AVOCADO (*Persea americana* Mill.) POLLINATORS IN ITS REGION OF ORIGIN

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SUMMARY

Insects visiting avocado flowers were collected over the course of five research trips to Mexico, in the states of Michoacan, Mexico, Puebla, Veracruz and Chiapas. Most of the specimens were identified at the species level, and the amount and distribution of pollen on their bodies were determined. Both the density and behavior of species found to carry a large amount of avocado pollen were observed on the avocado bloom. In commercial orchards sprayed with potent insecticides, only a small number of visitors of a few species were observed, most of them honeybees (*Apis mellifera*). In contrast, on unsprayed trees (in small plots, backyards, etc) large numbers of visitors of numerous species were usually observed. More than 1,000 individual insects, of about 100 species, were collected on avocado bloom, most of them of the orders Hymenoptera, Diptera, Coleoptera and Heteroptera. Apparently, some of the visitor species did not pollinate the avocado flowers, but most of them did contribute to its pollination. The following species were found to be effective pollinators of avocado: the honeybee, 8 to 10 species of stingless bees (*Apidae, Meliponinae*) and the "Mexican honey wasp" (*Brachygastra mellifica*). These species were the main pollinators of the three avocado races: Mexican, Guatemalan and West Indian. Honeybees were active on the avocado bloom at most sites; however, in some cases they abandoned the avocado bloom to collect nectar and pollen from nearby competing flowers. The stingless bee species and the Mexican honey wasp showed a greater preference for the avocado bloom. We assume that the original pollinators of the avocado, before the introduction of the honeybee to the American continent, were stingless bee and wasp species, which are better adapted for its pollination.

KEY WORDS: *Apis mellifera*, *Brachygastra mellifica*, competition for pollination, Meliponinae, pollination, foraging preference.

INTRODUCTION

There is a problem of inadequate pollination of avocado in Israel, the USA and probably also in other countries. Honeybees, which serve as the major pollinator for the avocado in most countries, tend to abandon avocado orchards when more attractive bloom is available. They also do not perform efficient cross-pollination, due to their location-constancy behavior (Angel, 1994; Bekey, 1986; Bergh, 1967, 1975; Davenport, 1986; Ish-Am & Eisikowitch, 1998a, 1998b, 1998c; McGregor, 1976; Peterson, 1955; Stout, 1923, 1933; Vithanage, 1990). Avocado originated in Central America, and evolved there for millions of years without the presence of the Old-World honeybee. Thus, it is not surprising that it did not develop the traits needed to make it very attractive to honeybees. However, it is reasonable to assume that it did develop traits that make it attractive to its natural pollinator or pollinators. There is little information about avocado pollination and pollinators in Mexico and Central America. Potential pollinators that have been reported to visit avocado flowers are honeybees, stingless bees, wasps, flies, beetles and even bats (Angel, 1984; Crane, 1992; Free & Williams, 1976; Papademetriou, 1976; Roubik, 1995). The efficiency of these visitors as avocado pollinators has not been investigated.

The avocado unique flowering behavior can be termed: diurnally synchronous protogyny dichogamous, with intermediate closing. The bisexual flower opens twice: at the first opening it functions as a female and at the second opening, usually on the next day, it functions as a male and pollen is released. The opening and the closing of the female stage flowers of a single tree (or cultivar), as well as that of the male stage flowers, occur simultaneously, each of the two flower stages at a different part of the day. All the avocado types are divided to two complementary flowering groups. 'Group A' types bear, in a warm weather, open female stage flowers from the morning to noon time, and male stage flowers during the afternoon. 'Group B' types, on the other hand, bear open female stage flowers in the afternoon and male stage flowers in the morning. These male and female flowering phases overlap for a daily period of 1-3 hr in some of the avocado cultivars. Under cool weather conditions there is a delay of the male and the female open-

ings, which may result in a complete reversal in the part of the day female and male flowers are open. At both male and female openings nectar is being secreted, thus, insects that collect nectar, or nectar with pollen, are the potential pollinators of the avocado. (Bergh, 1969; Davenport, 1986; Ish-Am & Eisikowitch, 1992; McGregor, 1976; Nirody, 1922; Peterson, 1955; Stout, 1923, 1933).

The aim of this study is to collect insects visiting avocado flowers in its region of origin, identify them and determine their effectiveness as avocado pollinators.

