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1) Soybean floral ecology and insect pollination.

The cultivated soybean (*Glycine max* (L.) Merrill) is an herbaceous annual, unknown in the wild, 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. (Probst and Judd, 1973). 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 (Probst and Judd, 1973) or perhaps, the ancestral soybean species has been lost (R. Bernard, personal communication).

Among the traits that may have been altered through man's selection and breeding is the soybean's natural pollination syndrome (Rubis, 1970). 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 (see Erickson, 1975a). 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. Note: We now know that a related species, *Glycine falcata* Benth., is insect pollinated (Anderson et al., 1983).

The subject of honey bee (*Apis mellifera* L.) foraging on soybeans has long been immeshed in controversy, and debated publicly for over 50 years (see Erickson, 1975abc). 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, as will become evident.

A somewhat complex picture of interactions between soybean cultivar and environment seems apparent. At certain locales and under certain circumstances, foraging by bees, the principal insect pollinators, 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.

Soybean flowers and honey bees   As I and others (Abrams et al., 1978; Erickson, 1975c, 1976; Erickson and Robins, 1979; Jaycox, 1970; Kettle and Taylor, 1979; Mason, 1979; Sheppard, 1975) have pointed out, certain cultivars of soybeans are more extensively visited by bees and produce greater quantities of nectar and aroma than 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 foraging cues and rewards (Robacker et al., 1982b; Robacker et al., 1983).

The flower   The soybean flower is variable in size; 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 flower has five petals. 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 (Carlson, 1973; Erickson and Garment, 1979).

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 (anthophilous) 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); 3) a tongue channel and guide (for pollinators -- probably bees); and 4) a highly differentiated discoidal nectary (Erickson and Garment, 1979) 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 (Robacker et al., 1982a). 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 nectar or pollen (Erickson and Garment, 1979). Yet, in cool climates or during cool weather, the flowers of most soybean cultivars are cleistogamous and, hence, are inaccessible to bees.

Two to 35 flowers are borne in racemes at the nodes of the stem and branches (Carlson, 1973). They first open at the base of the raceme and then open progressively upwards. Each soybean flower is open for only a single day (E. Erickson et al., unpublished data; Severson, 1983), but from one to 13 may be open simultaneously on a raceme depending upon the cultivar (Erickson, 1975a). When the leaf canopy is moved aside and several flowers are open simultaneously on each raceme, floriferous cultivars appear quite showy. The number of flowers produced per hectare is highly variable among cultivars. Sheppard et al. (1979) estimated a range of 1.3 to 4.1 million flowers per ha per day in Illinois. Generally, soybeans do not compete well with other legumes for the attention of bees, due to the relative numbers of flowers per hectare; other legumes, such as alfalfa and clover, may have up to 10 times the number of flowers per ha and greater numbers of flowers per cluster. 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 (Erickson and Garment, 1979). 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 (Erickson, 1975c; Severson, 1983). We see similar variability among cultivars in nectar production and attractiveness to bees in both southern and northern regions of the U.S.

In the central United States, soybean nectar production and bee visitation occur between 0900 and 1500 h 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 (Erickson, 1975c; Severson, unpublished data).

Several workers have examined soybean nectar and reported a mean nectar sugar content of 37.0 to 45.0% (Erickson, 1975bc; Jaycox, 1970). Kettle and Taylor (1979) reported a 39.5% sugar concentration for the cultivar 'Forest' in Kansas. Severson (1983) found that the total carbohydrate content in soybean nectar varied from 301 to 1354 μg/μl of nectar and from 15 to 134 μg per flower. Floral sugar concentration increased but volume decreased with time of day and temperature. Sugar ratios (i.e., fructose/glucose/sucrose) differ among soybean cultivars, as well as with time of day within a cultivar (Severson, 1983). Severson (1983) noted no differences in carbohydrate content between purple and white flowered cultivars. Nectar production from flower to flower appeared to be most consistent in volume and carbohydrate content (Erickson, 1975c) among white flowered cultivars; hence, white flowered cultivars were judged more attractive than purple flowered cultivars. But, later work by Mason (1979) and Severson (1983) seems to dispel this notion.

Sheppard (1975) and Sheppard et al. (1979) reported a mean sugar concentration of 39.9% (range 13.0 to 60.0%) for nectars of four soybean cultivars as taken from the honey stomachs of bees. Here, differences in sugar content among sampling dates varied as much as that among cultivars and fields. O'Keefe Van Der Linden (1981) reported sugar concentration in the stomachs of honey bees foraging soybeans in Iowa to be 28.0% (range 20.0-33.0%) in 1979 and 51.0% (range 38.0-63.0%) in 1980.

