

Major role of honeybee pollination in avocado as compared to wind

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Abstract

The purpose of this study was to determine the relative importance of honeybee (*Apis mellifera*) activity and wind in the pollination of avocado (*Persea americana* Mill.) trees. Data on the pollination rates of five avocado cultivars, honeybee densities, ambient temperatures, and wind velocities were recorded in an orchard in Israel, on 61 days over 7 years. The impact of wind velocity on avocado-flower pollen under laboratory conditions was also studied.

The rates of avocado pollination showed highly positive correlations with honeybee densities, whereas no correlations were observed with wind velocities. Pollination rates in days of very low honeybee activity were very low as well. Under laboratory conditions, no impact of wind velocities equalling those measured in the field was observed on avocado-flower pollen.

Our results agree with earlier works, in which avocado air-borne pollen found to contribute, at the most, 7% of the yield, and usually less. The avocado flower presents typical zoophilous (pollinated by animals) properties. The dependence of avocado pollination and yield on insect activity, mainly honeybees, found to be very high in most avocado growing territories, including in the tropical zone of Yucatán. Hence, we assume that contrasting data, which show a high effectiveness of wind pollination on avocados, are not relevant to most avocado-growing regions, including Israel and California. It is, therefore, recommended that the avocado growers continue using honeybees for pollination.

Importancia de la abeja domestica como polinizador de aguacate comparado con el viento

Resumen

El propósito de este estudio fue determinar la importancia relativa de la actividad de la abeja doméstica (*Apis mellifera*) y el viento en la polinización de árboles de aguacate (*Persea americana* Mill.). Datos sobre el porcentaje de polinización de 5 variedades de aguacate, densidad de abejas, temperatura ambiente y velocidad del viento fue registrado en un campo de aguacate en Israel por un período de tiempo de 61 días durante 7 años. El impacto de la velocidad del viento sobre el polen de las flores de aguacate fue también evaluado en condiciones de laboratorio.

Bajo condiciones de campo se observó una alta correlación positiva entre el porcentaje de polinización y la densidad de abejas, mientras que tal correlación no fue observada con relación de la velocidad del viento. El porcentaje de polinización en días de baja actividad de la abeja doméstica estuvo en el rango de entre 6% y 15%. Bajo las condiciones de laboratorio, la velocidad del viento, similar a aquellas observadas en las condiciones de campo, no tuvo ninguna influencia sobre el polen de las flores de aguacate.

Nuestros resultados están en acuerdo a estudios previamente publicados, donde se observó que la contribución del viento como agente polinizador no fue mayor a un 7% de la producción, y generalmente inclusive menos. La flor de aguacate presenta una estructura anatómica zoófila (polinizada por animales) típica. La dependencia del aguacate en la polinización por insecto, principalmente por abeja doméstica, para la producción, resulta ser muy alta en la mayoría de los territorios productores, incluyendo aquellos de las zonas tropicales de la península de Yucatan. Por lo tanto nosotros asumimos que los datos demostrando mayor importancia al viento como agente polinizador en el caso de aguacate, no son relevantes para la mayoría de los países productores. Por lo tanto es recomendado a los productores de aguacate la utilización de la abeja doméstica como agente polinizador.

Key words: avocado, honeybee-pollination, wind-pollination, temperature, air-borne pollen

Introduction

The unique flowering behaviour of avocado (*Persea americana* Mill.) may be termed "protogynous dichogamy with synchronous complementary flowering". The bisexual avocado flower opens twice, with an intermediate closing. The first opening is at the female stage and the second, usually the following day, is at the male stage. The male and female flower populations open simultaneously among trees at complementary times of day. Individual flowers within each population open successively, over 2 - 3 hours (h). Both female- and male-stage flowers attract insects by secreting nectar using different sets of nectaries (Bergh and Lahav 1996, p.113; Ish-Am and Eisikowitch 1991a, p.225; Robinson and Savage 1926, p.1; Stout 1927, p.145).

Avocado cultivars are divided into two complementary flowering groups. In warm weather, 'Group A' cultivars open in the morning with female-stage flowers, which are closed at mid-day, then re-open the following day at the male stage, from mid-day throughout the afternoon (a 34-h cycle). 'Group B' cultivars open female-stage flowers from mid-day throughout the afternoon, then re-open as male-stage flowers the following morning, and close towards the early afternoon (a 26-h cycle). In cool weather a delay occurs in the opening and closing times, which may result in a complete reversal in the part of the day in which female- and male-stage flowers open (Bergh *et al.* 1996, p.113; Bringhurst 1951, p.164; Davenport 1986, p.257; Ish-Am *et al.* 1991a, p.225; Papademetriou 1976, p.106; Robinson *et al.* 1926, p.1; Stout 1927, p.145).

