

Low attractiveness of avocado (*Persea americana* Mill.) flowers to honeybees (*Apis mellifera* L.) limits fruit set in Israel

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SUMMARY

Avocado in the Western Galilee region of Israel was found to be dependent on honeybees for fruit set. A significant initial fruit set required a density of at least five bees per tree during the female stage of flowering. The early-blooming avocado cultivars were visited by enough honeybees on fewer than one-third of their blooming days. Because they were visited mostly at the end of their blooming season, and due to rainy days, not more than 5% of their entire season's flowers were exposed to sufficient pollination to set fruit. The late-blooming cultivars however, were visited by many bees and exhibited high initial fruit set. The attractiveness to honeybees of various avocado cultivars and some other plant species, which were found to compete for pollination, was measured by the coefficient "r" obtained from correlations between bee density and reward measures of these plants, over the course of a day or season. At the beginning of the blooming season, the avocado flowers competed for nectar-foraging bees mainly with flowers of *Citrus* spp., and for pollen foragers with Brassicaceae and Fabaceae, all of which were more attractive to the bees. Since pollination was carried out only by nectar-collecting bees, *Citrus* spp. flowers presented the main limiting factor for initial fruit set in avocado. However, toward the end of its blooming season, the avocado competed with Poaceae, Asteraceae and Apiaceae flowers, and its relative attractiveness increased.

Avocado (*Persea americana* Mill.) is native to the tropics of Central America, and is also cultivated in other regions. However, it tends to yield well below its potential in Mediterranean climates (Bergh, 1967 and 1977), where it has been found to suffer from both frost and heat waves (Bergh, 1967 and 1977; Gazit, 1977; Stout, 1933), as well as from calcareous and heavy soils (Ben-Yaacov, 1977; Bergh, 1977; Stout, 1933). Inadequate pollination has been suggested as an important factor limiting avocado yield. Its main pollinator in Mediterranean regions is the honeybee (*Apis mellifera* L.), and many avocado growers place hives in the orchard throughout its blooming season to improve pollination (Bergh, 1969 and 1977; Eisikowitch and Melamud, 1982; Gazit, 1977; Ish-Am, 1985; Vithanage, 1990).

The inadequate pollination of avocado has two aspects: low pollination rate, which is a consequence of the honeybees' preference for flower species other than avocado (Bergh, 1967 and 1969; Clark, 1923; Eisikowitch and Melamud, 1982; Gazit, 1977; Ish-

Am, 1994; Stout, 1923 and 1933; Vithanage, 1990), and a low cross-pollination rate, resulting from both a lack of adjacent complementary pollen-donor cultivars and the low efficiency of honeybees as cross-pollinators (Bergh, 1967, 1969 and 1977; Degani *et al.*, 1989; Gazit, 1977; Gazit and Gafni, 1986; Gil *et al.*, 1986). Nevertheless, it has been suggested that a commercial yield of avocado can be obtained even with a very low pollination rate, due to the large number of flowers normally produced by its tree (Clark and Clark, 1926; Davenport, 1986; Gazit, 1977; Schroeder, 1954). Furthermore, it has been shown that in a tropical climate, such as that in Florida, the local avocado cultivars set most of their crop due to spontaneous self-pollination within the male-stage flower (Davenport, 1989 and 1991; Davenport *et al.*, 1994).

Our research was aimed at identifying the main plant species competing for honeybee pollination with avocado in Israel, measuring these competitors' attractiveness to honeybees, and assessing the implications of the competition on avocado fruit set.

MATERIALS AND METHODS

Observations and experiments were carried out during 1991 and 1992, in an orchard in the Western Galilee of Israel, about 4 km from the Mediterranean coast and 30 m above sea level. Adjacent plots of mature trees of the early-blooming avocado cultivars 'Hass' and 'Ettinger', the late-blooming avocado cultivars 'Reed' and 'Nabal', of orange (*Citrus sinensis* Osbeck cv. Valencia), and a neighbouring fallow field of wild mustard (*Sinapis alba* L.), were studied. Five trees in full bloom were chosen for each of the avocado cultivars and for the orange cultivar, and 1 m² squares were marked in the mustard field, in a heavy blooming area. Sixteen strong hives (four to five stories each) were placed in the avocado orchard, 200 m from the study trees, and pollen traps were fitted at the entrance of five of these (Free, 1959).

"Flower density" was measured by methods adapted to each species. Avocado flowers are carried in inflorescences spread throughout the canopy. Therefore, its flower density was represented by the number of open flowers borne on five medium-size inflorescences, marked on each avocado tree. Orange flowers, however, are borne in small inflorescences on the outer canopy surface only, and were accordingly counted in 1 m² of canopy surface, marked on each tree. In the mustard field, the number of flowers per 1 m² was calculated by counting both the number of open flowers per ten inflorescences, and the number of inflorescences per marked 1 m². Young avocado fruits were counted on the same inflorescences as the flowers. A young fruit was counted when it reached 2 mm (or more), either within the flower's tepals or after the flower had dropped.

