MG, especially in tropical latitudes. Such data would enable both the validation and refining of soybean phenology models (31).

The present experiment was undertaken to evaluate the effect of temperature and nitrogen nutrition on phenology of soybean from four maturity groups. Three field sites in an elevational transect located on the island of Maui, HI (part of the Maui Soil, Climate and Landuse Network: MauiNet) provided an opportunity to investigate the effect of temperature (elevation) on soybean phenology. The use of the above transect to study temperature effects on crop plants has been documented earlier (8, 9, 20). Nitrogen nutrition effects on phenology were evaluated by planting nodulating and nonnodulating isolines of all maturity groups at each site. The effect of photoperiod was minimized by planting at the different sites on the same day.

MATERIALS AND METHODS

Experimental design

Nodulating (nod) and nonnodulating (nonnod) isolines of five soybean genotypes representing four maturity groups (00, IV, VI and VIII) were grown at elevations of 320, 660, and 1050 m on the island of Maui, HI (site latitude ranged from 20°51' to 20°54'N). The experimental design was a randomized complete block with three replicates at each site.

Field and plant culture

Procedures followed for soil amendment, rhizobial inoculation, and plant culture were described previously (8). These procedures were aimed at minimizing the effect of soil environment on growth and phenology. Seeds of soybean maturity groups 00 (Clay, nod and nonnod), IV (Clark, nod and nonnod), VI (D68-0099, nod; D68-0102, nonnod; N77-4262, nod, indeterminate; and N77-4273, nonnod, indeterminate), and VIII (Hardee, nod and nonnod) were planted at each of the three sites on 29 July 1985. Seeds were sown in four rows 60 cm apart in 2.4 by 4.0-m plots to give a final population of 400 000 plants ha⁻¹. Daily maximum, minimum, and mean temperatures were determined from temperatures recorded at 1-min intervals by a Campbell Scientific CR-21 micrologger* (Campbell Scientific, Inc., Logan, UT) equipped with a thermistor (Fenwal Electronics, Medford, MA).

Sampling procedures

Phenological observations were made on a 1-m section of row in each plot. Plants were considered to have reached a particular phenological stage when 50%

* Mention of a brand name does not constitute an endorsement by the authors, University of Hawaii or the United States Agency for International Development.

of the plants in the 1-m row reached that stage. Growth-stage characterization was based on the system developed by Fehr *et al.* (7).

Three meters of row from the center of the two central rows were harvested at physiological maturity. Details of harvest procedures, dry weight determination, and total nitrogen analysis were described elsewhere (9).

Durations of vegetative and seed-fill phases were calculated, respectively, as days from planting to first flower (R1) and days to physiological maturity (R7) minus days to beginning seed (R5). Rate of seed dry matter accumulation was determined by dividing grain yield ha^{-1} by seed-fill duration. Growing degree days (19) were calculated using a base temperature of 7°C .

Data analysis

The data from the three sites were combined (21) and subjected to analysis of variance using SAS (24) procedures.

RESULTS

Mean maximum and minimum temperatures at the three elevations during the experiment were 27/20, 25/17, and $23/14^{\circ}\text{C}$, respectively. The decline in mean temperature from the start to the end of the experiment at a site was gradual and small (Fig. 1). The photoperiod decreased from 13 h at planting to 11 h at the end of the experiment. Total solar radiation from planting to the average days to harvest of the genotypes at each site was 1998, 1824, and 1926 MJ at the 320-, 660-, and 1050-m elevations, respectively.

Days to first flower (R1) and physiological maturity (R7) between sites and genotypes differed significantly (Table 1). Both phenological events were delayed considerably at the higher elevations compared to the lowest elevation. The effect of increasing elevation was progressively greater on higher maturity groups.

