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THE THERMAL-PHOTOPERIOD REQUIREMENT FOR FLORAL BUD GROWTH

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EPHRATH J. E. and HESKETH J. D. *The thermal-photoperiod requirement for floral bud growth*. BIOTRONICS 20, 1-7, 1991. Temperature and photoperiod effects on floral bud growth rates, between detection of a primordium with a dissecting microscope and an open flower, need to be quantified for plant growth and yield models. Plants of several crop and weed species were grown in controlled environment chambers at several daylengths. Degree-day values for bud growth were determined; bud growth rates were much slower under long days in long day sensitive plants. The node at which the first floral bud appeared and total nodes at first flower were also recorded. The soybean strains most sensitive to photoperiod initiated floral buds in a reasonable length of time (50 days, 29/19°C day/night temperatures), but their floral buds had not opened by the end of the experiment (over 125 days) and it seemed likely they never would. Large floral buds were produced on such plants, but these plants were too large to prevent shading in the growth cabinet.

Key Words : phenology ; degree-days ; base temperature ; crop systems-modeling ; *Glycine max* (L.) Merr. ; *Gossypium hirsutum* (L.) ; *Zea mays* (L.) ; *Abutilon theophrasti* Medic. ; *Datura stramonium* (L.) ; *Xanthium strumarium* (L.)

INTRODUCTION

Aitken (1) emphasized the importance of measuring three stages and three components of development in phenological studies. Her three stages were sowing to floral initiation, floral initiation to the first flower, and the first flower to ripe seed. Unfortunately, her second stage, floral initiation to first flower, has been ignored in many phenological studies. She published 15 tables and two figures showing species, maturity genotype, photoperiod and temperature effects on the duration of floral bud growth, with as much or more information about the other stages and components of development. She also discussed in detail the importance of correcting for the difference between temperature measured in a weather station and that in the floral bud or shoot meristem.

Her three developmental components included rate of leaf appearance, number of vegetative nodes at floral initiation, first flower and maturity and the

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rate of seed development. She listed definitions for various aspects of these developmental stages and components, and discussed the morphology involved, including the phytomer concept.

Following a long research tradition, she was trying to predict how well a variety might yield when introduced into a new area, within a range of known seasonal temperatures and photoperiods determined by latitude, elevation, and the planting date. She grew early and late cultivars at different latitudes, different elevations at one location, and in controlled environments.

Her research approach and results, concerned with problems associated with new plant introductions, are fundamental to simulating plant growth, development and yield, with computer models. Others (1), of course, have defined more stages and components, but few take into account floral bud initiation. The list of genotypes that need more morphological and phenological detail seems endless.

Jones and Laing (4) studies the time from floral bud initiation to first flower in soybean plants growing at different temperatures and the natural daylength at Sydney Australia (34° latitude). They reported temperature and photoperiod effects, the latter for photoperiods before and after the longest day of the year, and its rate of change. They measured 296 degree days per flower, 10°C base temperature, for 18/11–27/22 12-h day/night °C temperature regimes, with 392 and 460 degree days required for plants in 30/25 and 33/27 temperature regimes. Jones and Laing's (4) soybean strains were very sensitive to photoperiod ; Hesketh and Warrington (3) reported that 518 degree days, 7.2°C base temperature, were needed to grow a corn tassel from a primordium to anthesis. Jones and Laing (4) developed a computer phenological model for soybean, based upon these and field data.

We report here thermal requirements for floral bud growth and development for these and other species, including those for different Maturity Group genotypes of soybean. As Aitken (1) reported, the thermal requirement for bud growth is affected by photoperiod in late-maturing genotypes. In other words, floral bud growth and development is sometimes more affected by photoperiod than floral bud initiation.

MATERIALS AND METHODS

Plants were grown as described in earlier reports (2,6) under approximately 600 $\mu\text{mol m}^{-2} \text{s}^{-1}$ PAR. Three of the growth cabinets were modified to use outside air during the winter months for cooling. Two cabinets were cooled with air conditioners. Eighteen 100-W incandescent lamps were used to extend daylengths from 11 h of 600 $\mu\text{mol m}^{-2} \text{s}^{-1}$ PAR to 12, 13, 14, 15 and 16 h. Air temperatures were maintained at 29°C during the 11-h period of maximum light and at 19°C during the remaining 13-h.