An effective daily morning overlap therefore occurs between 'Group A' female-stage flowers and 'Group B' male-stage flowers, and *vice versa* in the afternoon. In most avocado cultivars grown in a Mediterranean-type climate, there is also a daily 1 - 3 h of self-overlap of bisexual flowering, when female-stage flowers and pollen-releasing male-stage flowers bloom simultaneously on the same tree. In contrast, in many West-Indian avocado cultivars grown in tropical regions, this bisexual self-overlap in flowering does not exist (Bringhurst 1951, p.164; Davenport, Parnitzki, Fricke and Hughes 1994, p.1200; Papademetriou 1976, p.106; Ish-Am *et al.* 1991a, p.225; Stout 1927, p.145).

Self-pollination within a single flower can only occur at the male-stage opening, during pollen release. Its effectiveness, namely its ability to accomplish fertilization of the male flower, is an open question. An inability of pollinated male-stage flowers to achieve fertilization has been demonstrated in Mexican and Guatemalan cultivars (Katz 1995; Sedgley 1977, p.27; Shoal 1987). On the other hand, in tropical regions, effective male-flower fertilization has been shown for local West Indian cultivars (Davenport 1989, p.844; Davenport *et al.* 1994, p.1200; Papademetriou 1976, p.106).

Close-pollination between neighbouring flowers occurs during the daily bisexual self-overlap period. During close-pollination, male- and female-stage flowers are in close proximity, and therefore its efficiency is high (Ish-Am *et al.* 1991a, p.225; Ish-Am and Eisikowitch 1991b, p.5). Cross-pollination occurs between 'Group B' male-stage flowers and 'Group A' female-stage flowers in the morning (under warm conditions), and *vice versa* in the afternoon (Ish-Am *et al.* 1991b, p.5; Nirody 1922, p.65; Stout 1927, p.145).

Avocado fruit is solely a product of pollination and fertilization. Parthenogenesis is not known in avocado. In growing areas such as Israel, California, Chile, and South Africa, the need for pollination represents a major limiting factor for yield. Self- or wind-pollination have both been found ineffective in those areas, and insect pollination, mainly by honeybees (*Apis mellifera*), has been shown to be essential for fruit production. Therefore, honeybee hives are regularly introduced into avocado orchards during bloom to ensure pollination (Clark and Clark 1926, p.85; Gazit 1977, p.88; Ish-Am and Eisikowitch 1993, p.175; Peterson 1955, p.163; Robbertse, Johansmeier and Morudu 1998, p.63). Moreover, in Central America native avocado pollinators, such as stingless bees and wasps, are also active (Bergh *et al.* 1996, p.113; Gazit 1977, p.88; Ish-Am and Gazit 2002, p.223; Peterson 1955, p.163). When there is not enough pollinator activity, rates of pollination are low and yields are significantly lower than average (Free and Williams 1976, p.125; Ish-Am and Eisikowitch 1998, p.195; Papademetriou 1976, p.106). In contrast, under the tropical weather conditions of Central America and Florida, insufficient pollination has not been found to be a significant yield-limiting factor in avocado (Davenport 1989, p.844; Davenport *et al.* 1994, p.1200; Papademetriou 1976, p.106). This effect has been explained as resulting from effective self-pollination, as well as wind-driven close- and cross-pollination. Such observations, with similar conclusions, have recently been reported from the Mediterranean climate of California (Davenport 2003, p.221; Ying, Davenport, Faber, Zheng, Schnell and Tondo 2009, p.255).

The purpose of this study was to determine the relative importance of honeybee activity and wind in the pollination of avocado trees under a Mediterranean climate.

Materials and methods

Observations

Observations were conducted in avocado orchards in Western Galilee, Israel, over seven flowering seasons (in 1982-1984 and 1989-1992). The cultivars Hass and Reed (Group A) and Fuerte, Ettlinger, and Nabal (Group B) were studied. Five trees in full bloom were selected for each cultivar in each season. Observations were conducted every 30 min over approx. 9 days of bloom per season for each cultivar. During each observation, flower stages (Ish-Am *et al.* 1991a, p.225), honeybee density (Ish-Am 2009, p.105), ambient temperatures and wind velocities were recorded.