Avocado and mustard nectar was collected in 5 µl microcapillary tubes, and its volume was read in microliters. Sugar concentration (percent w/w) was measured using a field refractometer (Stanley and Bellingham, UK) calibrated against standard sucrose solutions (Corbet, 1979). At each observation, nectar was collected from 5-10 marked flowers, which were not checked again. When the nectar's sugar concentration was too high, above collection ability, 2 µl of distilled water were added to each flower by micropipet, and the resulting liquid was collected and measured after about 30 sec (Corbet, 1979). The amount of sugar in a flower was obtained as the product of its

nectar volume and sugar concentration, converted from percent w/w to percent w/v (Bolten *et al.*, 1979). "Sugar density" was calculated as the product of the average amount of sugar per flower and flower density.

'Valencia' nectar was collected in 50 μ l micro-capillary tubes, and the values of sugar per flower and sugar density were calculated as in avocado. Honeybees visiting 'Valencia' were found to reach the nectar of only a small percentage of the flowers, and then to imbibe only part of it. Therefore, to estimate the amount of sugar available per flower, nectar was collected concomitantly from two flower types: those from which nectar had not yet been collected (with a closed staminal tube), and those from which nectar had already been collected, immediately after the collecting bee's departure. The average amount of available sugar per flower was represented by the difference between the average sugar amounts of the two flower types (Pleasant and Waser, 1985).

"Bee density" was measured on avocado and citrus trees by counting honeybees on the whole tree for 1 min, while walking around it (Mayer *et al.*, 1989), and on mustard by counting bees within the marked square for 1 min. Pollen-loads were collected after the pollen traps had been attached to the hives for 1 h. The collected pollen-loads were transferred to sealed plastic containers and kept at 4°C. They were later identified, with the aid of a light microscope, by comparing with known pollen grains, to species, genera or family level, sorted and stored accordingly. Standard meteorological equipment was installed beside the plots to record temperature and relative humidity.

Monitoring during a day

Measurements were carried out every 30-60 min during the course of a day, recording bee density and "plant-reward measures" (nectar volume and sugar concentration, and flower density) on the avocados, citrus and mustard. The citrus and mustard were observed for 2 d each, and each of the avocado cultivars was observed for 4 d.

Monitoring throughout the blooming season

Bee density, plant-reward measures and young-fruit density were recorded three times a week throughout the early-blooming avocado cultivars' bloom, concomitantly in 'Hass' and 'Ettinger' avocados, 'Valencia' citrus and mustard. Honeybee pollen-loads were collected at the same times. Observation times coincided with the daily full female-flowering stage in 'Hass' (A-type) and the male flowers' pollen release in 'Ettinger' (B-type). This usually occurs in the late morning (Stout, 1933) and shifts, according to the ambient temperature, to the early morning on hot days and to noontime on cool ones (Ish-Am and Eisikowitch, 1991 and 1992). Monitoring throughout the season of the late-blooming avocado cultivars was less complete, and was not accompanied by pollen-load collection.

Statistical analysis

Calculations were made according to Sokal and Rohlf (1981). Correlations between bee

density and plant-reward measures' courses (throughout a day or a season) were obtained, and employed as a measure of plant attractiveness.

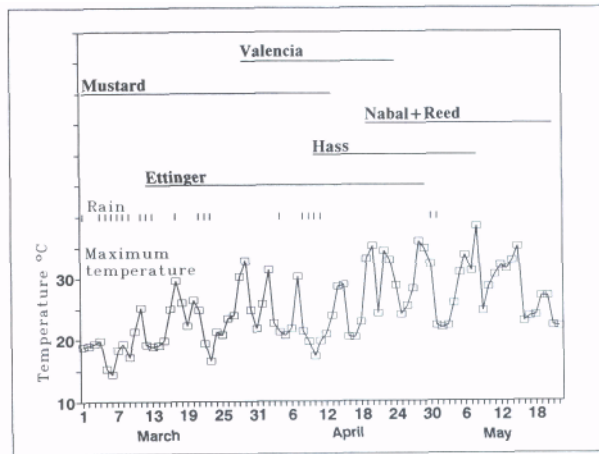


FIG. 1

Blooming period of avocado cultivars, mustard and 'Valencia', maximum daily temperatures and rainy days in 1991.

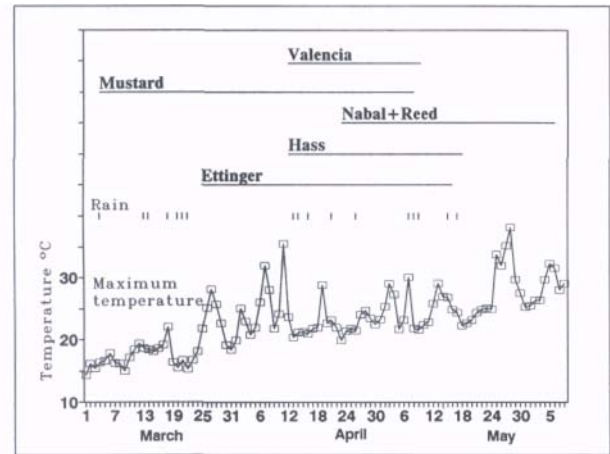


FIG. 2

Blooming period of avocado cultivars, mustard and 'Valencia', maximum daily temperatures and rainy days in 1992.

