

Variability of Floral Characteristics Influences Honey Bee Visitation to Soybean Blossoms¹

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ABSTRACT

Group O-III cultivars of soybean, *Glycine max* (L.) Merr., screened for floral variability (e.g. flower size, color, abundance, cleistogamy, aroma, nectar production, and blossom sequence) demonstrated a continuum between extreme limits for most of these factors. Cultivars potentially attractive to honey bees (*Apis mellifera* L.) were ranked from high to low, based on their rate of nectar secretion. The responses of late flowering under fluorescent light and temperature insensitivity at flowering (noncleistogamic) were found to be associated with higher production of nectar, which suggests possible methods of screening for potential bee attractiveness. The effect of weather in Wisconsin on the flowering and bee visitation for one soybean cultivar was studied in detail. Here, flowers failed to open and nectar secretion ceased at daily mean ambient temperatures below 21 C.

Additional index words: *Glycine max* (L.) Merr., *Apis mellifera* L. Pollination, Floral biology.

INVESTIGATIONS pertaining to the visitation of soybeans, *Glycine max* (L.) Merr., by honey bees (*Apis mellifera* L.) were undertaken at the USDA Bee Res. Lab., Madison, Wis., in 1971 because: beekeepers need more information concerning soybeans as bee pasture (6, 7); the potential for increasing soybean yield through honey bee pollination exists (4); and hybrid soybeans (2) will require insect pollination. The effort involves clarification of the factors that influence bee attractiveness of soybeans to bees and a determination of which cultivars are most attractive to bees.

Since all soybean cultivars are restricted geographically to narrow latitudes according to rate of maturation (maturity group), the data acquired in Wisconsin may not be directly applicable elsewhere. However, hopefully the data will stimulate similar investigations at other latitudes.

METHODS

1972 Test of Cultivars

Eighty-eight public and commercial soybean cultivars and experimental lines planted in 6-m long rows 91.4 cm apart at Madison in 1972 (uniform soybean tests) were used for the major portion of the study. These were sown in randomized block design with 49 replicated four times, 15 replicated twice, and the balance (mainly experimental lines) in single rows. A second experimental site at Clinton, Wis. with about 1,200 lines planted in 7.6-m long rows 76 cm apart was used for less intensive observations.

The screening procedures used to determine the extent of floral variation among soybean cultivars and experimental lines included nectar analysis for quantity and percentage dissolved solids, determination of flowering habit (early or late), classification of the flower (color and size), and susceptibility to eco-

logical cleistogamy or cleistoflory. Honey bee visitation of cultivars was noted and climatological data recorded at the Madison site. Unseasonably cool and wet weather permitted only intermittent observations and occasional nectar sampling. Nectar in the blossoms was sampled by using 1 μ l pipettes to remove the nectar from the blossom. In each sampling period (1.5 hours; each replicate $n = 4$), an attempt was made to collect nectar secreted by five blossoms in each row by using one or more pipettes/row; nectar from the five blossoms was then pooled. The percentage of dissolved solids in nectar removed from bees (10 bees/sample) foraging on soybeans at midday was read directly by a hand refractometer. Floral size variation was determined by measuring the extreme width of the large standard petal of the first flower appearing at a node (always noticeably larger than subsequent flowers) and the length from the base of the flower to the tip of the standard petal. The bloom of a cultivar was categorized as exceptional ("showy") when more than three comparatively large white or purple flowers were open simultaneously at each node. Cleistogamy was rated as: 1 = fully open, 2 = partially cleistoflorous, and 3 = cleistogamous.

1973 to 1974 Tests of Cultivars

Entries and procedures at both locations in 1973 were similar to those used in 1972 though there was some substitution. Also, in 1973 an effort was made to determine parental sources of potential attractiveness to bees among chasmogamous cultivars and lines that were considered showy and that produced the greatest quantities of nectar in 1972. These cultivars and lines, their common parent strains, and other selected cultivars and lines were therefore grown in nonreplicated randomized plots (three 6-m long rows/plot) at Madison. Similarly, cultivars and lines that ranked high in 1973 in potential attractiveness to bees and other selected cultivars and lines were grown at Madison and Urbana, Ill. in 1974. These special plots were evaluated as in 1972 except that bees were not sampled for nectar. In 1973, the nectar analyses were again based on five-blossom samples ($n = 8$), but in 1974, they were based on 25-blossom samples ($n = 3$). At Madison (1973), the quantity of nectar/blossom in 'Saranac' alfalfa (*Medicago sativa* L.) was similarly measured coincidentally for comparison.