Pollen Honey bee collection of soybean pollen is highly variable as is a cultivar's ability to produce quantities of pollen. Some cultivars produce twice as much pollen as others (Palmer et al., 1978). Erickson (1975abc) and others (see Erickson, 1975a) have noted that little soybean pollen may be gathered by bees in some areas. However, I (personal observation) and Jaycox (1970) determined that soybean pollen comprised over 50% of the total quantity of pollens gathered by many bee colonies in Arkansas and Missouri and Illinois. Soybean pollen pellets taken from the corbiculae of foraging bees are easily recognized by their grey-brown color, small size, and compaction.

The bees Many species of bees, including honey bees, forage soybeans for nectar and pollen. Honey bee populations may exceed a density of 1 bee per meter of row during peak foraging (Erickson, 1975c). Sheppard et al. (1979) found that Caucasian bees gathered a greater percentage of soybean pollen (0-54% by day) than did Carniolan and Italian bees. Rust et al. (1980) reported 29 additional species of bees that forage soybeans in three regions of the United States. They reported further that others had identified several species of bees foraging on soybeans: Missouri, seven species; North Carolina, six species; Indiana, three species. The contributions of bees other than honey bees to soybean yields are unknown.

Soybean honey production Beekeepers, particularly those in the central and southern United States, have been obtaining substantial yields (70-90 kilograms per colony) of light amber honey from soybeans for decades (Erickson, 1975a; Warren, 1983). 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 nonexistent productivity (Erickson and Robins, 1979). There is little doubt that many beekeepers unknowingly harvest large quantities of soybean honey. For example, O'KeefeVan Der Linden (1981) found soybean pollen in 15 of 15 honey samples taken from eight Iowa counties in 1979, and in 46 of 48 samples from 35 Iowa counties in 1980. Only samples from the northeast corner of the state failed to show soybean pollen in the stomach contents of bees. 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 (Erickson, 1975abc).

Nectar production in soybeans, as in other plants, is dependent in part upon weather (Erickson, 1975c; Severson, 1983). 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 three days to recover the ability to produce nectar following a period of cool weather, even though the 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 are required to insure nectar production (Erickson, 1975bc).

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, the most attractive to foraging bees (Erickson and Robins, 1979; Robacker et al., 1982ab; Robacker et al., 1983; Shuel, 1975). 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. For example, soybean yields are significantly reduced when a crop is grown on acid soils that have a pH level below 6.0. Soil nutrient availability (particularly phosphorus and potassium) is reduced with increasing soil acidity. Various soil micronutrients are similarly affected. At low pH, potassium, phosphorus, calcium, and boron interact with one another, inducing deficiencies. Thus, optimal soil pH and soil fertility are vital to the physiological well-being of the plant (Erickson and Robins, 1979), its ability to produce flowers, nectar and aroma (Robacker et al., 1982a; Robacker et al., 1983) and, probably, its yield response to bee pollination.

Soil texture, too, is important to soybeans, since it affects nutrient retention, soil moisture availability, and root penetration. In southern Missouri, 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 (Erickson and Robins, 1979). Fertility can be restored to these lands, but, unless good crop husbandry is practiced, nectar secretion and resultant honey production is likely to be poor (10-20 kg 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), and our experience has shown that high soybean honey yields (90 kg per colony) also can be expected. 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 (Erickson and Robins, 1979; Severson, 1983).

Studies conducted in a controlled-environment facility demonstrated that plant/flower characteristics, indicating greater plant vigor, were optimal at the intermediate day and night air temperatures (28 and 22-26°C), the higher soil temperature (28-32°C), and the higher (175 ppm) and lower (15 ppm) soil concentration of nitrogen (N) and phosphorus (P), respectively. Bioassays showed that honey bees preferentially visited soybeans that had more flowers which produced greater quantities of nectar (Robacker and Erickson, 1984). 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 (Robacker et al., 1983).

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 (Carlson, 1973). Moreover, large numbers of fertilized and unfertilized flowers (more than 75% in some cultivars) drop off the plant and do not set seed (Carlson, 1973). 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 disagree. Even though the soybean retains a high level of heterosis because it is a disomic polyploid, 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 have involved a misunderstanding of cleistogamy and the fact that soybean blossoms are open for only a single day. Recently, Robacker et al. (1982a), working in a controlled environment, found that only 33% of the 'Mitchell' soybean flowers examined were completely self-pollinated 3.5 hours after the onset of photophase; 58% were self-pollinated 6.5 hrs after the photophase began. These results suggest that early in the day soybeans exercise a cross-pollination strategy that 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 temporalization of these strategies may vary with the cultivar's relative abundance of pollen (Palmer et al., 1978) and with other factors as well.