RESULTS

Phenology

The 'Ettinger' blooming period started in mid-March and lasted for about seven weeks (Figures 1, 2). The 'Hass' bloom started in the second week of April, lasted for only 4-5 weeks, and mostly overlapped with the 'Ettinger' bloom, ending 2-9 d later. Both 'Nabal' and 'Reed' blooming periods started in the last third of April, lasted 5-6 weeks, and ended 2-3 weeks after flowering of the early-blooming cultivars. During both seasons, the mustard bloom started and ended 1-2 weeks before that of 'Ettinger', and overlapped with most of the 'Ettinger' bloom, but with only three blooming days of 'Hass' in 1991, and most of its blooming period in 1992. The mustard bloom did not overlap with the 'Nabal' and 'Reed' blooming period in 1991, and only overlapped with its first third in 1992. The 'Valencia' blooming period lasted four weeks during both seasons. It occurred within the 'Ettinger' blooming period, and overlapped with the main blooming period of 'Hass', but only with the first third of that of 'Nabal' and 'Reed'.

Weather

The numbers of rainy days in March, April and May, were 14, 6 and 1 in 1991, and 7, 5 and 5 in 1992, respectively (Figures 1, 2). During these days, honeybee activity was very limited, or totally prevented. The daily temperature, however, exceeded 16°C on all days, throughout both avocado blooming seasons (Figures 1, 2), and therefore did not interfere with honeybee activity (Free, 1993).

Honeybee activity and plant-reward measures Avocado

Honeybees visiting avocado usually moved freely among female and male-stage flowers, collecting nectar from the former and nectar with pollen from the latter. However, bees collecting pollen only (sometimes with a little nectar) were also observed on the male-stage flowers: these almost never visited the female flowers, and therefore could not perform pollination. On average, both male and female 'Ettinger' flowers contained 0.7 mg sugar ($n = 873$), whereas a 'Hass' male and female flower carried 0.4 and 0.15 mg sugar, respectively ($n = 448$). About 0.2 mg sugar was found per 'Nabal' flower ($n = 456$), and only 0.1 mg sugar was found per 'Reed' flower ($n = 540$). Five avocado inflorescences carried up to 300 open flowers, which contained 200, 100, 50 and 30 mg sugar in 'Ettinger', 'Hass', 'Nabal' and 'Reed', respectively (Figures 3-6). Meaningful correlations between the daily courses of bee density and avocado reward measures could be obtained only on days with more than five bees per tree, which occurred toward the end of the early-blooming cultivars' bloom (Figure 3) and during most of the late-blooming cultivars' season (Figure 4). These correlations were significantly positive (Table I), especially when bee density was related to flower or sugar density.

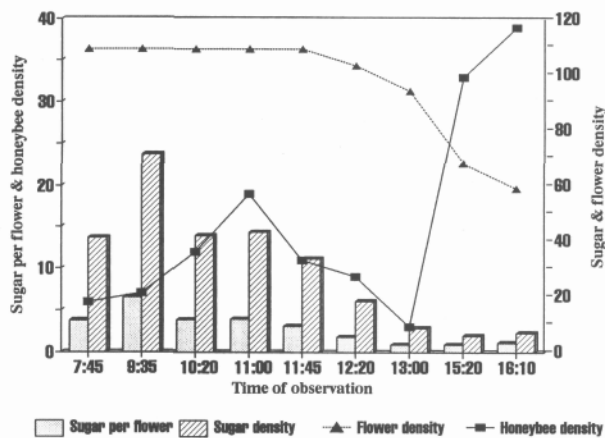


FIG. 3

One-day course of reward measures and honeybee density of 'Ettinger' avocado. Monitoring of a day with high bee activity, toward the end of seasonal bloom (April 24, 1991). The tree carried male-stage flowers during the morning and female flowers during the afternoon, with a 3-h overlap between them (from 1300 to 1600 hours). Units are: sugar per flower—1/10 mg, sugar density—mg per five inflorescence, flower density—per five inflorescences, bee density—per tree.

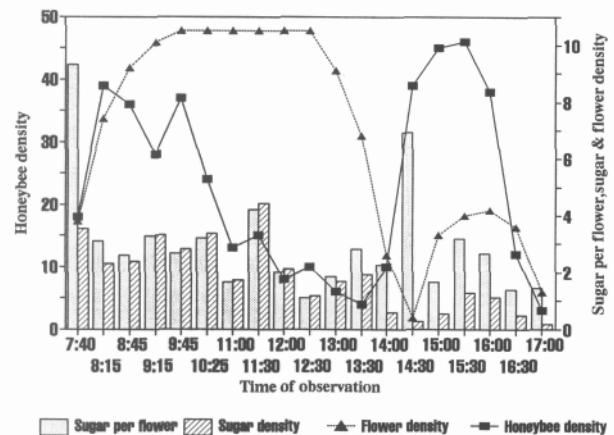


FIG. 4

One-day course of reward measures and honeybee density of 'Nabal' avocado. Monitoring of a day with high bee activity at peak seasonal bloom (May 11, 1991). The tree carried male-stage flowers during the morning and female flowers during the afternoon, with a half-an-hour overlap period between them (from 1400 to 1430 hours). The bees collected nectar from female flowers before opening. Units are: sugar per flower—1/100 mg, sugar density—mg per five inflorescences, flower density—(per five inflorescences)/10, bee density—per tree.