"Honeybee density", the number of honeybees visiting a tree during 1 minute (min), was recorded for each of the selected trees of each blooming cultivar, and was later converted to "bees per medium tree" by relating each tree size to a standard tree size of 5 meters (m) in height. A daily "maximum bee density" was documented for each day of observation, for each cultivar.

Ambient temperatures were recorded every 30 min by a standard meteorological station installed next to the research plot. The daily average temperatures were calculated using the maximum daily temperature and the previous minimum night temperature.

Wind velocity data were accepted from an adjacent Government Meteorological Station, and were also estimated in an open field 20 m from the orchard, and inside the orchard. The Beaufort scale of wind velocity was used, and was later converted to meter per second ($m\ sec^{-1}$). Wind velocity data were compared over the 1982 season by performing simultaneous measurements at the three stations. Both average and maximum daily wind velocities for the blooming hours (between 08:00 and 18:00 h) were recorded for each day of observation.

Simulation of wind effect

Under laboratory conditions, an electric hair dryer was used as a wind generator. Newly opened 'Hass' and 'Fuerte' male flowers were inserted in 1% weight/volume (w/v) agar in Petri dishes, ten flowers per dish. The flowers were held under stereoscopic observation for the three pollen-releasing male stages (Ish-Am *et al.* 1991a, p.225), and pollen drift was recorded. Wind velocity was adjusted by changing the power and distance of the wind source, and was measured using a "Datametric" wind detector.

Rates of pollination

A sample of 50 styles per cultivar (ten per tree) was harvested approx. once an hour during female flowering, and the termination stages of cross- and close-pollination were recorded (Ish-Am *et al.* 1991a, p.225; Ish-Am *et al.* 1991b, p.5). The harvested styles were placed on a microscope slide covered with fixation gel [2% (w/v) carboxymethyl cellulose in a 1:2:7 (v/v/v) mix of ethanol:glycerol:water, with addition of aniline blue, to create a light-blue solution]. The percentage of pollinated stigmas ("percent pollination") was recorded under a light microscope. A total of 506 samples were collected for the five cultivars on 61 days of flowering over the seven seasons. A daily sequence of percent pollination was recorded on 55 days, and the daily "maximum percent pollination" was documented for each day and cultivar. Since the percent pollination was affected by distance from the pollinizer cultivar, only data from trees that were next to a pollinizer tree were used for the analysis.

Statistical analysis

Data from the seven years of measurements were pooled for the analysis. "Maximum percent pollination" values, as the dependent variable, were analysed by ANCOVA using a model that included a fixed nominal variable: "cultivar", and three continuous variable covariates: "maximum bee density", and the maximum (or average) values of wind velocity and temperature. An interaction term between "cultivar" and the continuous variables was also included. To assess the correlation of the percent pollination to each of the four climate parameters, four separate analyses were conducted. In each analysis, the daily average, or the daily maximum values of both wind velocity and temperature were used. Since significant differences were found between cultivars, these were also analysed separately using a logarithmic transformation. The data were analysed using JMP 7 software (JMP, Version 7. SAS Institute Inc., Cary, NC.).

Results

Wind measurements in the open field yielded lower velocity values, by a factor of 0.3 to 0.6, than those recorded at the Standard station under light winds, and similar values at wind velocities greater than 8 m sec⁻¹ (Table 1). Wind speed inside the orchard was even lower, by a factor of 0.2 to 0.5. The highest wind velocity measured in the open field for the 61 days was 9.7 m sec⁻¹.

Table 1: Comparison of wind velocity measurements^a of the three meteorological stations

Station	Height above ground (m)	Beaufort units at the standard station				
		1	2	3	4	5
		Wind velocity measurements (m sec ⁻¹)				
Standard station	5	0.3-1.5	1.6-3.3	3.4-5.4	5.5-7.9	8.0-10.7
Open field	2	0.2-0.5	0.5-1.0	1.0-3.0	3.1-7.0	7.1-10.1
Inside the orchard	2	0.0-0.1	0.1-0.2	0.2-0.5	0.5-1.5	1.5-4.5

^a Measurements were simultaneously conducted in the three stations (1982 season).

No pollen dispersal was recorded from the male 'Hass' or 'Fuerte' flowers when subjected to wind velocities of up to 10 m sec⁻¹ in the laboratory. With a stronger wind (13-14 m sec⁻¹), slight pollen dispersal was observed. The pollen was not dispersed as separate grains, but in clusters. At a higher wind velocity of 15 to 16 m sec⁻¹, all pollen clusters were disconnected from the valves of the anthers.

