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Daily Patterns of Avocado Bloom and Honeybee Activity

Abstract - The daily course of avocado flowering and honeybee activity was studied. Daily flowering pattern was constant, differing between Type A and B cultivars. Flowering times were negatively correlated to average daily temperature. A daily self bisexual overlapping period was observed, which became shorter with increasing temperature. Daily honeybee activity pattern on the bloom was also constant, related to the daily flowering course. On Type B cultivars it lasted 12 hours with two activity peaks; on Type A, it lasted 10 hours with only one peak. The daily flowering course may support efficient pollination in Type A cultivars and oppose pollination efficiency in Type B. The daily bee activity course strengthens close-pollination possibility of Type A cultivars and lessens it in Type B. However, it decreases Type A cross-pollination possibility and supports its high efficiency in Type B. Honeybee daily activity in the two avocado types was a partial mirror image, which may further support their mutual efficient cross-pollination.

Keywords: *Persea americana* / *Apis mellifera* / daily flowering course / daily honeybee activity / temperature / pollination efficiency

Introduction

The avocado (*Persea americana*, Lauraceae) flower is bisexual, opening twice with an intermediate closing. The first opening is in the female stage and the second, usually on the following day, is in the pollen-releasing male stage. The appearance and disappearance of the daily female and male flower populations is synchronized within the tree (and cultivar). However, the population's individual flowers do not open and close simultaneously but rather one after the other, over a 2 to 3-hour period, which establishes a regular overlapping of subsequent flower stages on the tree, and enables extended pollen release. This unique flowering behavior is known as diurnally synchronous dichogamous protogyny, with intermediate closing (Peterson, 1955; Ish-Am and Eisikowitch, 1991b, 1992; Gazit and Degani, 2002).

The avocado cultivars are divided into two complementary flowering groups, according to their daily flowering sequence. "Type A" cultivars open female-stage flowers (in warm weather) from morning till noon, and reopen them the next day in the male stage from noon throughout the afternoon, for a flower blooming cycle of about 34 hours. "Type B" cultivars, on the other hand, open female-stage flowers from noon throughout the afternoon, and reopen them in the male stage on the following morning till early afternoon, a flower blooming cycle of about 26 hours. Thus, a daily effective overlap occurs between Type A female-stage flowers and Type B pollen-releasing male-stage flowers during the morning, and *vice versa* in the afternoon. Furthermore, some avocado cultivars also exhibit a regular daily self-overlap phase of female-stage flowers and pollen-releasing male-stage flowers on the same tree, lasting for 1 to 3 hours. It is well documented that this flowering behavior allows for both cross-pollination and close-pollination (within the cultivar), but, at least under Israeli conditions, prevents fertile self-pollination. In cool weather, a delay in both female- and male-opening periods occurs, which may result in partial or even complete reversal in the time of day during which female- and male-stage flowers are open. At both female and male stages, flower nectar is secreted, although by different sets of nectaries (Peterson, 1955, 1956; Sedgley and Grant, 1983; Ish Am and Eisikowitch, 1991a, 1991b, 1992; Gazit and Degani, 2002).

Today we are well aware of the importance of honeybees (*Apis mellifera*) for avocado pollination in Israel. Honeybees are the major- and usually sole-efficient avocado pollinator. However, in a competitive situation, honeybees usually prefer to visit flowers of citrus trees, litchi, or wildflowers. Hence, under conditions of competition for pollination, there is almost no honeybee activity on avocado trees, pollination rates are very low and the result is negligible fruit set (Ish-Am and Eisikowitch, 1991a, 1993, 1998a; Gazit and Degani, 2002; Ish-Am, 2005).

To execute pollination, the bees must alternately visit both pollen-carrying male flowers and female flowers. Furthermore, in most of the Israeli avocado cultivars, cross-pollination, mainly by a "potent" cultivar, has a better chance of effecting fertilization and fruit set than close-pollination (Gazit and Degani, 2002). Thus, for cross-pollination to take place, the bees must also move between different trees of female and male blooms. Pollination efficiency is, of course, dependent on bee density on the bloom. However, close-pollination efficiency is also dependent on the rate of the daily self-overlap phase of female-stage flowers and pollen-releasing male-stage flowers within the tree, while cross-pollination efficiency is dependent on the rate of overlap between male flowering of the pollenizer cultivar and female flowering of the pollenized one, on the distance between them, and on honeybee mobility (Ish-Am and Eisikowitch, 1991a, 1998a, 1998b, 1998c; Ish-Am, 2005).