'Valencia'

Most bees observed on the 'Valencia' trees collected nectar only, although a few collected both pollen and nectar. The nectar foragers did not touch the anthers, but grasped the petals and searched for an entrance into the nectar chamber within the filament tube. They reached the nectar in only 5.8% of the visited flowers ($n = 184$), and then imbibed it for a long period (average of 19 sec, maximum 2 min). The pollen-and-

nectar collectors, however, scratched the anthers first, and then searched for nectar, as described for the nectar foragers. A seasonal average of 9.7 mg sugar was found in the nectar of unvisited flowers (Figure 7), and 3.6 mg in flowers that had just been visited. Therefore, 6.1 mg sugar was accepted as an estimate of the seasonal average of available sugar per flower. One m² of the 'Valencia' blooming canopy carried up to 110 flowers, which contained 1.37 g sugar (0.67 g of available sugar). The daily correlations between the courses of bee density and reward measures in 'Valencia' were meaningless, since its reward measures was high and quite stable during most of the day, and bee density on it followed the usual honeybee daily activity pattern.

Mustard

On average, mustard carried only 0.014 mg sugar per flower (n = 86), although up to 60 mg sugar per 1 m² (3000 flowers per 1 m², Figure 8). Most visiting bees collected mainly pollen with a little nectar, although a few collected both pollen and nectar simultaneously. The pollen foragers were active throughout the day, scratched all the visited mustard flowers' anthers, and collected nectar from less than 10% of the flowers. The pollen-and-nectar foragers however, were active only in the early morning, collecting nectar from all the flowers visited and pollen from most of them. Since its nectar volume was undetectable during most of the day, we could not obtain correlations between the mustard's daily courses of bee density and reward measures.

TABLE I
Correlation coefficients (r) and probabilities (P) of bee density vs. reward measures of avocado and its competitor plants (1991 and 1992 data)

Plant	Period of correlation ¹	Reward measures		
		Sugar per flower	Flower density	Sugar density
'Hass'	season	*r = -0.25, n.s.	r = -0.55, P = 0.018	r = -0.42, n.s.
'Ettinger'	season	r = -0.37, n.s.	r = -0.46, P = 0.030	r = -0.37, n.s.
'Valencia'	season	r = +0.59, P = 0.026	r = +0.90, P = 1E-06	r = +0.72, P = 0.003
Mustard	season	r = +0.71, P = 5E-04	r = +0.79, P = 1E-05	r = +0.77, P = 7E-05
All avocados	day ²	r = +0.79, P = 0.002	r = +0.24, n.s.	r = +0.77, P = 0.004

Units of flower and sugar density are per five inflorescences for avocado and per 1 m² for 'Valencia' and mustard.

¹Daily correlations were obtained for avocados only (see text).

²Combined correlations of 12 d of a bee density of five or more bees per tree, of 'Hass', 'Ettinger', 'Nabal' and 'Reed' cultivars. The correlations' P values were combined using a χ^2 procedure to combine probabilities of independent tests of significance (Sokal and Rohlf, 1981).

Monitoring throughout the season

The 1992 seasonal courses of sugar quantity per flower, and of flower, sugar and bee density for 'Hass', 'Ettinger', 'Valencia' and mustard, as well as the avocados' initial fruit set, are presented in Figures 5 to 8, and correlations employing these data are summarized in Tables I and II. The 1991 seasonal data were similar, and are therefore not presented.

The seasonal pattern of honeybee-density course on 'Hass' and 'Ettinger' was very similar (r = +0.85, Figures 5, 6). Both cultivars attracted almost no bee activity throughout most of their blooming period, including their flower peak. They were visited by more than three nectar-collecting bees per tree only toward the end of their blooming period, for 7-12 d, although 'Ettinger' also received visits of three bees per tree during its first week of bloom. Significant avocado-pollen collection by the bees started, in 1992,

on April 30, and nectar collection on May 3, several days before the termination of mustard and 'Valencia' blooms, respectively (Figure 2). In 1991 avocado-pollen collection started on April 11, and nectar collection on April 19, again, in accordance with the end of mustard and 'Valencia' flowering (Figure 1). 'Nabal' and 'Reed' were barely visited by honeybees at the beginning of their blooming period, but later on, including their flowering peak, they attracted numerous bees. Both 'Valencia' and mustard attracted a high bee density throughout most of their blooming periods (Figures 7, 8).

Young fruits of both 'Hass' and 'Ettinger' were counted only several days after at least three bees per tree had been observed on the female-stage flowers (Figures 5, 6), and their initial fruit-set pattern was very similar ($r = +0.96$). In 1992 however, a few fruits appeared on 'Ettinger' earlier, but they were too few to be counted on the marked branches. During the period of high bee density, the 'Hass' trees accumulated a high number of young fruits, which soon began to drop. The 'Ettinger' initial fruit-set rate was lower, and almost no young fruits dropped during the observation period.