"Honeybee density" had a significant positive effect on the percentage of pollinated stigmas (Table 2), while neither maximum nor average wind velocities had any effect on this variable. The "average temperature" (positive effect) and the "Cultivar" had also a significant effect on percent pollination.

Table 2: Significance of the effect of the independent variables on the percent pollination of the avocado

Variable	Climatic variables included in each analysis ^a				
	Temperature	Average	Average	Maximum	Maximum
	Wind velocity	Average	Maximum	Average	Maximum
Model		<0.0001*	<0.0001*	<0.0001*	<0.0001*
Cultivar ^b		0.018*	0.012*	0.020*	0.013*
Maximum bees/medium tree		<0.0001*	<0.0001*	<0.0001*	<0.0001*
Average temperature		0.021*	0.020*	NR	NR
Maximum temperature		NR	NR	0.055	0.052
Average wind velocity		0.61	NR	0.71	NR
Maximum wind velocity		NR	0.48	NR	0.51

^a Four separate analyses were conducted using four combinations of daily average and maximum values of wind velocity and temperature.

^b The interaction terms were omitted from the model as no significant interaction between cultivar and the continuous variables was found.

* Significant *P* values.

NR – not relevant.

Pollination rates in each of the five cultivars were positively correlated with honeybee density, but none had a significant correlation with wind velocity (Table 3, Figure 1). Pollination rates on days of low honeybee activity (*i.e.* number of bees per tree ≤ 2) were 6.3%, 14.6%, and 12.5% for the early - blooming cultivars Hass, Ettinger, and Fuerte, respectively. Honeybee activity on the late-blooming 'Reed' and 'Nabal' was always high (≥ 10 bees per tree), and pollination rates were always high as well (≥ 40, and ≥ 50 in 'Reed' and 'Nabal', respectively).

Table 3: Correlations of percent pollination with honeybee density, and wind velocity, for each of the five cultivars

Cultivar	N	Correlations with honeybee density ^a			Correlations with wind velocity ^a		
		<i>r</i>	<i>r</i> ²	<i>P</i>	<i>r</i>	<i>r</i> ²	<i>P</i>
'Hass'	28	0.884	0.78	<0.0001*	-0.315	0.099	0.10
'Ettinger'	10	0.898	0.81	<0.0001*	0.210	0.044	0.92
'Fuerte'	13	0.772	0.60	0.0014*	0.040	0.0016	0.90
'Reed'	22	0.517	0.27	0.013*	0.146	0.021	0.52
'Nabal'	10	0.667	0.45	0.030*	-0.226	0.051	0.50

^a Logarithmic transformation.

* Values represent a significant correlation.

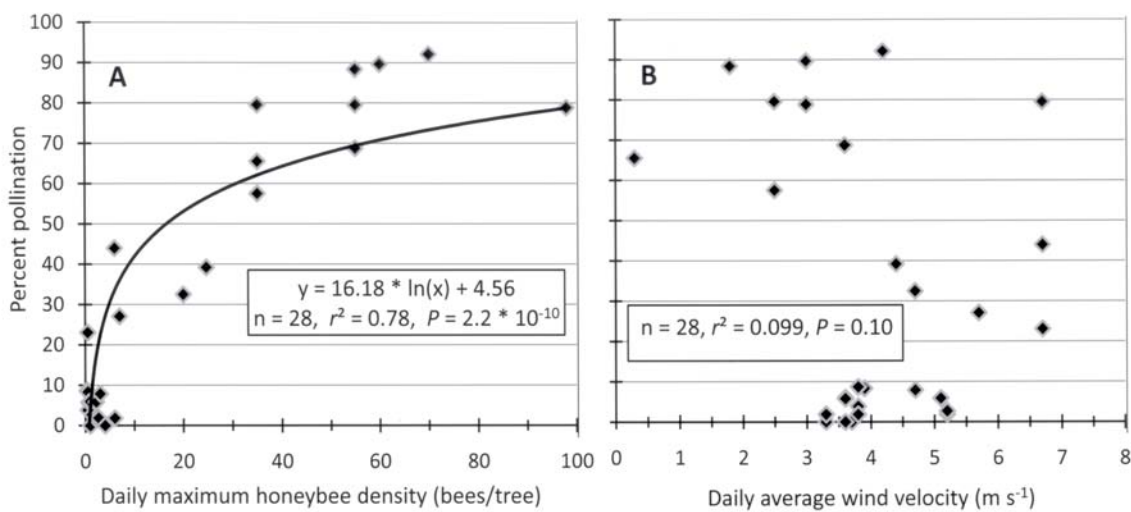


Figure 1: Correlations of 'Hass' daily maximum percent pollination, of trees close to a pollinizer cultivar, with daily maximum honeybee density (A), and the daily average wind velocity (B).