In most cases at least six plants were allowed to grow to flowering ; other plants were thinned to determine the time that the first flower was initiated, as detected using a standard dissecting microscope. One growing season in the

field was used to become familiar with the technique, using a standard soybean cultivar. Detecting floral bud primordia in soybean was difficult, compared to those in other species. In a few cases, we ran out of plants before detecting a bud. We also noted the number of nodes at floral initiation and flowering, which, of course, are the same when the main shoot terminates with a flower, as in maize.

Many of the species and strains used in these studies are listed in Tables 1 and 2. Soybean strains used, with their Maturity Group designations (00-IX), were [1] Acme (00), [2] Clay (0), [3] L71-920 (I), [4] L65-778* (I-II), [5] L63-3117(II), [6] L63-2404 (III), [7] Williams (III), [8] Clark (III-IV), [9] Pixie* (III), [10] L66-432 (IV-V), [11] L65-3366 (V), [12] Tracy* (VI), [13] D84-8400* (VI), [14] Bragg* (VII), [15] Braxton* (VII), [16] Hardee* (VIII), [17] Crockett* (IX), and [18] Padre* (VII-IX). The strains with an asterisk are determinate; all others are indeterminate. Wang *et al.* (5) described many of these soybean strains; they range from early (00) to late (IX) maturing, and from being insensitive (00) to very sensitive to photoperiod, for flowering and maturity. These strains are grown from southern Canada (00) to southern Florida (IX).

Table 1. Degree day requirement for growing a floral bud from the first detected primordium to open flower.

	Base Temper- ature (°C)	Daylength (h)				
		12	13	14	15	16
(Degree Days)						
Soybean (<i>Glycine max</i> (L.) Merr.)						
Acme (MG* 00)	10	248	230	297	284	270
Williams (III)	10	248	243	311	379	460
L65-3366 (V)	10	200	298	774	800+**	800+
Tracy (VI)	10		378	576		
D84-8400 (VI)	10		392	609		
Bragg (VII)	10		473			
Braxton (VII)	10		406			
Cotton (<i>Gossypium hirsutum</i> L.)						
Deltapine 90, late maturing	12			402	391	402
Paymaster 145, early maturing	12	495		391	437	403
Maize (<i>Zea mays</i> L.)						
Pioneer 3377	7	565		597		613
Velvetleaf (<i>Abutilon theophrasti</i> Medic.)						
	10		365	340	365	459
Jimsonweed (<i>Datura Stramonium</i> L.)						
				284		
Cocklebur (<i>Xanthium strumarium</i> L.)						
	10	338		311		

* Maturity Group designation. Maturity Groups range from 000 through IX (12 groups, with intergrades) in the USA and Canada, according to how early they mature at different latitudes.