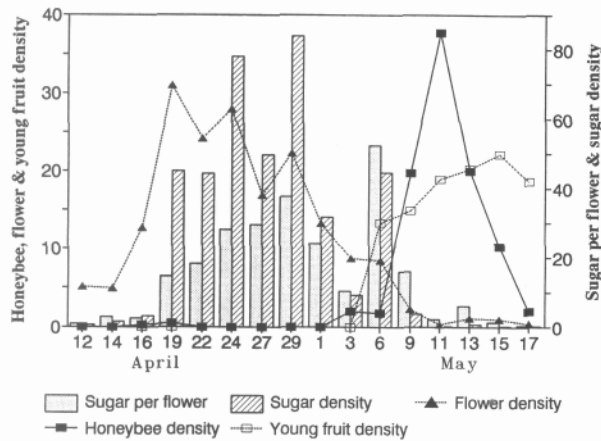


FIG. 5

Seasonal course of reward measures, bee and young fruit density of 'Hass' avocado (1992). Observations of five trees, three times a week, at the daily peak of female bloom. Units are: sugar per flower-1/100 mg, sugar density-mg per five inflorescences, flower and young fruit density-(per five inflorescences)/10, bee density--per tree.

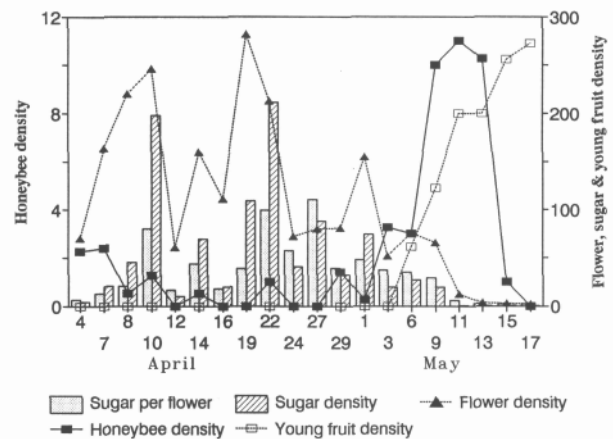


FIG. 6

Seasonal course of reward measures, bee and young fruit density of 'Ettinger' avocado (1992). Observations of five trees, three times a week, at the daily peak of male bloom. Observations started on April 4 on early-blooming trees and continued with later blooming ones on May 1. Young fruits could be counted on the marked branches from May 6, though a few were observed on the trees earlier. Units are: sugar per flower-1/100 mg, sugar density-mg per five inflorescences, flower and fruit density-per five inflorescences, bee density-per tree, young fruit density-(per five inflorescences) \times 10.

Correlations between bee density and plant-reward measures throughout the season (Table I) were significantly positive for 'Valencia' and mustard and negative for the avocados. These correlations were more significant when related to flower or sugar density, rather than to sugar quantity per flower. Correlations between densities of honeybees and young avocado fruits were significantly positive: $r = +0.72$ ($P = 8E-0.4$) for 'Hass' and $r = +0.52$ ($P = 0.013$) for 'Ettinger'.

Brassicaceae and Asteraceae pollen-loads were the main components of the pollen

collected by the bees during the first five weeks of the 1992 season (Figure 9), with mustard pollen accounting for 25% to 75% of the collected Brassicaceae pollen. The major pollens collected during the last 10 d of the season were of Asteraceae, Apiaceae and Poaceae. Citrus pollen was found only in small quantities throughout its blooming period and never exceeded 2% of the entire daily collection product. Avocado pollen appeared in small quantities (0.1% to 7.0%) during most of the 'Hass' and 'Ettinger' blooming period, and increased during the last 10 d of that period, to up to 50% of the collected pollen.

Correlations between each plant's pollen-load collection rate and bee density were significantly positive: $r = +0.86$ for 'Hass' and $r = +0.83$ for 'Ettinger' ($P = 5E-06$ for both); $r = +0.65$ ($P = 0.011$) for 'Valencia' and $r = +0.77$ ($P = 7E-05$) for mustard. The avocado pollen-load collection rate correlated negatively with that of Brassicaceae and Fabaceae ($r = -0.42$, $P < 0.05$). The correlations between both densities of honeybees and young avocado fruits and its competitors' bee and reward densities were mostly negative (Table II), being significant when related to 'Valencia' bee and flower densities and sugar per flower, to mustard's bee and flower densities and to pollen-load collection rate of Fabaceae (Table II). These correlations were more significant with regards to avocado initial fruit set than to its honeybee density.

TABLE II
Correlation coefficients (r) and probabilities (P) of the seasonal courses of honeybees' and avocado young fruits' density vs. its competitor plants reward measures (1992 data)

Competing plant and variable	Avocado cultivar (number of observations) and variable							
	'Hass' (18)				'Ettinger' (22)			
	Bee density		Young fruit density		Bee density		Young fruit density	
	r	P	r	P	r	P	r	P
'Valencia'								
Bee density	-0.62	0.006	-0.78	1E-04	-0.43	0.044	-0.53	0.011
Sugar/flower	-0.54	0.020	-0.75	4E-04	-0.47	0.026	-0.50	0.018
Sugar density	-0.38	n.s.	-0.53	0.025	-0.36	n.s.	-0.37	n.s.
Flower density	-0.54	0.022	-0.73	7E-04	-0.44	0.039	-0.49	0.020
Pollen-load rate	+0.02	n.s.	+0.43	n.s.	-0.22	n.s.	-0.57	0.058
Mustard								
Bee density	-0.39	n.s.	-0.54	0.020	-0.41	0.057	-0.50	0.018
Sugar/flower	-0.45	0.062	-0.59	0.011	-0.33	n.s.	-0.54	0.009
Sugar density	-0.38	n.s.	-0.52	0.028	-0.34	n.s.	-0.48	0.025
Flower density	-0.50	0.037	-0.68	0.002	-0.54	0.010	-0.64	0.001
Pollen-load rate ¹	-0.03	n.s.	-0.24	n.s.	-0.27	n.s.	-0.29	n.s.
Fabaceae								
Pollen-load rate	-0.62	0.006	-0.80	1E-04	-0.52	0.013	-0.70	3E-04

Units of bee density are bees per tree for avocado and 'Valencia' and bees per 1 m² for mustard. Units of flower, sugar and fruit density are per five inflorescences for avocado and per 1 m² for 'Valencia' and mustard.