Discussion

Avocado pollination by honeybees

In the present study of five avocado cultivars over seven seasons, significant positive correlations were found between pollination rate and honeybee density when analysing the data of all five cultivars together (Table 2), as well as those of each cultivar separately (Figure 1, Table 3). Vithanage (1990, p.81) came to similar conclusions in South-West Australia. Working on 'Hass' and 'Fuerte' he formulated a "pollinator index" as a means of measuring the efficiency of avocado pollinators. He found that honeybees were 16 to 200 times more efficient than other visiting insects, mostly fly species. Placing two beehives per hectare in the plantation increased both bee activity and avocado yield (3.5-fold). Adding one more hive per hectare further increased productivity by 20 to 38%. The need for honeybees was also demonstrated in Israel by Ish-Am *et al.* (1998, p.195), who recorded almost zero fruit set over the course of 3 weeks during which 'Hass' and 'Ettinger' trees in full bloom were not visited by honeybees. Heavy fruit set began immediately after the bees visited on the trees. When bumblebees (*Bombus terrestris*) were added, the yield increased further (Ish-Am, Regev, Peterman, Lahav, Degani, El-Batsri and Gazit 2000, p.119).p

Avocado pollination by air-borne pollen

Our results show no relationship between pollination rate and wind velocity. Levels of avocado pollination by air-borne pollen can be evaluated using pollination data under minimal honeybee activity. During part of the flowering season of 'Ettinger', 'Fuerte' and 'Hass' in Israel (March-April), bees hardly visit the avocado bloom (0.5-2.0 bees per tree), preferring to visit the blooms of citrus and wild flowers (Ish-Am *et al.* 1998, p.195). During that period we documented 6 to 22% avocado flower

pollination, as compared to 30-90% under higher honeybee visitation (Figure 1). The low percent pollination attributable to air-borne pollen, to flies, and also to the low honeybee visitation. The few honeybees pollinate 4 to 10% of the flowers, and the flies might also have contributed a few percent (Ish-Am 1994; Vithanage 1990, p.81). Hence, the contribution of air-borne pollen to avocado pollination can be estimated to be within a range of 2 to at most 12%. These findings are in agreement with Katz (1995), who sampled floating pollen of 'Ettinger', 'Fuerte', 'Pinkerton' and 'Reed' in Israel using oily slides and a Rotorod sampler. He found very low percentages of avocado pollen released into the air, mostly as clusters. Floating pollen (of 'Ettinger') was found up to 25 m from the source, and the amount decreased greatly with distance. This can explain our failure to observe avocado pollen movement in the laboratory under both low and medium wind velocities. Katz (1995) did not find any correlations between the amount of air-borne pollen and wind velocity in 'Ettinger' or 'Fuerte', and found a negative relationship in 'Pinkerton' and 'Reed'. This corresponds to our observed lack of correlation between pollination rate and wind velocity (Tables 2, 3 and Figure 1). Since the small number of avocado pollen released into the air does not relate to wind velocity, we suggest "air-borne pollination" as a more accurate term than "wind pollination".

Katz (1995) calculated probabilities for air-borne pollination. He found probability of 2.5% for close-pollination in 'Ettinger', and 0.8%, 0.3%, and 0.06% for 'Fuerte', 'Reed', and 'Pinkerton', respectively. For cross-pollination by a pollen donor 3 m away, these probabilities were three to five times lower. Katz also measured air-borne pollination rates in caged trees, finding 2.5% pollination in young 'Pinkerton' and 'Reed' trees positioned below a flowering 'Ettinger' tree, 4.7% in 'Reed' beside 'Nabal', but only 0.6% pollination in a secluded 'Ettinger' tree.