Floral Response of 'Hark.' In 1972, the floral response to weather was closely observed on Hark throughout bloom, weather permitting. Four nectar samples from flowers (25 flowers each) were taken at midday every other day from July 10 (first bloom) through August 13 (end of bloom). Nectar from foraging bees was sampled on alternate sampling days and reported as the mean of the percentage of dissolved solids (see above) in the nectar loads of 10-bee samples captured on blossoms at 10 AM, 12 noon, and 2 PM CST each sampling day.

RESULTS

1972 Test of Cultivars

Soybean cultivars and lines at Madison judged to be potentially most attractive based on flower size, color, flowering habit, nectar production, and chasmogamy are listed in Table 1. The color of the soybean flowers among the cultivars and experimental lines studied ranged from mauve accented with deep purple nectar guides to all white. The number of blossoms borne in racemes at the nodes of the stem and branches (and terminally) varied as did the number blooming simultaneously at a node (1 to 13). Also, some cultivars bloomed at many nodes simultaneously, and others bloomed progressively from the first node,

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Table 1. Potentially bee-attractive groups I to III of soybean cultivars and experimental lines in order of nectar secretion (1972).

Strain	Maturity group*	Nectar, μ l		n†	Flowering§	Color¶	Flower		Chasmogamy‡‡
		\bar{x} †	(S \bar{x})				Size††		
							Length	Width	
AX 227-31§§	II	0.063 ±.151			L	P	9.3	7.6	1
M61-224	I	0.063 ±.012			L	W	7.5	6.3	2-3
Hark	I	0.05 ±.01		20	L	P	8.0	7.1	2
W7-186	I	0.05 ±.007			E	P	8.0	6.5	3
Chippewa 64	I	0.038 ±.007			E	P	7.4	6.2	3
Wirth	I	0.038 ±.005			E	P	7.1	6.4	3
M63-217	I	0.038 ±.005		8	L	P	7.4	6.4	2
SRF-150	I	0.038 ±.019			—	P	7.5	5.7	2-3
W8-37	I	0.038 ±.005			E	P	7.7	6.5	3
C1512	II	0.035 ±.004		8	L	P	7.9	7.0	1
M62-263	I	0.033 ±.006			L	W	8.0	—	3
Provar	II	0.025 ±.004			L	P	8.0	6.0	2-3
Wells§§	II	0.025 ±.006			L	P	7.9	6.2	2-3
M63-194	I	0.025 ±.006			E	P	8.1	7.0	2-3
XK125	I	0.025 ±.004			—	W & P	7.1	6.8	2
XK505	III	0.025 ±.004			L	P	8.6	6.7	2-3
1-A	II	0.025 ±.004			—	P	8.0	6.6	2-3
Corsoy	II	0.017 ±.004			E	P	8.0	6.6	2-3
Steele	I	0.017 ±.006			E	P	7.6	6.4	3
Dunn	I	0.013 ±.003			L	P	7.8	6.8	3
Rampage	I	0.013 ±.003			E	P	7.3	6.1	3
FFR950386	II	0.013 ±.003			—	P	6.9	—	2-3
FFR955048	II	0.013 ±.003			—	P	8.3	6.4	2-3
SRF-100	I	0.013 ±.003			—	P	6.4	—	3
Beeson	I	0.008 ±.003			L	P	7.9	—	2-3
Amsoy 71	II	0.003 ±.001			L	P	8.5	6.7	2-3
L69D-133	II	trace		8	E	P	7.9	7.2	2-3
Blend 2§§	II	—			E & L	P	8.5	6.7	2-3
A66-1441-2	II	—			L	P	7.8	6.2	2-3
C1510	II	—		8	—	W & P	8.3	7.4	1

* Adaptation to narrow belts of latitude.

† Mean of four samples of five blossoms each taken over one, two, or four replicates.

‡ n = 16 unless otherwise noted.

§ Under fluorescent light with E = early flowering (about 35 days) and L = late flowering (about 70 days).

¶ P = purple, W = white.

†† Means of five blossoms

for each cultivar. All standard errors were < 0.3.

‡‡ 1 = chasmogamous (fully open), 2 = partially cleistoflorous, and 3 = cleistogamous.

§§ Showy: blossoms large, supernumerary at nodes, and conspicuous.

except that latent blossoms occurred sporadically at the lower nodes. Most cultivars fell between these extremes.

Variation in the size of soybean flowers was also evident among cultivars and experimental lines (Table 1). Some flowers were long and narrow, others were short and broad. Measurements of all cultivars and lines studied indicated that blossoms ranged from about 6 to 10 mm long (mean about 8 mm) and from 5 to 8 mm wide (mean about 6.5). Occasionally, cleistogamy prevented accurate measurement.

