

Soybean Pollination and Honey Production — A Research Progress Report¹

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IN LATE 1978 the North Central States Bee Research Unit, USDA-ARS, Madison, WI was the recipient of a special congressional appropriation in the amount of \$100,000 annually for the study of soybean pollination.² This appropriation was initially requested by the American Honey Producers Association whose members took the lead in guiding it through Congress. Because of widespread interest and support, an informal coalition of beekeepers from many states lent their support in a variety of ways and assured eventual passage of the appropriation.

Now, five years later we submit a progress report to those who supported this research, and to the American beekeeping public. For easy reference, we have provided a complete list of publications emanating from our soybean/honey bee research with those which were funded specifically from the special appropriation indicated by an asterisk. A narrative summary of our research on soybean pollination and honey production follows there after.

PUBLICATIONS

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4. Erickson, E. H. 1976. Bee pollination of soybeans. *Proceed. Sixth Soybean Seed Res. Conf.* pp 46-49.
5. Erickson, E. H., Berger, G. A., Shannon, J. G. and Robins, J. M. 1978. Honey bee pollination increases soybean yields in the Mississippi Delta Region of Arkansas and Missouri.

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- *7. Erickson, E. H. and Garment, M. B. 1979. Soya-bean flowers: Nectary ultrastructure, nectar guides, and orientation on the flower by foraging honeybees. *J. Apic. Res.* 18(1): 3-11.
- *8. Erickson, E. H. and Robins, J. M. 1979. Honey from soybeans: The influence of soil conditions. *Amer. Bee J.* 119(6): 444-445, 448-450.
- *9. Rust, R. W., Mason, C. E. and Erickson, E. H. 1980. Wild bees on soybeans, *Glycine max.* *Environ. Entomol.* 9(2): 230-232.
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- *13. Robacker, D. C., Flottum, P. K. and Erickson, E. H. 1982. A heat exchanger for soil temperature control of potted plants. *Agron. J.* 74: 147-148.
- *14. Severson, D. W. and Erickson, Jr., E. H. 1983. Variation in soybean (*Glycine max* (L.) Merrill) floral characteristics relating to honey bee (*Apis mellifera* L.) foraging preferences. Paper presented before North Central Branch of Entomological Society of America, St. Louis, MO.
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- *16. Severson, D. W. and Erickson, Jr., E. H. 1983. High performance liquid chromatography of carbohydrates in cucumber nectar. *J. Apic. Res.* 22(3): 158-162.
- *17. Erickson, E. H. 1984. Soybean floral ecology and insect pollination. *Soybean Genetics Newsletter* 11: 152-162.
- *18. Robacker, D. C. and Erickson, Jr., E. H. A bioassay for comparing attractiveness of plants to honeybees. (In preparation).

- *19. Robacker, D. C., Flottum, P. K. and Erickson, E. H. Soybean flower aroma: Chemical messages for pollinators? (In preparation).
- *20. Severson, D. W. and Erickson, E. H. Quantitative and qualitative variation in floral nectar of soybean cultivars in southeastern Missouri. *Environ. Entomol.* (In press).
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BACKGROUND

Soybeans, one of the five vital grains of ancient China (the others being barley, millet, rice and wheat) are the major agricultural product of the modern world. Their importance is reflected in the fact that in 1981 more than 51 million hectares (about 126 million acres) of soybeans were grown worldwide on an estimated 4 percent of all agricultural lands. Moreover, world soybean hectareage has increased 72 percent in the ten years from 1971 through 1980. In the United States, where they first achieved crop status in the early 1900's, soybeans are now the leading cultivated crop commanding up to 25% of the cropland in some areas. Since the early 1950's, the United States has committed more land to soybeans than any other country and in 1980, harvested over 27 million hectares (67 million acres) of soybeans; followed by Brazil (8.9 million hectares) and China (7.3 million hectares). Presently, the United States produces 66% of the total world soybean crop.

The explosion of interest in soybeans has resulted in a spectacular agricultural growth for countries like the United States and Brazil. Other countries will surely follow. The driving force behind this growth has been the number and diversity of products derived from this single farm commodity. Soybean products include those used for food (e.g. salad and cooking oil, shortenings, margarine, protein supplements, baby food, artificial meats and cheeses, soy sauce, and edible beans);

¹ Mention of a trade name does not constitute a guarantee or warranty of the product by the U. S. Department of Agriculture nor an endorsement over other products not mentioned.