Avocado fruit set under air-borne pollination

Previous research, in California (Gustafson and Bergh 1966, p.39; Peterson 1955, p.163), Israel (Gazit 1977, p.88), South Africa (Du Toit 1994, p.4; Robbertse *et al.* 1998, p.63) and in Tropical Yucatán (Can-Alonzo, Quezada-Euan, Xiu-Ancona, Moo-Valle, Valdovinos-Nunez and Medina-Peralta 2005, p.3), has shown that avocado trees that have been caged to exclude bees produce only a few fruits. Trees that were caged without a pollinizer cultivar carried only 1 to 3% of the fruits carried by un-caged trees, whereas trees caged with a pollinizer carried 4 to 6%. Another measure of the low efficiency of air-borne fertilization was achieved while using isoenzymes to identify fruits' male parent (Degani, Lahav, El-Batsri and Gazit 2003, p.1433). In caged trees, with a beehive but without a pollinizer tree, low but consistent rates of cross-pollinated fruit were found. On 'Tova' trees caged as above for four consecutive years, ca. 7% of the total fruit set (range of 3-14%) was the result of cross-pollination.

To understand the above data one must take into account both the requirement for at least 20 pollen grains per stigma to ensure a significant fertilization rate (Shoval 1987), and the advantage of cross- over self-pollination (Argaman 1983; Degani, Goldring and Gazit 1989, p.106; Degani, El-Batsri and Gazit 1997, p.813; Gazit and Gafni 1986, p.3; Peterson 1955, p.163; Robbertse, Coetzer and Johannsmeier 1996, p.63). The contribution of air-borne pollen to avocado pollination can be summarized as follows. An avocado tree carries on average 1 million flowers per season (Lahav and Zamet 1999, p.95). Therefore, the 2.5% of the flowers which are pollinated with air-borne pollen each day on a caged tree with no bees (Katz, 1995), sum to some hundreds of flowers per day, and many thousands per season. However, only very few of these flowers' stigmas accumulate 20 pollen grains (Davenport 1989, p.844; Ish-Am 1994; Katz 1995; Quiñones-Roldan, Castillo-Gonzales, Barrientos Priego, Avitia-Gacia, Gazit and Ish-Am 1999, p.81), the minimum amount for fruit set (Shoval 1987). Therefore, only a few (1-3%) of the fruits produced by the tree in a season are the result of air-borne pollen. Adding a pollinizer cultivar into the cage doubles fruit set (4-6%), because cross-pollination increases the probability of fruit set. Furthermore, introducing a beehive into the cage and placing a pollinizer tree out-cage, next to the net, results in a greater increase in air-borne cross-fruit set (ca. 7%). The bees accomplish efficient close-pollination, and the few floating cross-pollen grains that drift through the net from the adjacent pollinizer encounter pollinated stigmas carrying more than 20 grains, and therefore enjoy an improved chance of fertilization.

Avocado pollination by honeybees vs. by the wind

The avocado flower represents a typical zoophilous (animal-pollinated) flower (Faegri and Pijl 1979). Nevertheless, and in contrast to the above-presented evidence, it has been reported that most avocado pollination in Florida (West-Indian cultivars) results from air-borne pollen (Davenport 1989, p.844; Davenport *et al.* 1994, p.1200). Air-borne pollen is thought to contribute to both cross- and

close-pollination at the female stage, as well as to self-pollination at the male stage, which resulting in a commercial fruit set (Davenport 1989, p.844; Davenport *et al.* 1994, p.1200; Imbert 1998, p.99). More recently it has been reported that wind pollination is efficient in 'Hass' in California as well (Davenport 2003, p.221; Ying *et al.* 2009, p.255). These researchers claim that there is no direct evidence that honeybees significantly contribute to avocado pollination, and that wind pollination is the major productivity factor for all cultivated avocados. The results of our present study do not support these claims. Moreover, in Mediterranean avocado-growing areas, such as California, Chile and Israel, insect pollination, mainly by honeybees, is an essential condition for commercial production. The importance of bee pollination for avocado production has also been documented under subtropical summer-rain growing regions in South Africa (Du Toit 1994, p.4; Robbertse *et al.* 1998, p.63), Australia (Vithanage 1990, p.81), Mexico (Nieto Angel 1984, p.45; Quiñones-Roldán *et al.* 1999, p.81), and tropical Yucatán (Can-Alonzo *et al.* 2005, p.3). Air-borne avocado pollination does occur, but its contribution to cropping is small. At most, with a neighbouring pollinizer and under high honeybee activity, it is estimated to contribute an additional average of only 7% to total avocado production. It is, therefore, strongly recommended that avocado growers in the above growing regions continue using honeybee pollination, which is essential for the production of a commercial avocado crop.