MATERIALS AND METHODS

The field study was carried out in Mexico by a joint Israeli-Mexican research team during the years 1996 to 1999. At the beginning of the research we found out that in well managed avocado orchards the insect populations are severely diminished due to frequent spraying by potent insecticides. Later on we have concentrated on sites with avocado trees that are not exposed to spraying, in marginal or neglected plots, in backyards and avenues, in coffee orchards where avocado trees are used for shade, and escaped from cultivation trees. Precise and detailed information about the blooming season of the different avocado types throughout the research sites was not available, and was gathered in successive visits at different seasons.

Collecting, preserving and identifying the insects

Visitor insects were collected on avocado female, male and mixed bloom, of 'Group A' and 'Group B' flowering type trees. The collection was performed with insect nets and plastic collecting bottles. The collected insects were immediately placed in a poison jar, and later pinned, dried and kept in insect boxes. They were numbered and arranged according to their "collecting group", which is one, or more insect specimens that were collected at the same place and time, and appear to be of the same species. The insects were handled with care, in order not to remove the pollen carried on the insect body. Few representative insect specimens out of each "collecting group" were sent for identification, after being examined in the laboratory. Most insects were identified at the USDA Systematic Entomology Laboratory (SEL). The Meliponinae species were identified by Dr David Roubik, of the Smithsonian Tropical Research Institute in Panama. Many of the specimens were not identified at the species level, as the species had not yet been identified, the genus was under revision, or the needed specialist was not available.

Observations of insect behavior in the field

Pollination efficiency of insect species visiting avocado flowers was determined by examining the species density on the avocado (specimens per tree) and flower visitation rate (flowers per min), the rate of transits between male and female flowers (when open simultaneously) and the location and intensity of body contacts with stigmas and anthers of the avocado flower (Ish-Am, 1994; Vithanage, 1986).

Studying the insects in the laboratory

The collected and preserved insect specimens were checked under a stereomicroscope at x80 and x160 magnifications, to determine amounts of avocado pollen and distribution on their bodies. Special attention was given to the body zones that were found to touch the avocado flower stigma. Selected specimens were photographed by macro light photography and by SEM.

RESULTS AND DISCUSSION

Avocado types and the blooming seasons

Mexican race. In the states of Michoacan, Mexico, Puebla and Veracruz, at altitudes of more than 1,000 m, Mexican trees were in bloom from September until March.

West Indian race. In the state of Veracruz at low altitudes seedling and grafted trees of this type were in bloom throughout January to March.

Guatemalan race. In Chiapas, at altitudes of 1,000 to 2,500 m, seedling trees (called "On" in Chiapas) were in bloom from February to April.

Hybrid types. 'Hass', the main cultivated cultivar in Michoacan and Mexico states, has a long blooming season, from September to February. Its bloom comes later at higher elevations, and may change significantly from year to year. In the state of Veracruz, at altitudes of about 1,000 m, 'Hass', 'Fuerte' and other avocados, which are planted in coffee plantations, were in bloom from October to March. In Chiapas the local "Tzitzi" seedlings, Mexican -like Mexican-Guatemalan hybrids (Ben-Ya'acov and Bufler, not published) were in March close to the end of bloom, and still carried many flowers.

Avocado bloom visitors

More than 100 insect species were collected on avocado flowers (Table 1). Similar insect populations were collected on the three avocado races, and they were seen moving freely among them.

Commercial orchards. Insect populations were usually very limited in numbers and species. Honeybees from hives that were placed in the orchards and from feral nests, mostly of the African race (*Apis mellifera scutulata*), were the most common insects visiting the avocado bloom. In some orchards we also observed flies, wasps and beetles, and in few cases also bees of the Meliponinae and of other groups. The scarcity of the visitors is apparently related to the widespread use of potent insecticides, such as Parathion and Malathion.

Table 1. Insects that were collected on avocado bloom in Mexico.

Order	Sub order levels	Collected specimens (no.)	"Collecting groups"[z] (no.)	Species (estimated no.)[y]
Hymenoptera	Meliponinae	444	69	10
	Other bees	84	49	16
	Wasps	245	119	25
Diptera		153	103	40
Coleoptera		33	21	10
Heteroptera		44	13	8
Others		18	9	6
Total		1021	383	115

z"Collecting group" consists of one or more specimens of the same species that were collected in the same place and time.

ySpecies identification has not been completed.

Unsprayed trees. Much larger insect populations of greater species variety were found in orchards and on trees that were not sprayed, and were located near the forest, or in undisturbed areas. On such locations we sometimes observed hundreds specimens of bees, wasps, flies and other insect species per tree.

Avocado pollinators

Insects may visit avocado flowers without pollinating. To accomplish pollination the visitor should exhibit the following behavior traits (Faegri & Pijl, 1979; Ish-Am, 1994):

Visit both female and male-stage flowers.