The few cultivars or experimental lines with exceptional flower coloration, size, and abundance that appeared showy in comparison with others (Fig. 1) are noted in Table 1. These exceptions are not apparent to the casual observer because the flowers are concealed by the leaf canopy.

Intervarietal variations in flowering response to cool temperatures (facultative cleistogamy) were obvious (Fig. 2). Some cultivars or experimental lines (e.g., 'Illini' and AX 227-31) were noncleistogamous at temperatures that induced cleistogamy in others, but exceptionally cool temperatures did induce cleistogamy in Illini and AX 227-31, as well as in Hark. 'Chippewa' blossoms were open only slightly in Wisconsin, though at Urbana they were nearly but not fully open. Cleistogamic flowers rarely opened, but with the onset of favorable weather, succeeding blossoms on the same plant or cultivar sometimes opened fully, thus, weather change caused the cultivars and lines to respond variously during bloom.

Nectar secretion in 1972 was highly variable among cultivars and experimental lines. Table 1 reports those

that produced nectar and were thus potentially most attractive to bees in Wisconsin. The size of the standard errors can probably be attributed to daily weather change. Most cultivars and lines studied did not produce nectar even though they were not cleistogamous. Also, a few that were semi-cleistoflorous did produce nectar though the quantities were usually slight. None without nectar were considered showy. Cleistogamy and cleistoflory are unreported from southern latitudes. However, temperature sensitivity may influence nectar production among southern cultivars.

Although aromatic soybean flowers have infrequently been reported (10), I was unable to detect flower aroma in any of the cultivars or lines studied in 1972. However, 'Raiden,' brought to my attention by Richard L. Bernard of the USDA Regional Soybean Lab. at Urbana, that was sown at Madison and Urbana in 1974, did possess a faint floral fragrance at high temperatures.

The flowering response (early or late) is not known for all cultivars or lines listed. However, from those that are known, the late allele E_3 (3, 8) predominated among those considered most attractive to bees (true also in 1973-74), and the early allele predominated among non-nectar producing cultivars and lines. Similarly, maturity groups I, II, and III were common among those producing the greatest quantity of nectar (maturity groups I and II are favored at this latitude).

The extensive plantings at Clinton were screened empirically, and lines were noted that appeared superior in the categories also used in Table 1. However, 26 of 38 lines selected as superior in 1972 (also 43 of 53 lines selected in 1973) had as one or both



Fig. 1. Flowering of soybeans: A) sparse $\times 0.25$ and B) showy $\times 0.15$.

parents 'Wayne,' Hark, 'Amsoy,' and 'Habaro' (the first three possess the late flowering allele.)

1973 to 1974 Tests of Cultivars

The results of the 1973 and 1974 trials are summarized in Table 2. The same cultivars and experimental lines that were ranked high at Madison in 1973 were ranked high at Urbana in 1974. Both the late flowering allele and showiness were prevalent among but not wholly confined to the highly ranked cultivars. White blossoms were dominant among the cultivars, lines, and parents that ranked highest in attractiveness. In 1974 the slightly aromatic cultivar Raiden, a cleistogamy-resistant cultivar, selected for