¹Pollen-load rate of all Brassicaceae species, since sorting to species level was uncertain.

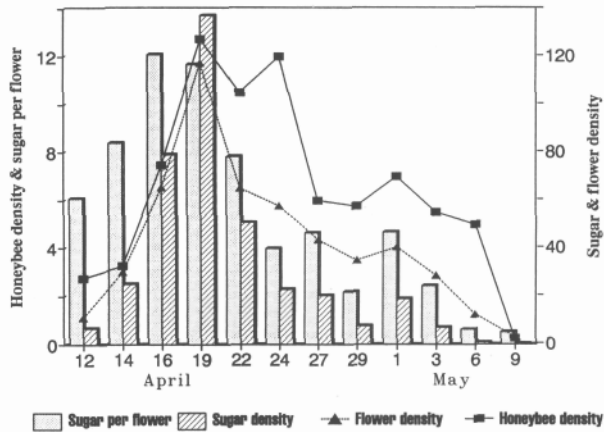


FIG. 7

Seasonal course of reward measures and bee density of 'Valencia' orange (1992). Observations on five trees, three times a week, at the same hour as the avocados. Units are: sugar per flower—mg (the whole sugar amount of the flower), sugar density— $10 \times$ mg per 1 m^2 , flower density—per 1 m^2 , bee density—per tree.

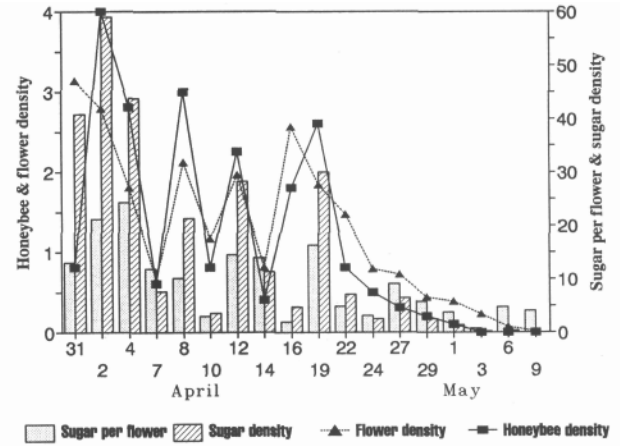


FIG. 8

Seasonal course of reward measures and bee density of wild mustard (1992). Observations on 1 m^2 , three times a week, at the same hour as the avocados. The observation square was moved to a new full blooming region on April 8, and again on April 16. Units are: sugar per flower— $1/1000$ mg, sugar density—mg per 1 m^2 , flower density—(per 1 m^2)/1000.

DISCUSSION

The main avocado competitors

Competition for pollination (CFP) has been defined by Waser (1983) as an interaction among sympatric plant species, resulting from the sharing of mutual pollinators, which reduces their reproductive success (fewer fruits and seeds per plant). He recognized two types of CFP: *competition through pollinator preference* (CPP), which occurs when one species' ability to attract pollinators away from another species lowers the latter's reproductive success, and *competition through interspecific pollen transfer* (CIPT), which occurs when a mutual pollinator transfers pollen among different plant species, leading to losses of both pollen and receptive stigma surface, which, in turn, results in lowering reproductive success. These two types of CFP may occur individually, or simultaneously.

Campbell and Molten (1985) suggested criteria to identify CFP, and to distinguish between its two types under field conditions. They assumed that CFP occurs among plant species which fit the following criteria: (1) they bloom at the same time and place, (2) they are pollinated by mutual pollinators, (3) in a closed space, some of them are preferred to others by the mutual pollinators, (4) under field conditions, their pollinator density is negatively correlated, (5) under field conditions, a decrease of the non-preferred species' yield is observed when the preferred species are present. In CPP, the competitor species should fit all of the above criteria, whereas in CIPT they need only fit criteria (1), (2) and (5); i.e. the pollination efficiency of the species is lowered when they are together, even though no decrease in pollinator density is observed on them.

According to our results, the early-blooming avocado cultivars, *Citrus* spp. and wild flowers of Brassicaceae and Fabaceae in the research area fit Waser's (1983) definition and act in accordance with Campbell and Motten's (1985) criteria, i.e.:

- (1) The early-blooming avocado cultivars bloom at the same time and place as the other plant species.
- (2) Honeybees, which are the main avocado pollinator, pollinate these species as well.
- (3) Although honeybee preference among these competitors in a closed space has not been studied, under field conditions we recorded a clear preference for 'Valencia' and mustard flowers over the avocados, when they flowered at the same time and place (Table II).
- (4) Negative correlations were obtained between bee density on the avocados and bee densities of both 'Valencia' and mustard, a significant one with regards to 'Valencia' (Table II, Figure 10). Avocado bee density was also negatively correlated with the reward measures of 'Valencia' and mustard (Table II).
- (5) Although we did not check for differences in avocado yield in the presence and absence of its competitors, these differences may be deduced from the high negative correlations found between the avocados' initial fruit set and both bee activity and reward measures of their competitors (Table II), noting the high correlations which have been found in Israel between initial fruit set and yield of the studied avocado cultivars (Lahav and Zamet, 1975).