** Floral buds took more than 800 degree days to open.

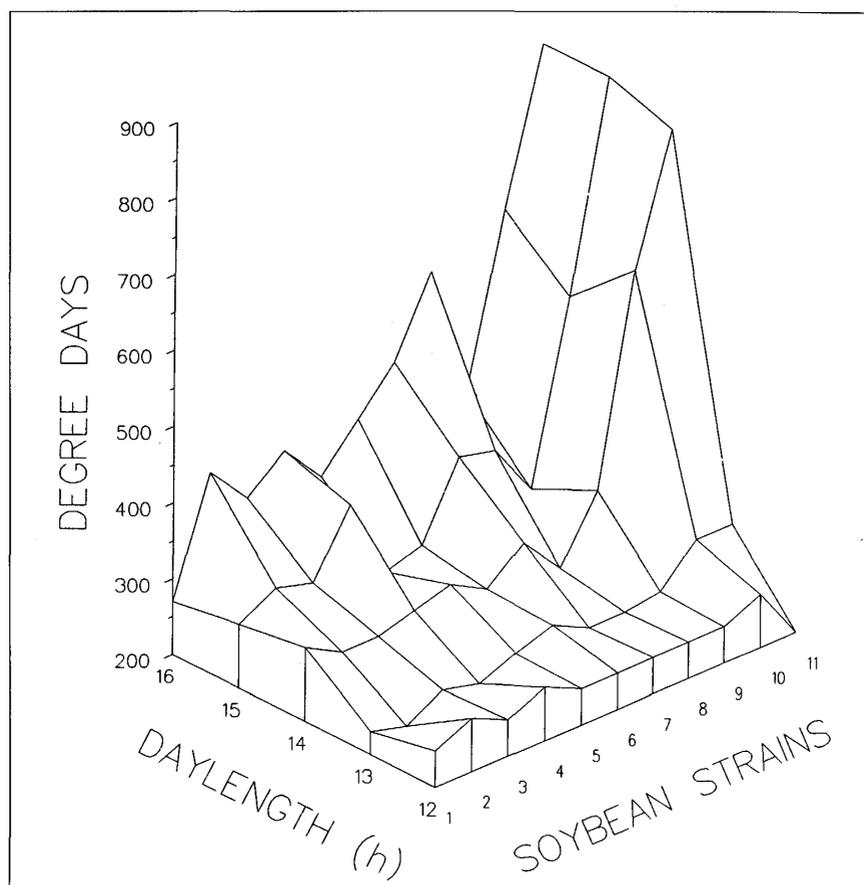


Fig. 1. Degree days from floral bud primordium to first flower in 11 soybean strains under 5 daylengths, with the same day/night temperature. The strains used, which ranged from early (1) to late (11) maturing, are defined in the Materials and Methods. The maximum value shown is 800 degree days.

RESULTS AND DISCUSSION

Table 1 and Fig. 1 show the degree day requirement for growing a floral bud from initiation, as detected with a dissecting microscope, to open flower, with the base temperature used in its calculation, for early and late maturing soybean strains and cotton cultivars, maize and three weed species. The first flower aborted in jimsonweed in four treatments out of five; since no values have ever been reported, we report here our one treatment mean value.

The soybean experiment was stopped after some 800 degree days had accumulated from the detection of the first floral bud in the late-maturing soybean strains. Jones and Laing (4) used a very late-maturing cultivar in their experiments, and measurements were made under daylengths (approximately 11 to 13 h), prevailing at 34° latitude, by varying the sowing date. Our measurements under long days for the later maturing genotypes were greater than any reported by Jones and Laing (4), documenting the daylength effect that

they anticipated. This means that floral bud initiation alone cannot be used in daylength studies among photoperiod sensitive soybean genotypes, when attempting to quantify time or degrees to the first open flower. Our strains 12 to 15 flowered 380 to 470 degree days after floral buds were detected in 13 h daylength, Table 1; Strains 12 and 13 did the same in 570 to 610 degree days in 14 h daylength. These and the remaining plants, that had not flowered but had initiated floral buds by at least 50 days from planting, were quite large, did have large floral buds, but obviously were going to take considerable time to open a flower, if ever, at 125 days after planting. It was difficult to prevent shading among such plants in the growth cabinets, but plants in the field under long days have behaved similarly (unpublished results). At this point the experiment was ended.

All the other species were relatively daylength insensitive, except for cocklebur, which had not produced a visible floral bud by the end of the experiment under 16-h daylength. These plants did flower at 15-h (Table 2), but we ran out of plants before detecting the floral bud.

Table 2 and Fig. 2 give the node where the first flower or floral bud appeared, as well as the total mainstem nodes at flowering, for these and some more species. The mainshoot terminates in a flower in the determinate soybean strains, maize and jimsonweed, with some complex sympodial branching in the latter. We counted a mainstem node if the associated leaf had extended 10mm; a floral bud primordium first appeared some two nodes higher in velvetleaf, cotton and soybean. Floral bud primordia appeared more rapidly than leaves from that point on; floral buds were usually detectable at higher nodes when the first one was seen. We are now working on this aspect of the problem, as well as positional effects, for field-grown plants. Zur *et al.* (6) and Hesketh and Warrington (3) reported 6 additional mainstalk leaves above the tip when a

Table 2. Total mainstem nodes at first flower and the node of the first flower.

	Daylength (h)				
	12	13	14	15	16
Cotton					
Deltapine 90, late maturing	15/5.0	18.3/7.7	16/6.3	14/4.6	16/5.8
Paymaster 145, early maturing	—/4.1		—/4.3	—/4.5	—/4.5
Velvetleaf	—/5	14/7.7	15.5/9.5	16.5/12	20.7/14
Cocklebur	8.1		9.2	19/16.5	22/—
Jimsonweed		6.5	8	9	8
Maize	17.3		18.5		19.6
Soybean strain, (Maturity Group)					
L71-920 (I)	6.5/2.2	7/3	6.3/2.3	10/2.2	7.5/2.8
Williams (III)	6.3/2.0	8/3.7	8.7/4.4	10.5/4.7	13/9
L65-3366 (V)	7/3.3	11/6.5	18/11	24/11	23/11
Tracy (VI)	6/2	12/8	18/10	26/12*	28/12.7*

* Total nodes at the end of the experiment /node of first floral bud ; all others total mainstem nodes at first flower/flowering node.