References

- Argaman, E 1983, *Effect of temperature and pollen source on fertilization, fruit set and abscission in avocado* (*Persea americana Mill.*), M.Sc. Thesis, The Hebrew University of Jerusalem, Rehovot, Israel, 111 pp.
- Bergh, BO and Lahav, E 1996, 'Avocados', *Fruit Breeding*, Volume I. In: Tree and Tropical Fruits (Janick, J. and Moore, J.N., Eds), John Wiley & Sons, West Lafayette, IN, USA, 113-166.
- Bringhurst, RS 1951, 'Influence of glasshouse conditions on flower behavior of Hass and Anaheim avocados', *California Avocado Society Yearbook* 35, 164-168.
- Can-Alonzo C, Quezada-Euán JJG, Xiu-Ancona P, Moo-Valle H, Valdovinos-Nunez GR and Medina-Peralta S 2005, 'Pollination of 'criollo' avocados (*Persea americana*) and the behaviour of associated bees in subtropical Mexico', *Journal of Apicultural Research* 44(1), 3-8.
- Clark, OI and Clark, AB 1926, 'Results of pollination and other experiments on avocados at the orchards of Point Loma Homestead', *California Avocado Association Annual Report*, 11, 85-94.
- Davenport, TL 1986, 'Avocado flowering', *Horticultural Review*, 8, 257-289.
- Davenport, TL 1989, 'Pollen deposition on avocado stigmas in Southern Florida', *HortScience*, 24, 844-845.
- Davenport, TL 2003, 'Evidence for wind-mediated, self and cross pollination, of 'Hass' avocado trees growing in Mediterranean environments', *Proceedings of the 5th World Avocado Congress*, Granada-Malaga, Spain, 221-225.
- Davenport, TL, Parnitzki, P, Fricke, S and Hughes, MS 1994, 'Evidence and significance of self-pollination of avocados in Florida', *Journal of the American Society for Horticultural Science*, 119, 1200-1207.
- Degani, C, Goldring, A and Gazit, S 1989, 'Pollen parent effect on outcrossing rate in 'Hass' and 'Fuerte' avocado plots during fruit development', *Journal of the American Society for Horticultural Science*, 114, 106-111.
- Degani, C, El-Batsri, R and Gazit, S 1997, 'Outcrossing rate, yield and selective fruit abscission in 'Ettinger' and 'Ardith' avocado plots', *Journal of the American Society for Horticultural Science*, 122, 813-817.

Degani, C, Lahav, E, El-Batsri, R and Gazit, S 2003, 'Caging single avocado trees with a beehive does not guarantee exclusive formation of selfed progeny', *HortScience*, 38, 1433-1434.

Du Toit, AP 1994, 'Pollination of avocados, mangos and litchis', *Plant Protection News*, 35, 4-5.

Faegri, K and Van Der Pijl, L 1979, *The Principles of Pollination Ecology*, 3rd Edition, Pergamon Press, Oxford, UK, 244 pp.

Free, JB and Williams, IH 1976, 'Insect pollination of *Anacardium occidentale* L., *Mangifera indica* L., *Blighia sapida* Koenig and *Persea americana* Mill', *Tropical Agriculture*, 53, 125-139.

Gazit, S 1977, 'Pollination and fruit set of avocado', In: *Proceedings of the First International Tropical Fruit Short Course: The Avocado* (Saults J.W., Philips R.L. and Jackson L.K., Eds), University of Florida, Gainesville, FL, USA, 88-92.

Gazit, S and Gafni, E 1986, 'Effect of hand pollination with different pollen donors on initial fruit set in avocado', *Israel Agriseach*, 1, 3-17.

Gustafson, CD and Bergh, BO 1966, 'History and review of studies on cross-pollination of avocados', *California Avocado Society Yearbook*, 50, 39-49.

Imbert, FM 1998, 'Delayed pistil senescence causes an overlap in 'Tonage' avocado (*Persea americana* Mill.)', *California Avocado Society Yearbook*, 81, 99-106.

Ish-Am, G 1994, *Interrelationship between avocado flowering and honey bees and its implication on the avocado fruitfulness in Israel*, Ph.D. Thesis, Tel Aviv University, Tel Aviv, Israel, 157 pp.

Ish-Am, G 2009, 'Daily patterns of avocado bloom and honeybee activity', *California Avocado Society Yearbook*, 91, 105-127.