² See: Gibson, Glenn. 1979. Soybean Research — A New AHPA Sponsored Project. *Am. Bee J.* 19(1): 60-61.

for animal and honey bee feed (e.g. whole and cracked grain, meal, and finely ground protein supplements); and in industry (e.g., oils, plastics, resins, paints, varnishes and in products for chemistry) just to name a few.

The cultivated soybean is an herbaceous annual, with uncertain ancestry. Most believe that its origin was in Eastern Asia, probably Northeastern China, where it was first cultivated about the 11th Century B.C. Like corn, the soybean may have been selected and bred by ancient man from a more primitive form that was different in growth habit and floral development. Existing primitive soybeans and the cultivated soybean may be the same species or perhaps, the ancestral soybean species has been lost.

Among the traits that may have been altered through man's selection and breeding is the soybeans' natural pollination syndrome. This could have occurred because selection of the cultivated soybean out of its wild parent was likely carried out in agricultural areas relatively free of insect pollinators. Hence, unwitting selection against bee pollinated types in the modern soybean would have been made. Couple this conjecture with numerous observations of good crop yields in the apparent absence of bees, and it is not surprising that many believe that bees cannot influence soybean yields. However, those who hold this view overlook four key points: 1) that the structure of soybean flowers definitely encourages bee visitation with concomitant pollination; 2) that bees forage extensively in soybeans; 3) that, in the

past, studies regarding the relative effect of pollinating insects on soybeans were usually conducted without knowledge of pollinator populations at the study site(s); and 4) that in the absence of an identified wild progenitor there has been no consideration given to the pollination of the ancestral parents of the cultivated soybean. We do know that a related species is insect pollinated.

The subject of honey bee foraging on soybeans has long been immersed in controversy, and debated publicly for over 50 years. There are those who have steadfastly maintained that bees do visit soybeans to gather nectar and pollen (and perhaps pollinate them) while others hold the opposite view with equal conviction. Both observations may, in fact, be accurate.

A somewhat complex picture of interactions between soybean cultivar and environment seems apparent. At certain locales and under certain circumstances foraging by bees on a soybean cultivar may be extensive; at other locales, it may be limited or nonexistent. As a result, floral nectar may or may not be secreted and bean yield may or may not be affected.

RESEARCH PROGRESS

SOYBEAN FLOWERS

Certain cultivars of soybeans are more extensively visited by bees and produce greater quantities of nectar and aroma than do others. Moreover, since soybean cultivars are restricted geographically to narrow latitudes based upon rate of maturation, those

cultivars known to be preferred by bees in one area may or may not produce nectar or aroma and therefore may not be attractive to bees at other localities. Hence, when referring to soybeans one must consider the specific cultivar involved. Cultivars grown within the range of their maturity group seem to elicit the most intense bee/flower interactions.

Other factors further contribute to optimal floral development and pollinator foraging. Soybeans have long been and in some areas are still considered a secondary crop, grown only in deference to other row crops such as corn and cotton. For this reason, perhaps more than any other, the best soybean husbandry practices such as optimizing plant density and nutrient fertilization have not always been followed. For example, many farmers do not follow existing recommendations and adjust their planter to narrower rows for soybeans after planting corn or cotton. And frequently, farmers plant their best land to other crops giving their fields of lesser productive capacity over to the beans. Poor crop husbandry contributes to reduced bee visitation due to altered bee foraging cues and rewards.

The Flower

The soybean flower is variable in size among varieties: some are long and relatively narrow while others are short and broad. Petal color ranges from white through mauve to purple, yet most cultivars possess pigmented flowers. Each zygomorphic (petals are unequal in size) flower has five petals (Fig. 1). The standard petal is bound on either side by a smaller wing petal while two tightly clasped ventral keel petals partially enclose the sexual column.

Previously published depictions and descriptions of soybean nectaries create confusion because of their inaccuracies. It is quite clear that soybean blossoms possess most, if not all, anatomical characteristics of bee-pollinated flowers including: 1) nectar guides (both in the visible and ultraviolet spectra), 2) a characteristic aroma (detectable at higher temperatures, e.g. above 27°C = 80°F), 3) a tongue channel and guide (for pollinators — probably bees), and 4) a highly differentiated nectary (Fig. 1) that produces substantial quantities of nectar. Preliminary data suggest that floral aromas may inform pollinators of flower pre-readiness, readiness and post-readiness for visitation (pollination) with separate chemical messages. Further studies are now underway to identify and bioassay flower volatiles and to confirm this concept. The structure of the flower and the approach behavior of the foraging bee ensure that bees will contact the sexual parts of the flower whether gathering