Cross pollination   Various workers have estimated natural cross pollination at from less than 0.5% to 35% (see Caviness, 1970; Erickson, 1975ab; Koelling et al., 1981; Sadanaga and Grindeland, 1981) with outcrossing most evident among lines in which pollination occurs the morning the flower opens (see also Robacker et al., 1982a). Note: See later section on hybrid soybeans for additional evidence of natural cross-pollination.

Outcrossing rates are a real measure of specific field circumstance, but one can neither consider them to be a measure of overall bee visitation nor a measure of pollination within a soybean genotype. While distance between pollen and seed parent and other factors have been shown to be related to outcrossing rates (Carter et al., 1983a; Nelson and Bernard, 1979), the primary limiting factors are undoubtedly the number of bees present and the level of fidelity to a single genotype practiced by individual bees. These must be determined, then bee pollination both within and between genotypes must be measured to ascertain the net result of pollinator activity.

Unfortunately, the true meaning of rates of outcrossing in insect-pollinated plant species has been misinterpreted by many people. Foraging honey bees normally discriminate among and retain a fidelity to a single floral source. And, so, just as honey bees discriminate among plant species, so do they often discriminate among cultivars or genotypes that differ in foraging cues (e.g., flower color and aroma) or reward within a species (see Erickson, 1983). This is true for soybeans (Severson, 1983). Outcrossing in soybeans is most frequently monitored between white and purple flowered cultivars (color differences that bees readily discriminate between) due to ease of evaluation based upon seedling hypocotyl color (e.g., Burton and Carter, 1983; Carter et al., 1983b). The fact that intraspecific crossing is usually low, when measured in this fashion, is hardly surprising given the well-known floral constancy of foraging bees. Apiculturalists would be surprised if it were otherwise!

Soybean yield increases   Recently, studies have shown that bees may increase soybean yields by as much as 20% (or more) for plots caged with bees vs. caged without bees. Erickson (1975a) demonstrated a yield increase of 13.9% for the cultivar 'Corsoy' in 1971 and 5.2% and 16.3% for 'Hark' in 1972 and 1973 in Wisconsin. In the Mississippi Delta, Erickson et al. (1978) obtained a combined yield differential of 21.6% 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 per pod and weight per seed did not vary. C. E. Mason (unpublished data), in Delaware, obtained three-year yield increases in cages with bees of 7.8%, 2.2%, and 15.8% for the cultivar 'Williams' and 16.0%, 2.7%, and 14.3% for the cultivar 'Essex' in 1978-80, respectively (data for the years 1978 and 1980 are significant at the 5% level). Kettle and Taylor (1979) obtained yield increases of 5.1%, 19.9%, and 36.0% ($\bar{X}$ = 20 percent -- significant at the 5% level for pooled result), respectively, at each of three study sites in Kansas for the cultivar 'Forrest'. A second cultivar, 'Woodworth', grown at yet another site, had a yield differential of 10% (significant at the 2% level). In Brazil, Juliano

(1976) noted a significant increase in both the number of pods and weight of total seed (37.9% and 40.1%, respectively) in open plots versus plots caged to exclude pollinators. In Italy, Pinzauti and Frediani (1981) obtained yield differentials in excess of 100%, in both seeds and pods, with bee pollination on two cultivars ('Grangeneuve' and 'Hei-iee-Jin'). Unfortunately, they, like Juliano, caged only the plot without bees and, thus, failed to evaluate the effect of the cage which, on soybeans, can be great (Erickson et al., 1978). Hence, while their conclusions may be correct, their exceptional results are likely due in part to the effect of the cage.

In open field trials in Arkansas and Missouri, Erickson et al. (1978) 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 those of Abrams et al. (1978): both data sets show a high yield near the bees (5-15 m from the apiary), a still higher yield at 20-35 m and then a progressive decline at greater distances from the colonies (Table 1). Similar patterns are common in other insect-pollinated crops.

Table 1.

Distance from apiary	Average number of seeds per sample[a] Arkansas	Missouri	kg/ha[b] Indiana
5-15 meters	785 a[c]	836 a	2654 a
20-35	839 a	931 a	2719 a
50-65	619 b	776 a	2473 a
85-100	630 b	529 b	2350 a
115-150	594 b	--	2350 a

[a]Each sample consisted of all seeds from 10 plants.

[b]Combined field data (Abrams, 1977).

[c]Within columns, values followed by different letters are significantly different at the .05 level.