When there is sufficient bee activity, one can witness significant changes in that activity on the avocado bloom throughout the day. The daily pattern of those changes over female and male blooms of Type A and B avocados is crucial for pollination efficiency. Since the daily avocado flowering pattern is markedly influenced by temperature changes, these changes also have an essential impact on avocado pollination (Ish-Am and Eisikowitch, 1991b, 1992; Ish-Am, 2005).

Research objective: to study the daily pattern of avocado flowering and honeybee activity on the flowers, and their relation to each other and to temperature, in four avocado cultivars.

Materials and Methods

Terminology

The following terms are used throughout this report (Faegri and van der Pijl, 1979; Ish-Am and Eisikowitch, 1992).

Self bisexual overlapping: the tree carries receptive female flowers and pollen-releasing male flowers simultaneously. Close-pollination within the tree is possible.

Cross bisexual overlapping: one cultivar carries pollen-releasing male flowers (“pollenizer cultivar”) while another cultivar carries receptive female flowers)pollenized cultivar”).

Stages of the avocado flower: the avocado flower’s flowering course may be divided into the following stages:

C1 – closed flower before opening.

F1 – opening of the functionally female flower.

F2 – open female flower.

F3 – closing of the female flower.

C2 – closed flower in an interim overnight pause.

M1 – opening, and open functionally male flower, before pollen release.

M2 – male flower releases pollen from the anthers’ lower valves.

M3 - male flower releases pollen from both the lower and upper valves of the anthers.

M4 – closing of the functionally male flower.

C3 – closed flower that has ended its flowering process.

Observations

Observations were performed in avocado orchards in the Western Galilee in Israel, in the years 1982-1984 and 1989-1992. The early-blooming cultivars ‘Hass’ and ‘Ettinger’, and the late-blooming ‘Reed’ and ‘Nabal’, flowering type A and B in both pairs, respectively, were studied. To monitor the daily course of flowering and bee activity, five medium-size trees (5-6 m in height) in full bloom were selected and marked for the season for each cultivar. Observations were implemented every half hour over the course of about 10 days during the flowering season. At each observation, temperature and relative humidity were recorded, flower stages were checked and honeybees were counted on each of the marked trees. The maximum temperature during the day (Tmax) and the minimum temperature during the previous night (Tmin) were also recorded. The average temperature of the observation day (Tavg) was calculated as the average of these two temperature records: Tavg = (Tmin + Tmax)/2.

Bee Density

Honeybees visiting the avocado tree were counted using a manual counter, while slowly walking around the tree for about a minute (Ish-Am and Eisikowitch, 1998b, 1998c). When the number of bees on a single tree was above 100, the bee count was implemented on one-half or one-third of the tree, and was then multiplied accordingly. Bee-density daily records (of days that bees-per-tree value exceeded 10) were attributed to the observation hour, temperature, and flower stages on the tree.

Results

Daily Flowering Course (Figs. 1-4)

Each of the four studied cultivars exhibited a regular daily flowering course, which lasted 10 to 12 hours. A similar daily flowering course was found in 'Hass' and 'Reed', the Type A cultivars, while a significantly different flowering course was found in the Type B 'Ettinger' and 'Nabal'. Significant negative linear correlations were found between the flowering times of the four cultivars and the average daily temperature (Figs. 1-4; see also Ish-Am and Eisikowitch, 1991b, 1992): the warmer the day, the earlier the flower stages' blooming. Therefore, on cooler days, the stages' flowering time was delayed and the last stages of the day were postponed into the night, or even the next morning. The earlier blooming 'Hass' and 'Ettinger' (Figs. 1-2) showed a great sensitivity to temperature changes: on warm days (Tavg > 20°C) their flowering commenced before 6:00, and at times even at 4:00, and ended at around 16:00, while on cool days (Tavg < 14°C), their flowering commenced at 10:00, or even at 12:00, and ended only at night, or the next morning. 'Reed' and 'Nabal' (Figs. 3-4), which bloom later in the season in warmer weather, showed less sensitivity to temperature changes: on cooler days (Tavg < 20°C) they commenced flowering at 8:00 and ended around 18:00, and on warm days (Tavg > 24°C), they flowered between 6:30 and 16:00.

Self Bisexual Overlapping (Tab. I, Figs. 1-4)

A self bisexual overlapping period was observed in all four cultivars, and in most cases became shorter with increasing temperature. In 'Ettinger' (Fig. 2), no shortening of the self bisexual overlapping was found, while in 'Nabal' (Fig. 4) it was maximal, and on warm days with average temperature exceeding 24°C, it disappeared all together. On those days, the 'Nabal' trees closed their last male flowers, which had been open since the morning, between 12:00 and 13:00, remained without any open flowers for an hour or two, and then started to open their afternoon female flowers.