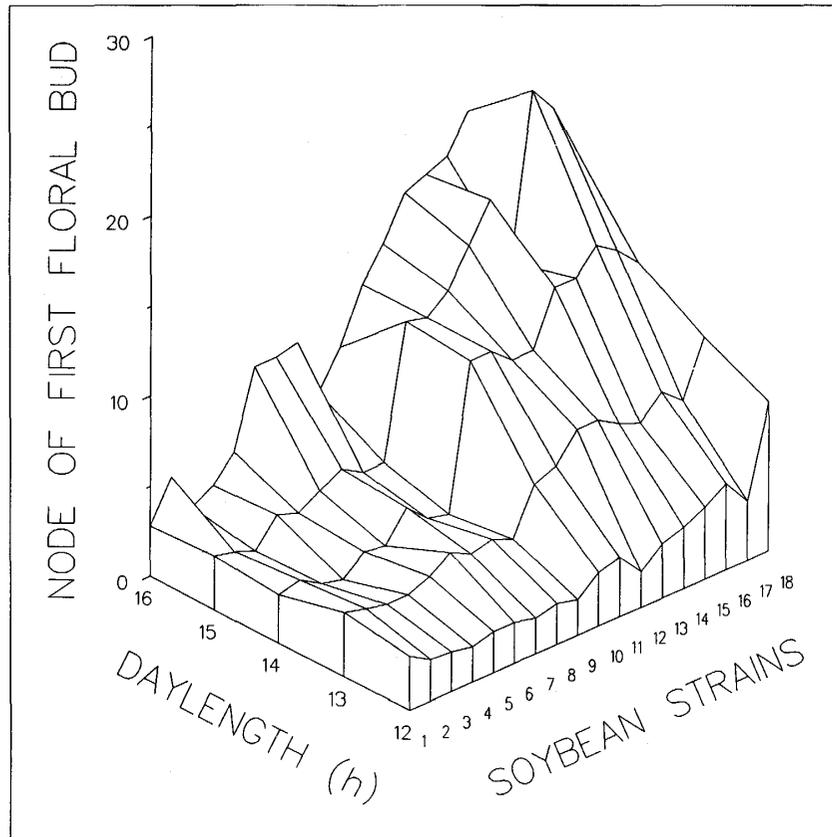


Fig. 2. The node number of the first flower or floral bud of 18 strains of soybean under 5 daylengths with the same day/night temperature. The strains used are defined in the Materials and Methods. The maximum value shown is 21 nodes. Floral buds had not opened in the late-maturing strains growing under the longer daylengths, by the end of the experiment, see text.

maize tassel appeared at the stalk apex.

Table 2 gives some values for total mainstem nodes, up to and including the one with a 10 mm leaf, at flowering. When grown at a range of climates, Aitken (*1*) found that for an early pea cultivar, there was a simple temperature requirement for the appearance of the first floral bud, flower and ripe seed. In a late cultivar, experiencing a wider range of climates because of a longer growth period, and being much more sensitive to photoperiod, there was no clear relationship, or if anything, the response to temperature was reversed. We show here for soybean what the photoperiod component of the response might have looked like. Aitken (*1*) discussed in detail situations when cool temperatures seem to hasten flowering or seed growth. She had to contend with the cold requirement for floral induction in winter wheat.

For actual floral bud primordia initiation to open flower, one would need to add some additional thermal time, to take into account bud growth between initiation and when we could detect a bud with our dissecting microscope. Such values can be used to determine the photoperiod (cf. Wang *et al.*, *5*) and other

weather characteristics at approximately the time that a flower is initiated, if the date of flower opening is known. Of course, a few dissections near floral initiation should result in better estimates of when this event occurred. Such information is needed from field and controlled environment studies to learn how predict better the effects of climate on phenology.

NOTE : J. F. Thomas (7) summarized earlier her published data showing that the growth of soybean floral buds is slow for a late maturing cultivar growing under long photoperiods. The reader should check her review and earlier papers for details.

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