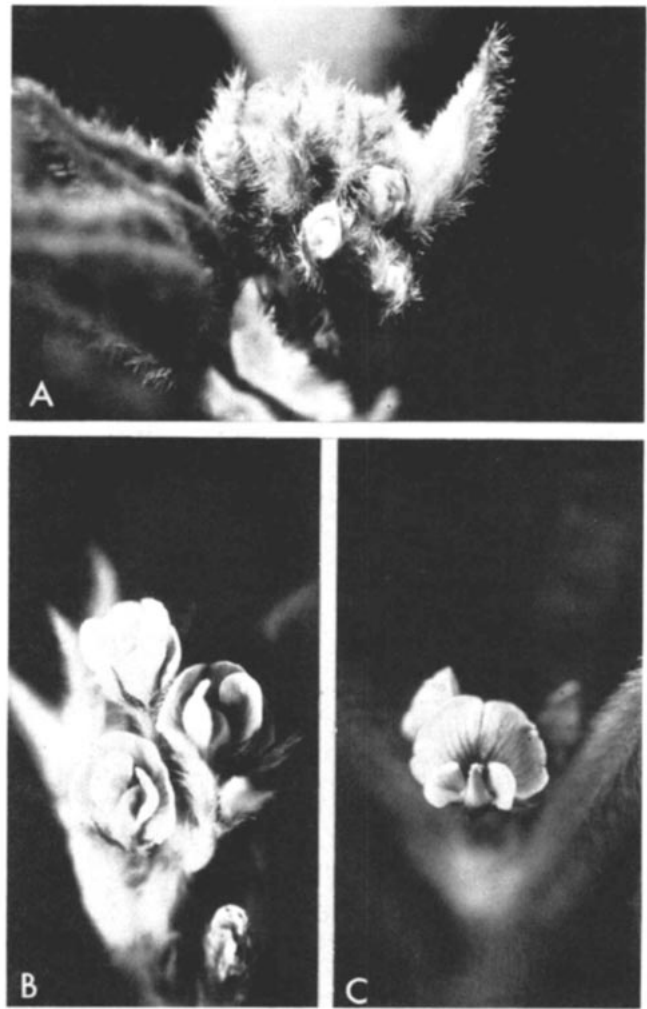


Fig. 2. Soybean blossoms: A) cleistogamous, B) partially cleistoflorous, and C) completely open $\times 2.5$.

areas of northern Japan, exceeded all other cultivars and lines studied in showiness, resistance to cleistogamy, and quantity of nectar produced (Urbana only, nectar production at Madison in 1974 was too slight for comparison).

During 1973, most cultivars or lines grown at Madison were nearly cleistoflorous or cleistogamous (Table 2) because of the below normal temperatures and above normal precipitation during bloom. The mean quantity (μ l) of nectar produced from each five-blossom sample ($n = 8$) in cultivars or lines judged less than cleistogamous, but not listed in Table 2 were: SRF 150, 0.11; FFR 950794, 0.07; IRV 1120, 0.07; FFR 950200, 0.06; SRF 200, 0.06; A 72119, 0.05; A 72133, 0.05; and SRF 69691, 0.05.

Floral Response of Hark. Figure 3 and the following data illustrate the effect of weather on flowering of and bee visitation to Hark, a cultivar that is more resistant to cleistogamy than most and is now known to be attractive to honey bees. The mean quantities (μ l) of nectar removed from flowers and the dates sampled were as follows: 0.36, 7/14; 0.08, 7/21; 0.01, 7/28; 0.45, 7/30 (10 flowers/sample, $n = 10$); 0.05,

Table 2. Floral biology of soybean parent and selected strains (1973 & 1974).

Strain	Maturity group*	Maximum nectar production, μ l†		Flowering‡	Color§	Flower		Chasmogamy††
		Madison	Urban a			Size¶		
						Length	Width	
		1973	1974			mm		
Raiden‡‡§§	III	—	0.8	—	P	9.5	8.5	1
Illini‡‡§§	III	0.2	0.6	L	W	8.8	7.0	1
Wayne	III	—	0.7	L	W	L	6.3	1
Lincoln‡‡	III	0.05	0.3	L	W			1
Williams	III†	—	0.25	L	W	M	7.3	1-2
L73-1411	III†	—	0.15	—	—			1
Mukden	II†	0.1	0.1	L	W	8.3	7.3	1
Adams	III	0.1	0	L	W	8.8	6.9	1
XK125	I	0.1	—	—	W & P	7.1	6.8	2-3
Corsoy	II	—	0.05	E	P	8.0	6.6	2
A227-31‡‡	II	—	—	L	P	9.3	7.6	1-2
AK Harrow‡‡§§	III	—	—	L	W	7.7	6.4	1
Clark‡‡	IV	—	—	L	P	M	7.0	1-2
L71L-06-4‡‡§§	III	—	—	—	W & P			2
Mandarin	I	—	—	E	P	M	6.3	2-3
Manchu	III	—	—	L	P			2-3
M61-224	I	—	—	L	W	7.5	6.3	2-3
Mandarin Ott.	I	—	—	E	P	M	6.2	2-3
Richland	II	—	—	E	P			3
Blackhawk	I	—	—	E	W	M	6.2	3
Chippewa	I	0	0	E	P			3
Checks								
Saranac alfalfa	N/A	0.1	—	N/A				
Hark soybeans	II	0.1	0.5	L	P	8.0	7.1	1-2

* Adaptation to narrow belts of latitude. L = late flowering (about 70 days). value is omitted. M = medium, L = large. supernumerary at nodes, and conspicuous.

† Five blossoms/sample, n = 8 (1973); 25 blossoms/sample, n = 3 (1974).
‡ P = purple, W = white.
§ Means of five blossoms for each cultivar. Standard errors were < 0.3. Size estimated where
†† 1 = chasmogamous (fully open), 2 = partially cleistoflorous, and 3 = cleistogamous.
§§ Bees abundant on flowers.