Make contact with both anthers and stigmas with the same parts of the body (the "pollinating zones").

Carry avocado pollen on the "pollinating zones".

For carrying out cross-pollination - move among, and visit flowers of trees of different cultivars.

Indeed, we observed beetle species that collected pollen and visited only male flowers; Hover flies, which collected nectar while fluttering, without making contact with anthers or stigmas; and wasps that efficiently touched the flower reproductive organs but carried no avocado pollen on their smooth bodies. Nevertheless, many of the avocado flowers' visitor species did effect its pollination, sometimes not efficiently. Among these pollinators were all the bee species, most of the fly species and some of the wasp, beetle and plant bug species.

The avocado efficient pollinators

Honeybees (*Apis mllifera*). At present the honeybee populations in Mexico consist of the African race (*A. m. scutellata*) and its hybrids with the European race. The African race reached Mexico about 15 years ago, and today exists there as domesticated, as well as a feral honeybee (Roubik, 1998). In most research sites honeybees were the main visitors to the avocado flowers and behaved as efficient pollinators (Table 2). However, in several situations they were found to prefer other blooms over the avocado's. In some cases we observed an all day long low honeybee activity on the avocado trees, while they were visiting in high density other flowers, like yellow weed bushes (*Senecio saligmus*) and *Citrus* bloom in the vicinity. At the same time the avocado flowers were visited by stingless bees, wasps and flies, sometimes at high densities. In other cases honeybees were highly active on the avocado flowers during the morning but left toward noon time, while the activity of stingless bees and wasps, which was also high in the morning, increased rapidly up to a thousand specimens per tree. This behavior of the honeybees may be interpreted either as a competitive exclusion by the other avocado visitors, mainly by the stingless bees, or as a preference for the competing species' flowers over that of the avocado. Only the second explanation is pertinent when the honeybees neglect the avocado bloom while other visitor population is sparse.

Stingless bees (Meliponinae, Apidae). Nine species of this subfamily were found to visit avocado flowers (Table 2). These bees seem to be well adapted for avocado pollination: they are smaller than the honeybee and, while visiting avocado flowers, they achieve efficient contact with stamens and stigmas by both ventral and the lateral sides of the thorax and the abdomen (Figure 1). On these "pollinating zones" they collect large amounts of avocado pollen (Figure 2), which are later transferred to the hind legs and used for building up the pollen loads (Figure 3). Six of these species were observed visiting flowers of the three avocado races in high densities, and moving frequently among male and female stage flowers when they were simultaneously open. Some stingless bees were found in all the research sites while some only in a limited region (Table 2).

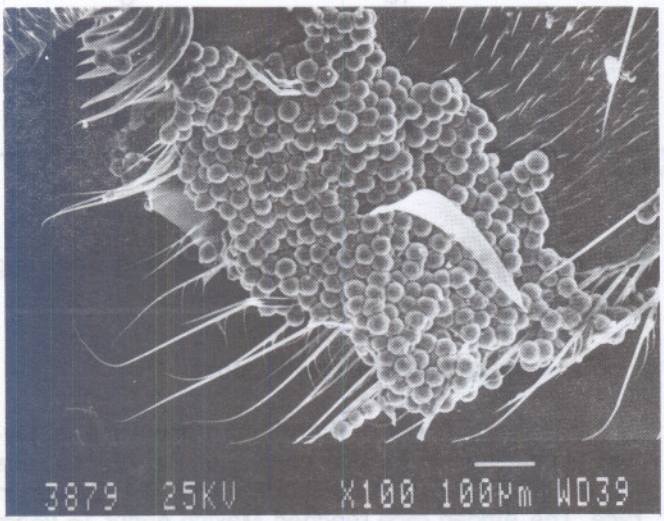

Figure. 1. The stingless bee *Geotrigona acapulconis* collects nectar from 'Hass' female-stage flower.

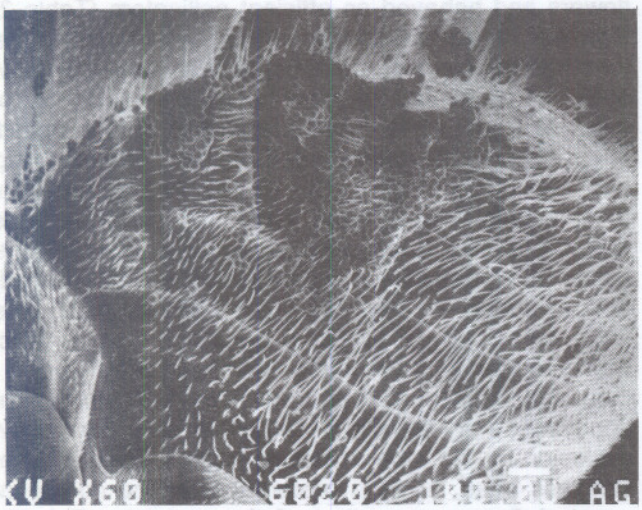

Figure 2. Large amount of avocado pollen carried on the ventral abdomen of the stingless bee *Geotrigona acapulconis*. SEM picture, x 60.