It is therefore deduced that:

- a. In the Western Galilee of Israel, the main competitors of the early-blooming avocado cultivars are the *Citrus* spp. for nectar-foraging bees, the Brassicaceae with Fabaceae species for pollen foragers (see also Levin and Anderson, 1970; Rathcke, 1983; Waser, 1983).
- b. The avocado flowers' nectar and pollen attractiveness is low relative to the *Citrus* flowers' nectar, and to both Brassicaceae and Fabaceae species' pollen (see also Bergh, 1967 and 1969; Eisikowitch and Melamud, 1982; McGregor, 1976; Stout, 1923; Vithanage, 1990).
- c. Since pollination of female avocado flowers is performed only by nectar-collecting bees (mainly by nectar-and-pollen collectors), *Citrus* spp. flowers are the main competitors for pollination of the early-blooming avocado cultivars in this region. This conclusion is also supported by the avocados' initial fruit-set seasonal patterns (Fig ures 5, 6), which were more highly correlated with both honeybee and reward densities of *Citrus* spp. than to these of mustard (Table II).

However, it is worth noting that toward the end of 'Hass' and 'Ettinger' blooming season, and despite their decline in both flower and nectar densities, they became more attractive while competing with flowers of Asteraceae, Poaceae and Apiaceae species (Figures 3, 5, 6, 10, Table I), and the late-blooming cultivars 'Nabal' and 'Reed', although having less nectar per flower, were even more attractive (Figure 4, Table I).

One may conclude that bee density on the early-blooming avocados, while competing with the aforementioned plant species, is not controlled by their own reward properties, but mostly by that of their competitors. The avocado flowers' low attractiveness to honeybees is intriguing, since an avocado tree in full bloom may offer the bees similar amounts of nectar and pollen as its competitors (Ish-Am, 1994), and during part of the

season it is also well-visited. New evidence, however, indicates that the avocado flowers' low attractiveness may result from their nectar and pollen being poorly adapted to the honeybee's needs (Ish-Am, 1994). It should be noted that the honeybee, which is native to the Mediterranean region, serves as the avocado's generalist pollinator there, but since it does not exist in the avocados' native countries, no mutual adaptations have developed between them (Eisikowitch and Ish-Am, 1996; Valentine, 1978). This important issue should be explored by studying adaptations between avocado flowers and their native pollinators, probably *Meliponinae* and *Polistinae* species (Crane, 1992; Davenport, 1986; Free and Williams, 1976; Papademetriou, 1976).

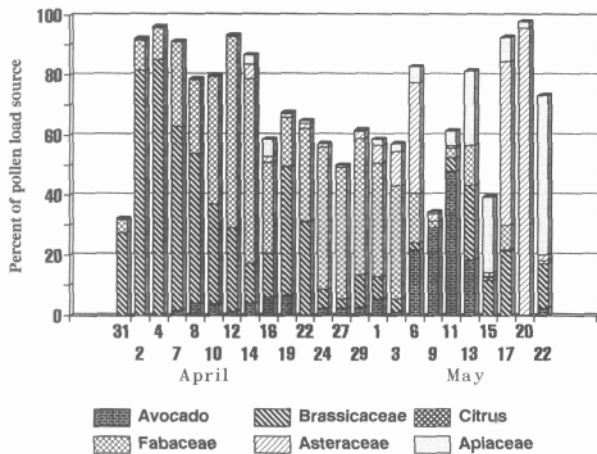


FIG. 9

Seasonal course of pollen-load sources (1992). Sum of 1 h collection in five hives, carried out three times a week, concomitantly with the avocado observations. The complementary percent of accumulated bars denotes pellets of other species' pollen, mostly of the Poaceae, as well as *Laurus*, oaks and undetermined pollen sources.

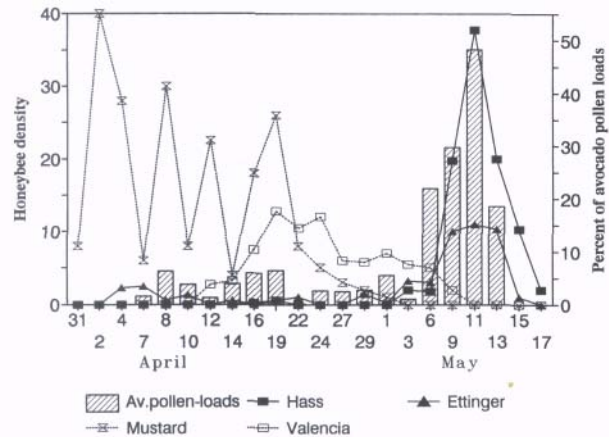


FIG. 10

Seasonal courses of avocado pollen collection rate, and honeybee density on the avocados and their competitor plants (1992). Compiled data from Figures 5 to 9. Bee density is presented as bees per tree for avocado and 'Valencia', and as bees per 10 m² for mustard.