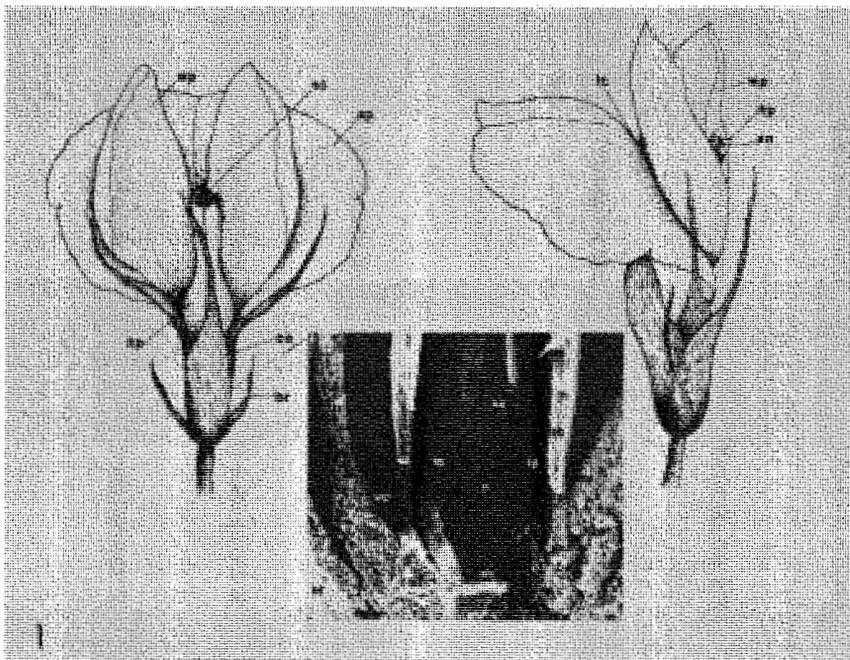


FIG. 1. Drawings of a soybean flower with center photograph (magnified 25 times) inset to show the nectary and its position in the flower. Abbreviations are as follows: an — anther; br — bract; ca — calyx; kp — keel petal; n — nectary; ob — ovary base; sc — staminal column; sp — standard petal; ss — single stamen; tc — tongue channel; tg — tongue guide; wp — wing petal.

nectar or pollen. Yet, in cool climates or during cool weather the flowers of most soybean cultivars never open (are cleistogamous) and hence are inaccessible to bees.

Two to 35 flowers are borne in racemes (clusters) at the nodes of the stem and branches. They first open at the base of the raceme and then open progressively upwards. Each soybean flower is open for only a single day but from one to 13 may be open simultaneously on a raceme, depending upon the cultivar. When the leaf canopy is moved aside multiflowered cultivars appear quite showy. The number of flowers produced per hectare is highly variable among cultivars. A soybean field is usually in bloom for 4 to 6 weeks and in agricultural areas where early and late adapted cultivars bloom in succession, a 6-9 week flowering period ensues.

Nectar

Soybean blossoms have functional nectaries. Each flower of most cultivars produces only slightly less nectar than alfalfa in northern regions. Sugar concentrations in soybean nectars are 5-10% higher than those of alfalfa when growing conditions are favorable. We see similar variability among cultivars in nectar production and attractiveness to bees in both southern and northern regions of the United States.

In the central United States soybean nectar production, and bee visitation, occur between 0900 and 1500 h (9:00 am-3:00 pm) each day. Peaks in these activities, like the time of day when the flower is first fully open, may vary depending upon the cultivar and local weather conditions. Soybean nectar volume per flower, greatest in warmer climates, varies significantly among cultivars ranging from none to 0.2 microliters per flower, with some flowers having as much as 0.5 microliters (Note: the honey stomach of a worker honey bee holds 35-50 microliters.).

We and others have examined soybean nectar and reported a mean nectar sugar content of 37.0 to 45.0 percent. In Missouri and Arkansas, the total carbohydrate content in soybean nectar varied from 301 to 1354 micrograms per microliter of nectar and from 15 to 134 micrograms per flower. Floral sugar concentration increased, but volume decreased with time of day and temperature. Nectar sugar ratios (ie. fructose:glycose:sucrose content) differ among soybean cultivars as well as with time of day within a cultivar. We noted no differences in carbohydrate content between purple and white flowered cultivars. Earlier in Wisconsin, nectar production from flower to flower appeared to be most consistent in volume and carbohydrate content among white flowered cultivars, hence, white flowered cultivars were judged more attractive than purple cvs. But, later work in Missouri



FIG. 2. Honey bee gathering nectar from a soybean flower.

seems to dispel this notion.