Cross Bisexual Overlapping (Tab. II, Figs. 5, 6)

The daily cross bisexual overlapping periods lasted longer than the self-overlapping ones. The morning cross-overlapping periods, in which Type A cultivars were pollenized by Type B ones, were distinctly longer than the afternoon overlapping ones. For the most part, the cross bisexual overlapping periods' sensitivity to temperature changes was low, except for the period of 'Hass' cross-pollenization by 'Ettinger', which became much longer with increasing temperature.

The Daily Course of Honeybee Activity on the Avocado Bloom (Figs. 7, 8)

The daily course of honeybee activity on the bloom of each of the four cultivars also revealed a constant pattern, which was related to the constant daily flowering course of the cultivar. That is to say, the daily peaks of bee activity did not show up at set hours, but they appeared earlier on warmer days and later on cooler ones, in accordance with the trees' flowering stages. Like the daily flowering course, a similar daily course of bee activity was found in 'Hass' and 'Reed', the Type A cultivars, while a significantly different bee-activity course was characterized in the Type B 'Ettinger' and 'Nabal'.

The daily honeybee activity on 'Ettinger' and 'Nabal' (Type B) lasted for about 12 hours, with two clear activity peaks (a bimodal daily pattern). On a day with average temperatures, there was a morning activity peak on the male pollen-releasing flower, and a second peak at the full female flower opening in the afternoon. Around noon, a decline in bee activity was observed, coinciding with their self bisexual overlapping period. The decline more noticeable in 'Nabal', which on warm days showed neither self bisexual overlapping period, nor bee activity during this period.

The daily honeybee activity on the Type A 'Hass' and 'Reed' lasted only about 10 hours, starting later in the morning and ending earlier in the afternoon. Bee activity on these two cultivars had only one clear daily peak, at around noon (on an average temperature day), that lasted about 2.5 hours and included their self bisexual overlapping period. Thus, honeybee activity on Type A cultivars was a partial mirror image of the activity on Type B cultivars (Figs. 7, 8): the highest bee activity on the cultivars of one type coincided with the lowest bee activity on the cultivars of the other type.

Discussion

The daily self bisexual overlapping period, which was found in all four studied cultivars, has also been found in other commercial cultivars studied in Israel and California (Ish-Am, unpubl. data). This is in contrast to other reports of this daily period absence in 'Hass' in California (Davenport, 2003). The daily self bisexual overlapping period enables effective close-pollination, and therefore provides an adequate explanation for the abundance of self-pollinated fruits found in avocado orchards (Peterson 1955; Ish-Am and Eisikowitch, 1991a; Gazit and Degani, 2002; Ish-Am, 2005). It is, in fact, a preferred explanation for the suggested wind-mediated self-pollination of the male-stage flowers (Davenport, 2003).

In previous research (Ish-Am and Eisikowitch, 1998a), it was concluded that under a significant bee activity of 10 honeybees or more per medium-size avocado tree, the day-to-day fluctuations of bee activity on the trees match, and are probably dictated by, the seasonal changes in the tree's reward quantity. Here we obviously found that under these same conditions, fluctuations in honeybee activity during the day faithfully follow the trees' daily flowering routine as well, and also seem to be directed by changes in the trees' reward amounts (see also Herrera, 1990).

The conditions for both cross- and close-pollination, with regard to the daily flowering course, were found to be more convenient for Type A cultivars than for Type B. Cross-pollination (Tab. II; Figs.

5-6) takes place in Type A, as the pollinated cultivar, for 4.5 hours or more on hot days and up to 7 hour on cool days, occurring in the morning and the afternoon. In contrast, in Type B cultivars, cross-pollination can only occur for a 2 to 3-hour period, in the afternoon on warm days, but in the evening and later on cool days. Close-pollination occurs in Type A cultivars (Tab. I, Figs. 1-4) when male flowers are opening and releasing pollen (M2 beginning), whereas, in Type B cultivars it occurs when the male flowers, which finished releasing pollen much earlier, are closing (M4). As for the Type B 'Nabal', close-pollination becomes less and less probable with increasing temperature, disappearing altogether on warm days.

The single daily peak of honeybee activity on Type A cultivars (Figs. 7, 8) adds to their extremely efficient close-pollination possibility, since it takes place during their self bisexual overlapping period. In contrast, in Type B cultivars, a daily minimum of bee activity is observed during this period, which may further decrease close-pollination efficiency. Interestingly, an inverted picture is revealed for cross-pollination efficiency, regarding honeybee activity. In Type A cultivars, bee activity is relatively low during this period, while in Type B cultivars, it is reaching its afternoon peak.