Figure 3. A hind leg of *Geotrigona acapulconis* carries avocado pollen load at the biginning stage of building up. SEM picture, x 100.

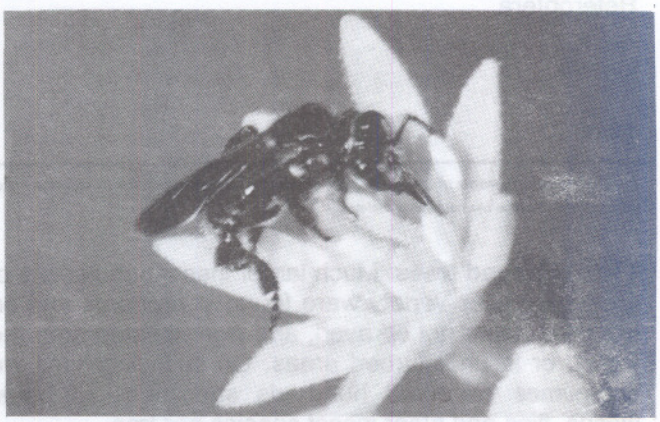

Figure. 4. The "Mexican Honey Wasp" *Brachygastra mellifica* collects nectar from avocado male-stage flower

Wasps (Hymenoptera). Many wasp species visited the avocado flowers (Table 1), but some did not contribute to pollination because they did not carry avocado pollen on their hairless bodies. The main avocado pollinator of this group was the "Mexican honey wasp" (*Brachygastra mellifica*) (Table 2). These social wasps collect honey to feed their larvae, and carry large amounts of pollen, including avocado pollen, on their hairy head, thorax and legs, and inside unique thoracic cavities. We found this wasp species on avocado bloom in all research sites (Figure 4), sometimes in high densities of tens of specimens per tree. Many species of the genera *Polistes* (Table 2), *Mischocyttarus* and others were sometimes observed visiting avocado flowers in high densities, but with low pollination efficiency due to low flower visitation rate and small to medium amounts of avocado pollen carried on their bodies. Some hairy wasp species were collected while visiting avocado flowers. Although these wasps carried large amounts of avocado pollen, their contribution to the avocado pollination was low, as only few specimens were active on the flowers, visiting them at a low rate.

Flies (Diptera). Many fly species were collected visiting avocado flowers (Table 1), and sometimes they were

observed at high densities (tens and even hundreds per tree). Some species of the Calliphoridae (Table 2), Muscidae and Syrphidae carried large amounts of avocado pollen and created effective contact with stamens and stigmas, but their pollination efficiency was not high because of low flower visitation rate.

Plant bugs (Heteroptera). On a large seedling Mexican avocado tree in a backyard in Tingambato (Michoacan) we observed hundreds individuals of the species *Stenomacra marginella* (Table 2) entering to the evening male flowers, perhaps for a night's sleep. On this species' body we found large amounts of avocado pollen, but we did not see them visiting female flowers, and it is not clear whether and how much they contribute to the avocado pollination.

CONCLUDED DISCUSSION

Who are the original avocado pollinators?

The avocado flower has an open "general form", with exposed nectar and easy to collect pollen. It exhibits features of the typical bee, wasp and fly flowers (Faegri & Pijl, 1979), and therefore is not suitable for a specific pollinator. Indeed, insects belonging to those groups were reported to visit avocado flowers in California, Israel, South Africa, Australia and the Antilles (Bekey, 1986; Bergh, 1975; Du Toit, 1994; Eardley & Mansell, 1993, 1994; Free and Williams, 1976; Ish-Am, 1994, Visscher & Sherman, 1998; Vithanage, 1986). It was not surprising to find a similar picture in Central America (Table 1). Most of the avocado visitors were found to contribute to pollination, but which of them were the original main pollinators? Evidently not the honeybee, which was only brought to the "New World" at the beginning of the 16th century by the Europeans (Roubik, 1998). Our data (Table 2) indicates that before the arrival of the honeybee a large number of stingless bee species (ten were identified so far) and the Mexican honey wasp had been the main avocado pollinators. All these were social Hymenopterans, which were adapted for mass food collection from many flower types throughout the year. It seems that the avocado bloom constitutes an important food source for them.