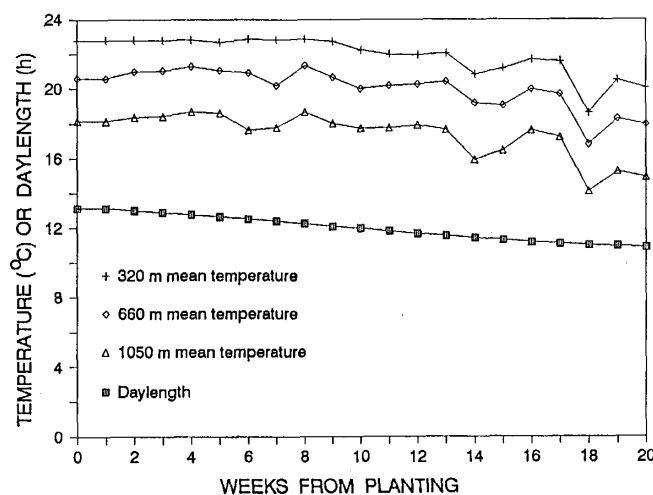


Fig. 1. Weekly mean temperatures and daylengths during the growth of five soybean genotypes at three elevations on the island of Maui, Hawaii.

Table 1. Days to first flower (R1) and physiological maturity (R7) of nodulating isolines of five soybean genotypes grown at three elevations on the island of Maui, HI

Genotype	First flower			Physiological maturity		
	320 m	660 m	1050 m	320 m	660 m	1050 m
	(days)					
Clay (00)†	28E‡	31E	40E	73E	78E	93E
Clark (IV)	30D	35D	46D	87D	92D	107D
D68 (VI)	34C	41C	56C	90C	101C	112C
N77 (VI)	38B	49B	66B	94B	105B	128B
Hardee (VIII)	42A	54A	74A	106A	117A	133A
Mean	34c	42b	56a	90c	99b	115a

† Maturity grouping.

‡ Means followed by the same upper case letter within a column or lower case letter within a row for each category are not significantly different ($P=0.05$) by Duncan's multiple range test.

Table 2. Cumulative growing degree days (GDD) during vegetative growth and crop duration for nodulating isolines of five soybean genotypes grown at three elevations

Genotype	Vegetative phase†			Total crop duration‡		
	320 m	660 m	1050 m	320 m	660 m	1050 m
	(Growing degree days §)					
Clay (00)¶	451E#	450E	472E	1190E	1116E	1083E
Clark (IV)	488D	509D	539D	1406D	1316D	1223D
D68 (VI)	548C	600C	658C	1453C	1428C	1280C
D77 (VI)	619B	707B	777B	1512B	1482B	1425B
Hardee (VIII)	691A	788A	867A	1686A	1642A	1471A
Mean	559c	611b	662a	1449a	1397b	1297c

† Period from planting to flowering (R1).

‡ Period from planting to physiological maturity (R7).

§ Calculated using a base temperature of 7°C.

¶ Maturity grouping.

Means followed by the same upper case letter within a column or lower case letter within a row for each category are not significantly different ($P=0.05$) by Duncan's multiple range test.

Flowering of Clay (00) was only 12 days later at 1050 m than at 320 m while Hardee (VIII) flowered 31 days later at the highest site. Similarly, Hardee flowered 15 days later than Clay at the 320-m site, but was 34 days later than Clay at 1050 m. Phenological development was consistent with maturity group number within a site; plants in the lower maturity groups flowered and matured more rapidly than did plants in higher maturity groups. Thus, within a site, each event was recorded first and last, respectively, for Clay and Hardee. The indeterminate maturity-group-VI genotype N77 required a significantly greater number of days than the determinate VI genotype D68 to reach both R1 and R7.

Growing degree days accumulated before R1 for all genotypes increased slightly with increasing elevation (Table 2). Because the seed-fill period was

approximately constant between sites, GDD for the total crop duration actually decreased with increasing elevation. Higher maturity group genotypes required a greater number of GDD to reach R1 and R7 at all sites.

The differences in duration of the seed-fill phase were much smaller than differences in durations of vegetative and total crop growth. Genotypes differed significantly in duration of seed-fill (R5 through R7) (Table 3). Differences between sites in seed-fill duration, although significant, were small. Clay, the earliest maturing genotype, had the shortest seed-fill duration. The other maturity groups were inconsistent in seed-fill duration. When averaged across sites, Clark and Hardee had the longest seed-fill period (Table 3). The rate of seed dry-matter accumulation declined significantly with increasing elevation and was lowest for the two early genotypes at the 1050-m site (Table 4). When averaged across sites, N77 had the highest rate of seed dry-matter accumulation.