Daily bimodal activity of pollinators on avocado, similar to the two daily peaks of honeybee activity on Type B cultivars noted here (Figs. 7, 8), has also been found in Jamaica by Free and Williams (1976), and in Mexico by Ish Am and Gazit (unpubl. data). Kubitzki and Kurz (1984) also described daily bimodal pollinator activity on the bloom of a number of Lauraceae species in Brazil's rainforest. It thus seems that this daily pattern of bimodal pollinator activity characterizes avocado and other members of its family. It should be noted, however, that Herrera (1990) also observed daily bimodal pollinator activity on *Lavendula* bloom, which matched its daily pattern of nectar secretion.

Since honeybee peak activity on the male-stage flowers of one type cultivar always preceded their peak activity on the female-stage flowers of the other type (Figs. 7, 8), thus, twice a day, the maximal bee activity "moves" from pollen-loaded male flowers of one cultivar to the open female flowers of the other type cultivar, a move that could favor efficient cross-pollination. A similar phenomenon has been observed by Augspurger (1980) and by Frankie and Haber (1983) on tropical and subtropical trees which, like avocado, carry many small flowers ("mass flowering"). They explained this movement of the "bee cloud" as a mechanism that enhances cross-pollination probability. They assumed this mechanism to be the product of selection for temporal coordination between nectar secretion and pollen release of female and male blooms, respectively. Whether this shift of honeybee activity peak from male- to female-blooming avocado trees does, in fact, represent a direct move of pollen-loaded bees from the male flowers to the female ones, which would greatly enhance cross-pollination, or whether the pollen-loaded bees actually first return to the hive, unload the pollen, and then these bees, or other bees, leave the hive towards the female trees, remains an open question. This issue should be studied with respect to honeybees, as well as with respect to the stingless bees (Meliponinae), which have been found to be the original pollinators of avocado in Mexico (Ish-Am et al., 1999; Ish-Am and Gazit, 2002).

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Table I. Duration of self bisexual overlapping period

Cultivar	Flowering type	Duration of self bisexual overlapping on cool days	Duration of self bisexual overlapping on warm days
'Hass'	A	85 min	30 min
'Ettinger'	B	130 min	130 min
'Reed'	A	135 min	30 min
'Nabal'	B	95 min	No overlap on days of Tavg > 24°C

Table II. Duration of cross bisexual overlapping period

Pollenizer Cultivar	Pollenized cultivar	Duration of cross bisexual overlapping on cool days	Duration of cross bisexual overlapping on warm days
'Ettinger'	'Hass'	4 1/4 h	7 h or more
'Hass'	'Ettinger'	2 h	2 3/4 h
'Nabal'	'Reed'	5 1/4 h	5 1/4 h
'Reed'	'Nabal'	3 1/4 h	3 h

Legend for Figures 1-6

F1 begin – beginning of female bloom
F3 end – end of female bloom
M1 begin – beginning of male bloom before pollen release
M2 begin - beginning of pollen release
M2 end – end of pollen release, male flowers are still open
M4 end – end of male bloom

Note: In 'Ettinger', F3 end occurred mostly at night, and then could not be detected. Therefore F2 end was measured.

F2 end – end of full-open female flowers bloom. Closing (half-open) female flowers remain for another hour or so.