Measuring attractiveness

The attractiveness of a particular flowering plant to honeybees depends on its own flowers' qualities, on the honeybees' population needs, and on environmental factors, such as characteristics of the competitor plant species, activity of other pollinators and the weather (Campbell and Molten, 1985; Levin and Anderson, 1970; Rathcke, 1983). In an attempt to measure attractiveness quantitatively, it has been expressed as the difference (or ratio) between the competitor plants' reward measures (Free, 1960; Levin and Bohart, 1955; Waller *et al.*, 1972), bee density on the plants (Free and Spencer-Booth, 1964), the frequency of bee visits to their flowers (Campbell and Motten, 1985; Chesson, 1983; Levin and Anderson, 1970), collection rate of the species' pollen-loads by the bees (Free, 1959), and net energy collection rate of the bees on these plants (Heinrich, 1983; Pleasent and Waser, 1985).

All of these methods utilize a direct comparison of measures among different species; however, a meaningful comparison of this type can be performed only among cultivars within the same species, or between closely related species (DeGrandi-Hoffman *et al.*,

1991; Free, 1960), and not between unrelated ones (Dafni *et al.*, 1988; Southwick *et al.*, 1981). We therefore developed a method to measure attractiveness of a flowering plant to honeybees employing only the variables of the plant itself, producing a value comparable among different plant species and environments. We measured, under field conditions, the attractiveness of a plant's flowers to honeybees by the coefficient " r ", obtained from the correlations between reward measures and bee density of this plant, over the course of a day or the flowering season. This method is based on the assumption that the higher the attractiveness of a blooming plant, the stronger its influence on the bees' distribution among food sources, and, in turn, the higher the correlations between its reward density and bee density over its flowers. Nevertheless, it should be stressed that attractiveness is always measured in a specific environment, and the same plant's attractiveness may differ in different ones. Although the plant reward measures may not be changed, the obtained " r " values are changed in accordance with the environment.

Using this method (Tables I, II) we verified quantitatively the early qualitative hypothesis regarding the avocado flowers' low attractiveness to honeybees (Bergh, 1967 and 1969; Eisikowitch and Melamud, 1982; McGregor, 1976; Stout, 1923; Vithanage, 1990). Furthermore, we found (Table I) that r was generally more significant when related to the plant rewards' density (as well as to the net energy collection rate, Ish-Am, 1994) and less significant when related to sugar per flower values. Therefore, it would appear that while allocating honeybee workers among food resources, the bees mainly estimate both the whole-plant reward and the expected rate (cal per min) of energy collection on it.

Consequences regarding avocado fruitfulness

Previous qualitative studies in Israel have shown that on days of low bee activity, when less than 10% of the avocado stigmas are pollinated, initial fruit set is almost nil (Eisikowitch and Melamud, 1982; Ish-Am, 1994). The present work demonstrates quantitatively (Figures 5, 6) that at least three nectar foragers per medium tree are needed for some initial fruit set, and over five are required for a measurable set (the corresponding pollination-rate values have been studied elsewhere: Ish-Am, 1985 and 1994). The early-blooming avocado cultivars 'Hass' and 'Ettinger' were exposed to the activity of three (or more) bees per tree during only 26% and 32% of their blooming periods, respectively (Figures 5, 6), and due to both bloom decline and rainy days, only about 5% of their flowers were actually exposed to an adequate level of honeybee pollination.

These conclusions may seem to contradict data from Florida, where the local avocado cultivars were found to set most of their crop under very low pollinator activity and female flower pollination rate, due to spontaneous self-pollination within the male-stage flower (Davenport, 1989 and 1991; Davenport *et al.*, 1994). Nevertheless, in Mediterranean regions it has been found that no fertilization occurs out of self-pollination within the male-stage flower (Katz, 1995; Peterson, 1956; Sedgley, 1977; Sedgley and Grant, 1983; Shoal, 1987; Snir, 1971). Therefore, we assume that, with regards to this issue, the avocado may behave differently under Mediterranean

conditions than in tropical climates.

In Israel most avocado orchards are close either to *Citrus* plantations or to fallow fields. Since blooming season of the early blooming avocado cultivars, as 'Hass' and 'Ettinger', significantly overlap that of *Citrus* and spring wild flowers, and since the honeybees prefer the latter to the former, these avocado cultivars are subjected to severe competition for pollination. Blooming periods of these avocados and their competitor plant species vary among years and regions, and, together with the weather, determine the number of effective pollination days (see also Rathcke, 1983). Therefore, and according to our results and earlier works (Snir, 1971; Gazit, 1977; Shoval, 1987; Eisikowitch and Melamud, 1992; Ish-Am, 1994) we conclude that, in many places and years, competition for pollination is the main factor limiting the yield of the early blooming avocado cultivars. These cultivars constitute 85% of the avocado area in Israel. However, the late-blooming avocado cultivars flower at a much more favourable time, from both weather and competition standpoints. If hives are present in the vicinity, they are visited by many bees throughout most of their blooming period. Note that honeybees, when they do visit avocado, pollinate it efficiently within the cultivar, although less so between cultivars (Ish-Am, 1994; Ish-Am and Eisikowitch, 1993), these avocado cultivars achieve a high pollination rate (Ish-Am, 1994), and usually set good yield.

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