Table 3. Duration of seed-fill† of nodulating isolines of five soybean genotypes grown at three elevations

Genotype	Elevation (m)			Mean
	320	660	1050 (days)	
Clay (00)‡	36	35	38	36D§
Clark (IV)	47	43	46	45A
D68 (VI)	42	45	40	43B
N77 (VI)	39	39	44	41C
Hardee (VIII)	47	46	43	46A
Mean	42a	42b	42a	

† Days from beginning seed (R5) to physiological maturity (R7).

‡ Maturity grouping.

§ Means followed by the same upper case letter within a column and lower case letter within a row are not significantly different ($P=0.05$) by Duncan's multiple range test.

Table 4. Rate of seed dry-matter accumulation† of nodulating isolines of five soybean genotypes grown at three elevations

Genotype	Elevation (m)			Mean
	320	660	1050 (kg ha ⁻¹ day ⁻¹)	
Clay (00)‡	90	80	14	61D§
Clark (IV)	95	71	30	65C
D68 (VI)	101	83	47	77B
N77 (VI)	91	90	58	79A
Hardee (VIII)	102	78	43	75B
Mean	96a	80b	38c	

† Determined by dividing grain yield ha⁻¹ by duration of seed fill (R5–R7).

‡ Maturity grouping.

§ Means followed by the same upper case letter within a column and lower case letter within a row are not significantly different ($P=0.05$) by Duncan's multiple range test.

Table 5. Mean days to first flower (R1) and physiological maturity (R7) for nodulating (nod) and nonnodulating (nonnod) isolines of five soybean genotypes

Genotype	First flower (R1)		Physiological maturity (R7)†	
	Nod	Nonnod (days)	Nod	Nonnod
Clay (00)‡	33a§	33a	75a	71b
Clark (IV)	37a	37a	90a	85b
D68 (VI)	44b	47a	96a	91b
N77 (VI)	51b	52a	100a	96b
Hardee (VIII)	57b	62a	112a	106b

† Data averaged for the Kuiaha (320 m) and Haleakala (660 m) sites. Reproductive stage determination after R1 was not realistic for nonnods at the 1050 m site because of the severe N stress and stunted plant growth.

‡ Maturity grouping.

§ Means followed by the same letter within a row for each category are not significantly different ($P=0.05$) by Duncan's multiple range test.

Table 6. Mean tissue nitrogen concentrations at physiological maturity of nodulating (nod) and nonnodulating (nonnod) isolines grown at three elevations

Genotype	320 m		660 m		1050 m	
	Nod	Nonnod	Nod	Nonnod (g N kg ⁻¹)	Nod	Nonnod
Clay (00)†	37a‡	15b	35a	23b	40a	11b
Clark (IV)	38a	18b	38a	21b	36a	14b
D68 (VI)	40a	13b	36a	20b	32a	15b
N77 (VI)	38a	18b	35a	19b	37a	15b
Hardee (VIII)	43a	21b	36a	20b	32a	20b

† Maturity grouping.

‡ Means followed by the same letter within a row for each elevation are not significantly different ($P=0.05$) by Duncan's multiple range test.

Nonnodulating isolines flowered later and matured earlier than their nod counterparts. When averaged over sites, the nonnod isolines of Clay and Clark were similar in days to R1 (Table 5), but nonnod isolines of other genotypes were late to flower. Nodulating isolines had significantly greater N concentrations than did the nonnods (Table 6).

DISCUSSION

We isolated temperature as the major variable in the experiment by using elevations within the same latitude which received similar rainfall and irradiance. The effect of soil environment on growth and phenology of soybean was minimized by maximizing the availability of essential nutrients except N, by equalizing pH between sites, and maintaining soil moisture at field capacity. The delay in the occurrence of R1 (Table 1) due to increasing elevation was therefore, primarily due

to a 5°C decline in mean daily temperature from the lowest to the highest site. Since the effect of the prevailing photoperiod on flowering was the same at the three sites, differences between sites in days to flowering are mainly due to differences in temperature. The consistent delay in phenological responses of all maturity groups in response to increasing elevation further indicates that temperature was the dominant effect. A delay in flowering of soybean due to low temperature has been reported by many investigators from controlled environment research (10, 12, 28, 30) and field experiments (17, 18, 25, 26). Our results, while in general agreement with the above reports, are the first which quantify the effects of temperature on flowering of several soybean maturity groups in isolation from photoperiodic effects in actual field conditions. Although Seddigh *et al.* (26) minimized the confounding of photoperiodic and temperature effects on soybean phenology, only genotypes from MG 000, 00, and 0 were used. Our research addressed phenological development of a wide range of maturity groups in a tropical latitude.