Pollen

Honey bee collection of soybean pollen is highly variable as is a cultivar's ability to produce quantities of pollen. Little soybean pollen may be gathered by bees in some areas. However, soybean pollen may comprise over 50% of the total quantity of pollens gathered by many bee colonies. Soybean pollen pellets taken from the corbiculae of foraging bees are easily recognized by their grey-brown color, small size and compaction.

SOYBEAN HONEY PRODUCTION

Many species of bees, including honey bees (Fig. 2), forage soybeans for nectar and pollen. Honey bee populations may exceed a density of 1 bee per meter (= 3-3 ft) of row during peak foraging. Working in cooperation with others, we reported 29 additional species of bees that forage soybeans in three regions of the United States. The pollination contributions of, or benefits to bees other than honey bees foraging soybeans are unknown.

Beekeepers, particularly those in the central and southern United States, have been obtaining substantial yields (70 to 90 kg = 150 to 200 lbs per colony) of light amber honey from soybeans for decades. In so doing they have identified those agricultural lands where ample soybean honey production can be expected as well as those areas that are of unreliable or non-existent productivity. There is little doubt that many beekeepers unknowingly harvest large quantities of soybean honey. Often, soybeans are not exploited by beekeepers for the production of this honey which has a distinctive aroma and flavor and is easily identified with experience.

Nectar production in soybeans as in

other plants is dependent in part upon weather. During cool periods mature flowers remain partially or fully closed and have no nectar. In 1973 I was able to observe that plants in more northern climates (e.g. Wisconsin) required 3 days to recover the ability to produce nectar, following a period of cool weather even though subsequent flowers were open each day. The quantity of nectar produced per flower following cool weather usually will not reach the level that was present during the preceding favorable period. Temperatures above 22-24°C (= 72-75°F) are required to ensure soybean nectar production.

Intuitively, the most vigorous plants given optimal plant husbandry should produce the greatest quantities of nectar. Since most of the basic components of nectar, including sugars, are products of photosynthesis, the healthiest plant receiving the maximum amount of light and grown in the most suitable soil is likely to be the greatest producer of flowers with quality nectar and aroma and thus be the most attractive to foraging bees. Other researchers have shown that soybean seed yields are sensitive to the presence and availability of certain soil nutrients, soil pH, (a pH level of 6.0-6.5 is considered optimum) and soil moisture, as well as sunlight. Optimal soil pH and soil fertility are vital to the physiological well-being of the plant, as well as its ability to produce flowers, nectar and aroma and probably its response to bee pollination.

Soil texture, too, is important since it affects nutrient retention, soil moisture availability, and root penetration. In southern Missouri, others have shown that sandy, coarse loamy, and coarse silty soils provide the least amount of available water to the plant followed by the clayey soils; the fine

loamy and fine silty soils supply the greatest amount. Moisture stress reduces photosynthesis as well as flowering and pod filling. Coarse soils are readily leached and so are usually acid and low in fertility. Fertility can be restored to these lands, but unless good crop husbandry is practiced, our studies show that nectar secretion and resultant honey production is likely to be poor (10-20 kg = 22-44 pounds per colony). Heavier soils are less acid, more fertile, and retain their productivity partly because they are difficult to till. As a result, crop yields are usually high (2.6-4.3 kl/ha = 30-50 bu/acre), and our experience has shown high soybean honey yields (90 kg = 200 lbs. per colony) can also be expected. Similarly, nectar secretion in various other plant species has been shown to be adversely affected by low soil moisture availability, low soil nutrient availability, and low pH. Nectar secretion is generally low on soils with either too much or too little drainage (Table 1).

Our data from studies conducted in a controlled environment facility demonstrate that plant/flower characteristics, indicating greater plant vigor, were optimal at the intermediate day and night air temperatures (28 and 22-26°C = 82.5 and 72-79°F), the higher soil temperature (28-32°C = 82.5-90°F), and the higher (175 ppm) and lower (15 ppm) soil concentration of nitrogen (N) and phosphorous (P), respectively. Bioassays showed that honey bees preferentially visited soybeans that had more flowers which produced greater quantities of nectar. The predominant environmental factors contributing to attractiveness of soybeans to bees were moderate and high air temperature and high and low soil concentration of N and P, respectively.