In other studies, soybean yield differences due to bees have not been observed. E. H. Erickson and E. S. Oplinger (unpublished data) were unable to show significant yield differences in five cultivars ('Hark', Williams, 'Illini', 'Wayne' and 'Mukden') over three years, although caged treatments with bees were 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 higher productivity than the earlier trials (Erickson, 1975a) with Corsoy and Hark. Sheppard et al. (1979) were unable to demonstrate significant yield differences in open field studies in Illinois of 'Amsoy' and Williams, although their data show a slight trend of yield decline (similar to those in Table 1) with increasing distance from the apiary for Williams.

Soybean cultivars are often identified as being determinant (cease vegetative growth before beginning to flower) or indeterminant (flower while continuing to grow). In reality, all soybeans are indeterminant, but individual cultivars vary in their tendency towards determinancy with later maturity group cultivars tending to be more determinant (R. Bernard, personal communication). Even so, unlike Sheppard(1975), Sheppard et al. (1979) and Mason (1979), 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 (Erickson, 1979). Substantial interest was generated after Brim and Young (1971) reported the discovery of genetic male sterility in soybeans. Bradner (1977) attempted to produce hybrids using a genetic characteristic for open flowers that would enhance outcrossing. It was suggested that hybrid soybeans would be available in five to ten years. The present status of hybrid soybeans is uncertain, as genetic male sterility presents some difficult problems if it is to be considered for development of commercial hybrids and the work initiated by Bradner is not progressing as expected. Cytoplasmic male sterility in soybeans is as yet unknown.

Some studies have shown that there may be a relatively high level of cross pollination (62%) in at least one genetic male-sterile soybean (Sadanaga and Grindeland, 1981). Koelling et al. (1981) found a significant increase in seed set on male-sterile soybeans caged with bees versus caged without bees (honey bees, 39 seeds per plant; alfalfa leafcutter bees, 40 seeds per plant; no bees, 3 seeds per plant). Similarly, Nelson and Bernard (1979) obtained fewer than 10 seeds per plant at 15 m from the pollen parent to more than 70 seeds per plant at 1.5 m in studies to determine the relationship of distance from pollen source to pollination of male-sterile soybeans. In these studies, the male-sterile plants produced an average of 27 seeds per plant -- far less than the normal production of 70 to 100 + seeds per plant (Erickson, 1975a; Erickson et al., 1978). Again, these data must be interpreted carefully considering the discriminative foraging behavior of bees discussed earlier. Inadequate pollination is a major factor limiting the production of hybrid soybeans (Nelson and Bernard, 1984), just as it has limited hybrid production in other crops (Erickson, 1983).

Whether hybrid soybeans will become a commercial reality remains to be seen. Some researchers feel that it is just a matter of time; others think it unlikely that hybridization will ever become sufficiently practical for commercial seed production. Certainly, hybridization would contribute substantially to the research programs of plant breeders by reducing the necessity for hand-crossing and for obtaining large-scale outcrossing for recurrent selection (Burton and Carter, 1983; Carter et al., 1983a). Meanwhile, forthcoming soybean flower-pollinator data will enhance our knowledge of the pollination ecology of entomophilous plants. If hybrid soybeans become a reality, plant breeders must pay strict attention to floral characteristics and include selection for pollinator cues and rewards to ensure floral compatability between seed parents in their breeding programs (see Erickson, 1983; Rubis, 1970). Also, they should carefully evaluate grossly abnormal flower mutants (see Erickson et al., 1982ab; Johns and Palmer, 1982) in the light of pollinator requirements.

Conclusions The data presented indicate that bees produce substantial honey crops from soybeans and may increase soybean yields in some fields/localities, but not in others. Hence, the convictions of those on both sides of the issue appear equally valid. Only intransigence and imprecise descriptions of circumstances predisposing each conclusion can be faulted. Regardless of opinions to the contrary, many soybean growers continue to encourage beekeepers to locate apiaries near their fields and report increased yields with bees present.

Differences in soybean honey production and soybean yield due to bee pollination seem attributable in part to heritability factors and geoecology. Interpretation of all bee/soybean data suggest that greatest honey yields occur on the most productive soils in warm climates, while soybean yield increases resulting from insect pollination have been highest on poorer soils. Further research is needed to clarify these hypotheses. Some cultivars are more attractive to pollinators than others. Many cultivars have yet to be studied in this regard. Bees rarely visit soybeans in geographical areas with low median temperatures because soybean flowers do not open or produce nectar and aroma in these areas. Studies are needed to ascertain the nature of bee/flower interactions for each agricultural zone. Perhaps, as new knowledge is developed, new avenues can be pursued to maximize soybean yields for growers and honey yields for beekeepers.

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