Ish-Am, G and Eisikowitch, D 1991a, 'Possible routes of avocado tree pollination by honeybees', *Acta Horticulturae*, 288, 225-233.

Ish-Am, G and Eisikowitch, D 1991b, 'Avocado pollination within and between cultivars', *Alon Hanotea* 46, 5-15.

Ish-Am, G and Eisikowitch, D 1993, 'The behaviour of honey bees (*Apis mellifera*) visiting avocado (*Persea americana*) flowers and their contribution to its pollination', *Journal of Apicultural Research*, 32, 175-186.

Ish-Am, G and Eisikowitch, D 1998, 'Low attractiveness of avocado (*Persea americana* Mill.) flowers to honeybees (*Apis mellifera* L.) limits fruit set in Israel', *Journal of Horticultural Science*, 73, 195-204.

Ish-Am, G, Regev, I, Peterman, Y, Lahav, E, Degani, C, El-Batsri, R and Gazit, S 2000, 'Improving avocado pollination with bumblebees: 3 seasons summary', *California Avocado Society Yearbook*, 92, 119-135.

Ish-Am, G and Gazit, S 2002, 'Pollinators of Avocado', *Excerpted and adapted from Wysoki M, Van Den Berg MA, Ish-Am G, Gazit S, Peña JE and Waite GK: Pest and Pollinators of Avocado, In: Tropical Fruit Pests and Pollinators*, Peña, JE, Sharp, JL and Wysoki, M, Eds, CABI Publishing, Wallingford, Oxford, UK. 223-293.

Katz, E 1995, *Avocado productivity: pollination, pollenizers, fruit set and abscission*, M.Sc. Thesis, The Hebrew University of Jerusalem, Rehovot, Israel, 130 pp.

Lahav, E and Zamet, D 1999, 'Flowers, fruitlets and fruit drop in avocado trees', *Revista Chapingo Serie Horticultura 5 Num. Especial*, Proceedings of Fourth World Avocado Congress, 95-100.

Nieto Aigel, R 1984, 'Observacion preliminar de la polinizacion entomofila en aguacate *Persea americana* Mill', *Revista Chapingo*, 45-46, 54-55.

Nirody, BS 1922, 'Investigations in avocado breeding', *California Avocado Association Annual Report*, 1921-1922, 65-78.

Papademetriou, MK 1976, 'Some aspects of the flower behavior, pollination and fruit set of avocado (*Persea americana* Mill.) in Trinidad', *California Avocado Society Yearbook*, 60, 106-153.

Peterson, PA 1955, 'Avocado flower pollination and fruit set', *California Avocado Society Yearbook*, 39, 163-169.

Quiñones-Roldán ML, Castillo-González AM, Barrientos Priego AF, Avitia-García E, Gazit S, Ish-Am G 1999, 'Pollination and fruit set in three cultivars of avocado (*Persea americana* Mill.)', *Program and Summaries of 4th World Avocado Congress*, Mexico 1999, p 81-82.

Robbertse PJ, Coetzer LA, Johannsmeier MF 1996, 'Hass yield and fruit size as influenced by pollination and pollen donor – a joint progress report', *South African Avocado Growers' Association Yearbook* 19, 63-67.

Robbertse PJ, Johannsmeier MF, Morudu TM 1998, 'Pollination of Hass avocados', *South African Avocado Growers' Association Yearbook* 21, 63-68.

Robinson, TR and Savage, EM 1926, 'Pollination of the avocado', *USDA Department Circular No. 387*, Washington D.C., USA, 16 pp,

Sedgley, M 1977, 'Reduced pollen tube growth and the presence of callose in the pistil of the male floral stage of the avocado', *Scientia Horticulturae*, 7, 27-36.

Shoval, S 1987, *Pollination Rate and Pollen Tube Growth of Avocado, in Relation to Yield*, M.Sc. Thesis, The Hebrew University, Rehovot, Israel, 161 pp.

Stout, AB 1927, 'The flowering behavior of avocados', *Memoirs of the New York Botanical Gardens*, 7, 145-203.

Vithanage, V 1990, 'The role of the European honeybee (*Apis mellifera* L.) in avocado pollination', *Journal of Horticultural Science*, 65, 81-86.

Ying Z, Davenport TL, Faber B, Zhang T, Schnell RJ, Tondo CL 2009, 'Re-evaluation of the roles of honeybees and wind on pollination in avocado', *Journal of horticultural science & biotechnology*, 84(3), 255-260.