‡ E = early flowering (about 35 days).
¶ Means of five blossoms for each cultivar. Standard errors were < 0.3. Size estimated where
†† Showy: blossoms large,

8/4; and 0.5, 8/16. The percentages of dissolved solids (sugar concentration) in the nectar removed from the honey stomachs of worker bees, density of honey bees foraging in the field, and dates samples were: 35.8%, 1 bee/2.1 m row, 7/25; 39.7%, 1 bee/2.1 m row, 7/30; and 33%, 1 bee/0.9 m row, 8/17 (all n = 10). Foraging bees were absent from the field on 7/28 and 8/14. Weather prohibited sampling on all other dates between 7/10 and 8/17.

Plainly, chasmogamy occurred after the cool temperatures of 7/26 and 8/9, and foraging bees returned to the field about two days after nectar was again being secreted. However, the brief warming period that followed the 8/3 temperature drop was not sufficient to stimulate nectar production; also foraging was prevented by rain. Thus, nectar secretion in this cultivar appeared to be inhibited and cleistogamy induced at mean daily temperatures below about 21 C (low daily temperatures below 16 C). Confounding effects of daily temperature fluctuation and duration of the cool period were evident.

DISCUSSION AND CONCLUSIONS

The quality of soybean nectar (30 to 50% dissolved solids) appears to be average to slightly above average (see also 4). In general, plants compete well for the attention of bees with nectar sugar concentrations above 25%. The rate of nectar secretion in plants is controlled by a complex of interacting climatic and edaphic factors as well as inheritance (9), therefore, the low temperature threshold of 21 C evident in Fig. 3 is not absolute for nectar secretion in Hark. It appears that the response of this cultivar to temperature is comparable to other competing plant species.

The flowers of certain soybean cultivars opened only partially or not at all in southern Wisconsin, but it

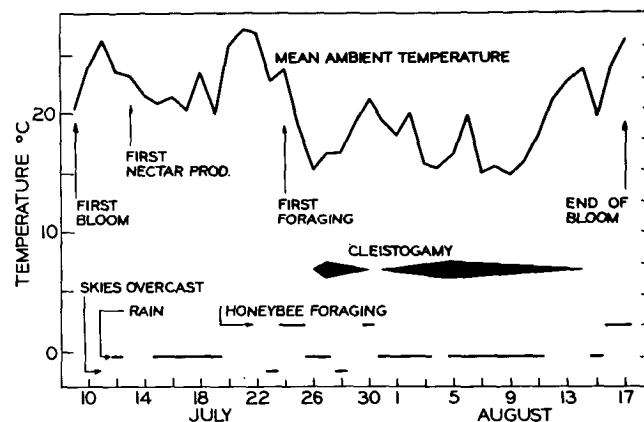


Fig. 3. The chronology of flowering and bee visitation for Hark soybeans at Madison, Wis., during 1972.

was not finally determined whether the ability of a soybean cultivar to resist cleistogamy (9, 11) is an indicator of its ability to secrete nectar under less than optimum climatic conditions, however, the data seem to support this hypothesis (1, 5). Cultivars that were semicleistoflorous usually continued to secrete a small amount of nectar at lower temperatures, but nectar was obtained from few cultivars that were cleistogamous. It is not likely that bees will visit these closed flowers (4).

Since soybean cultivars may bloom early to late in the season, peak bloom does not occur simultaneously, but samples of nectar were taken when all trial cultivars were blooming coincidentally. These data reflect comparability of climatic and edaphic factors but not plant maturity, so comparisons are valid, though absolute values may not be representative. Since all floral characteristics should be considered simultane-

ously, the apparent similarity in the volume of nectar produced by some soybean cultivars and by alfalfa in 1973 may not adequately reflect their relationships under other conditions.

The significance of the late flowering allele E_3 in relation to nectar production should be studied further. Susceptibility to temperature-induced cleistogamy may provide a way to screen for some aspects of attractiveness of soybean cultivars to honey bees, particularly nectar and aroma production.

Attractiveness to bees appeared to be heritable in soybeans as it is in most insect pollinated plants (9). Once genetically defined, this characteristic(s) might be combined with other desirable characteristics to develop male-sterile lines to be used in producing hybrid soybeans. Certainly the numbers of foraging bees observed on attractive cultivars and lines were sufficient to effect pollination of a male-sterile system. These data further suggest that it may be possible to improve soybean yields (4) through selection of lines and cultivars attractive to bees. The cultivars listed in this paper are those deemed exceptionally attractive to bees in southern Wisconsin, however, they may not perform as well as other cultivars in other localities.

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