BEE POLLINATION OF SOYBEANS

Soybeans are classified as self-fertile and automatically self-pollinating. It is said that pollination may occur before the blossom opens. Moreover, large numbers of fertilized and unfertilized flowers (more than 75% in some cultivars) drop off the plant and do not set seed. Thus, it would appear that soybeans normally set a full complement of seed and therefore have little biological need for insect pollination among cultivars and hence little need for the kind of floral development characteristic of insect pollinated plants. Indeed, many argue that such is the case. Others of us believe some outcrossing would be beneficial. The question is; how much interfloral pollen transfer both within and between cultivars occurs naturally?

One must now wonder whether the earlier observation that soybeans self-pollinate before the flower opens may

Table 1. Honey production in relation to soil conditions.

	Low Honey Production 13.5 kg (30 lbs) per colony	High Honey Production 90 kg (200 lbs) per colony
Soil pH	below 5	above 6
Fertility	low	high
Structure	coarse (sandy)	relatively fine (loamy)
Water holding capacity	low	high
Soybean yield	0.9-2.2 kl/ha (10-25 bu/acre)	2.6-4.3 kl/ha (30-50 bu/acre)

have involved a misunderstanding of cleistogamy and the fact that soybean blossoms are open for only a single day. Our studies in the controlled environment found that only thirty-three percent of the 'Mitchell' soybean flowers examined were completely self-pollinated 3.5 hours after the onset of photophase (artificial dawn): fifty-eight percent were self-pollinated 6.5 hrs after the photophase began. These results suggest that early in the day soybeans exercise a cross-pollination strategy which is followed by a self-pollination strategy later in the day. Follow-up field studies are now needed to examine this aspect of floral development under field conditions. If corroborated, we should expect that the timing of these strategies may vary with the cultivar's relative abundance of pollen and with other factors as well.

Our studies have shown that bees may increase soybean yields by as much as 20 percent for plots caged with bees vs caged without bees. I demonstrated a yield increase of 13.9 percent for the cultivar 'Corsoy' in 1971 and 5.2 and 16.3 percent for 'Hark' in 1972 and 1973 in Wisconsin. In the Mississippi Delta, we obtained a combined yield differential of 21.6 percent on the cultivar 'Pickett' at two study sites in Arkansas and Missouri in 1975. Here significant differences in the numbers of filled and empty pods were also noted. These differences were attributed to increased pod set since seeds pod and weight per seed did not vary. These results have since been corroborated by scientists working elsewhere in the United States and abroad.

In open field trials in Arkansas and Missouri, we obtained significant yield differences between that side of the field near the apiary versus the far side of the field. These data compare favorably with subsequent data sets: All show a high yield near the bees (5-15 m 16.5-50 ft from the apiary), a still higher yield at 20-35 m (= 65.5-115 ft) and then a progressive decline at greater distances from the colonies (Table 2). Similar patterns are common in other insect pollinated crops.

In other studies soybean yield differences due to bees have not been noted. We were unable to show significant yield differences in five cultivars ('Hark,' 'Williams,' 'Illini,' 'Wayne'

Table 2. Distance from apiary	Average number of seeds per sample*	
	Arkansas	Missouri
5-15 meters (16.5-50 ft)	785a**	836a
20-35 . . . (65.6-115 ft)	839a	931a
50-65 . . . (164-213 ft)	619b	776a
85-100 . . (279-328 ft)	630b	529b
115-150 . . (377-492 ft)	594b	-

* Each sample consisted of all seeds from 10 plants
** Within columns, values followed by different letters are significantly different at the .05 level.

and 'Mukden') over three years although caged treatments with bees usually slightly above those caged without in total beans and pods. Some cultivars during some years did show a significant difference in numbers of beans per pod. These studies were conducted in an area in southern Wisconsin on land of much higher productivity than the earlier trials with 'Corsoy' and 'Hark.'

Soybean cultivars are often identified as being determinant (cease vegetative growth before beginning to flower) or indeterminate (flower while continuing to grow). In reality all soybeans are indeterminate, but individual cultivars vary in their tendency towards determinancy, with later maturity group cultivars tending to be more determinant. I have yet to discern differences in foraging by bees or yield response resulting from bee pollination that can be explained based upon level of determinancy at flowering.

HYBRID SOYBEANS

The development of hybrid soybeans is a topic of interest both for beekeepers and plant breeders as well as others in agriculture. Substantial interest was generated after the discovery of genetic male sterility in soybeans. Others have attempted and are working to produce soybean hybrids. The present status of hybrid soybeans is uncertain as genetic male sterility presents some difficult problems if it is to be considered for commercial development of hybrids. Other forms of male sterility better suited for commercialization are yet unknown in soybeans. Once male sterility is discovered, in-