One may find a close relationship between the avocado flowering behavior, of simultaneous exposure of many new flowers (tens of thousands per tree), and the social pollinators' ability to recruit a large number of workers to exploit a rich food source. The insects' food collecting efficiency increases when a large amount of food is released in one place and time, and the increase of their density at the food source also amplifies their pollination efficiency. Moreover, the high density of the social insects may exclude the less efficient pollinator species, which can not compete for the food with the formers, and as a result increase even more both the pollinator food collecting efficiency and the pollination rate.

Are the Central America avocados exposed to competition for pollination?

A study of "competition for pollination" demands an extensive work under field conditions (Campbell and Motten, 1985), which was not possible to perform within the limits of the present research. However, the data that has been accumulated suggests some preliminary conclusions:

Commercial sprayed orchards. The average yield in many commercial orchards in Mexico is low. In most of them we observed a very low insect activity. If the low productivity is the outcome of an insufficient pollinator activity than it may stem from both the destruction of the natural pollinator population by the insecticide spray, and the attraction of the honeybees, which are the only remaining pollinator in the orchards, by a competing bloom. Indeed, in several cases we observed honeybees abandoning the avocado bloom and visiting yellow weed and *Citrus* flowers in the orchard's vicinity, a well known picture in other avocado growing countries (Bergh, 1967, 1975; Ish-Am & Eisikowitch, 1998a, 1998c; McGregor, 1976; Stout, 1923, 1933; Vithanage, 1990). At least in some of these cases it was evident that the honeybees had left the avocado bloom because they preferred the competing flowers.

Unsprayed avocado trees. The insect population in most of the unsprayed research sites, and in all of those that were close to the wild, was very dense, consisting mainly of honeybees and numerous species of the stingless bees, wasps and flies (Table 1). Even when the honeybees abandoned the avocados to forage on competing bloom, a big population of the other insect species, mainly stingless bees and wasps, remained. It seems that, unlike most of the avocado growing countries out of its region of origin, in Central America many non-Apis wild pollinators use the avocado bloom as an important food source, and prefer it over other available food sources. Their presence in high numbers is apparently beneficial for the avocado pollination, and should be encouraged. Evidently, limiting the regular insecticide treatments in the commercial orchards would enable the recovery of wild insect populations, which in turn would improve the cultivated avocado's pollination efficiency, and may increase the yield as well.

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Table 2. Efficient pollinators of avocados in Mexico.

Name	Description	Body length (mm)	Collecting: Nectar	Collecting: Pollen	Avocado pollen Amount	Avocado Pollination efficacy	Found in States[z]	Nesting Sites[yx]
Apis mellifera	social bee	10	+	+	Large	very high	all	2,5,6,
Geotrigona acapulconis	social bee, stingless	6	+	+	Large	very high	M,X,	1,
Trigona nigerrima	social bee, stingless	8	+	+	Large	very high	V,	3,
Partamona bilineata	social bee, stingless	6.5	+	+	Large	very high	all	4,5,
Nannotrigona perilampoides	social bee, stingless	4	+	+	Large	very high	X,M,V,	2,5,6,
Scaptotrigona pectoralis	social bee, stingless	6	+	+	Large	very high	V,	1,2,5,6,
Trigona nigra	social bee, stingless	5	+	+	Large	very high	V,	3,5,6,
Scaptotrigona mexicana	social bee, stingless	6	+	+	Large	very high (?)	V,	1,2,
Trigona fulviventris	social bee, stingless	7	+	+	Large	very high (?)	V,	1,2,5,6,
Plebeia frontalis	social bee, stingless	4	+	+	Medium	very high (?)	V,	2,5,
Bombus spp.	social bees	10-20	+	+	Large	very high	all	1,
Exomalopsis spp.	solitary bees	8	+	+	medium	high (?)	all	?
Brachygastra mellifica	Social wasp	8.5	+	?	large	very high	all	3,
Polistes spp.	Social wasp	10-20	+	-	medium	Medium	all	3,
Chrysomya megacephala	blowfly	14	+	-	medium	Medium	all	
Stenomacra marginella	plant bug	14	-	-	medium	?	M,X,C,	

[z]**States**: C=Chiapas, M=Michoacan, P=Puebla, V=Veracruz, X=Mexico

[y]**Nesting sites:** 1=under the ground, 2=inside hollow trunks, 3=on tree and bush canopy, 4=on trunks & walls, 5=on artificial walls or cavities, 6=were domesticated by people.

[x]**Sources**: Crane, 1992; Roubik, 1983