According to Hadley *et al.* (10), the reciprocals of the days taken to flower (rate of progress towards flowering) by soybean were linear functions of mean diurnal temperature in photoperiods shorter than the critical daylength. Thus, under a constant temperature regime and photoperiod below critical values, soybean genotypes would flower about the same time regardless of their maturity-group classification. In our experiment, flowering in order of progressively increasing maturity group number indicated that the prevailing photoperiods were longer than the critical values of the higher maturity groups. The large increases in GDD prior to flowering of the higher maturity groups within a site is further evidence for a photoperiodic effect. When photoperiods are longer than the critical value, the rate of progress towards flowering is a linear function of both temperature and photoperiod with no interaction between the two (10). Since, critical day-lengths for soybean are shorter in cooler than warmer temperatures (10), plants at the higher elevations in this experiment were subjected relatively more to photoperiods longer than their critical value. The effect of temperature on critical photoperiod values may have further delayed flowering at those sites compared to the lowest elevation. The overall effect was to increase the crop duration for successive maturity group numbers at high elevations.

Since flowering in Clay (00) is relatively insensitive to photoperiod (3, 18), delays in flowering of 12 and 43% at the intermediate and highest sites, respectively, is concluded to have been due entirely to lower temperatures. The similar GDD accumulated before R1 by Clay across elevations further supports the above conclusion.

The increased number of days to flowering at the higher elevation, however, did not result in a similar increase in days to physiological maturity (Table 1). Therefore, temperature had relatively less effect on reproductive stages after flowering compared to flowering itself. Further, the data indicate that the effects of temperature on the seed-fill duration (R5 through R7) was minimal (Table 3). Our results are essentially in agreement with the report by Seddigh and Jolliff (25) of similar time intervals between R1 and R7 for soybean grown at night tempera-

tures of 10, 16, and 24°C. They indicated that the period R3 through R7 was unaffected by temperature. Also, the finding of Hesketh *et al.* (12) that reproductive duration was relatively unaffected by temperatures in the range of 21 to 30°C may have been due to similar seed-fill durations.

Despite similar seed-fill durations, the rate of seed dry-matter accumulation decreased substantially with decreasing temperature. Genotypic differences in seed-fill durations were not related consistently to differences in grain yield within a site (Tables 3 and 4) (9). The above observation is in contrast to reports by others (4, 5, 11) that grain yield of different genotypes is strongly related to seed-fill duration with the rate of seed dry-matter accumulation being a constant. In the present experiment, grain yield increased with increasing vegetative-growth period, indicating vegetative dry-matter production is more critical to grain yield than seed-fill duration.

The differences in the response to temperature of nod and nonnod isolines indicate how nitrogen nutrition can alter soybean phenological development. The net result of delayed flowering and shortened reproductive and seed-fill durations was hastened maturity by the nonnods. The significantly lower N concentrations of nonnods compared to nods (Table 6) indicated N insufficiency in nonnod plants. Early maturity of nonnods was apparently due to N insufficiency. The cause of the delayed flowering of the nonnod isolines is unknown although Huxley *et al.* (15) reported that while flowering was substantially delayed by lower night temperature, low N levels also delayed flowering in soybean cv. TK5. Therefore, N nutrition is another important consideration in comparing phenological development of soybean across temperature regimes.

The effects of temperature on phenological development of a wide range of soybean maturity groups under field conditions with minimal confounding effects of photoperiod were demonstrated in this experiment. The results indicate that low temperature substantially delayed flowering of all soybean maturity groups. The extended vegetative growth due to decreasing temperature may be a response by the soybean plant which compensates for decreased rates of growth. Duration of seed-fill was relatively unaffected by temperature under similar N nutritional levels, but seed dry-matter accumulation per day per unit land area was decreased substantially by cool temperature. Nitrogen nutrition was found to be an important determinant of flowering and physiological maturity of soybean and needs to be incorporated into soybean phenology models.

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