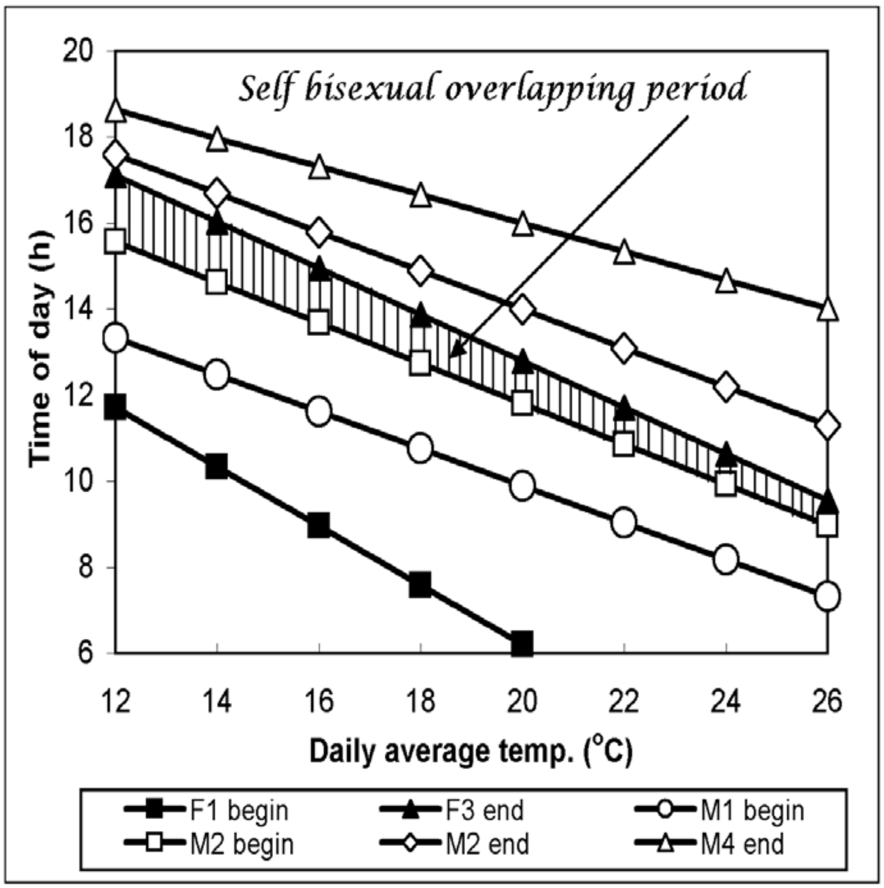

Figure 1: Correlation between daily flowering course and temperature in the Hass cultivar (adapted from Ish Am and Eisikowitch, 1991b)

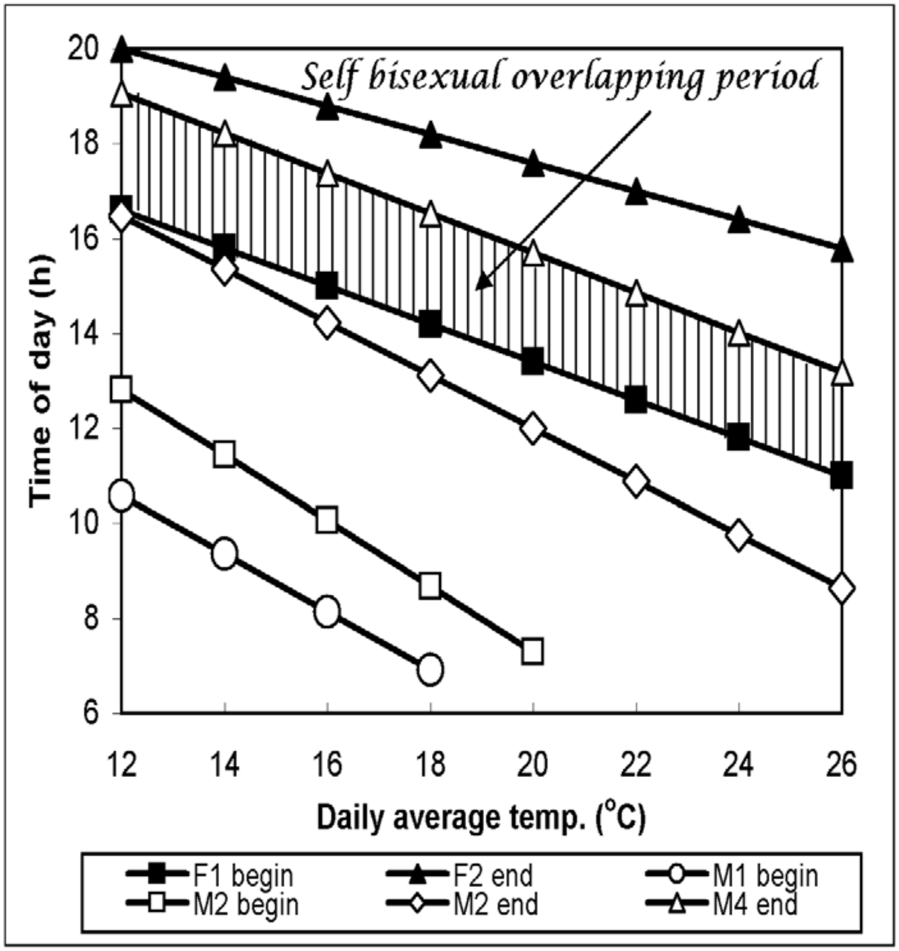

Figure 2: Correlation between daily flowering course and temperature in the Ettinger cultivar

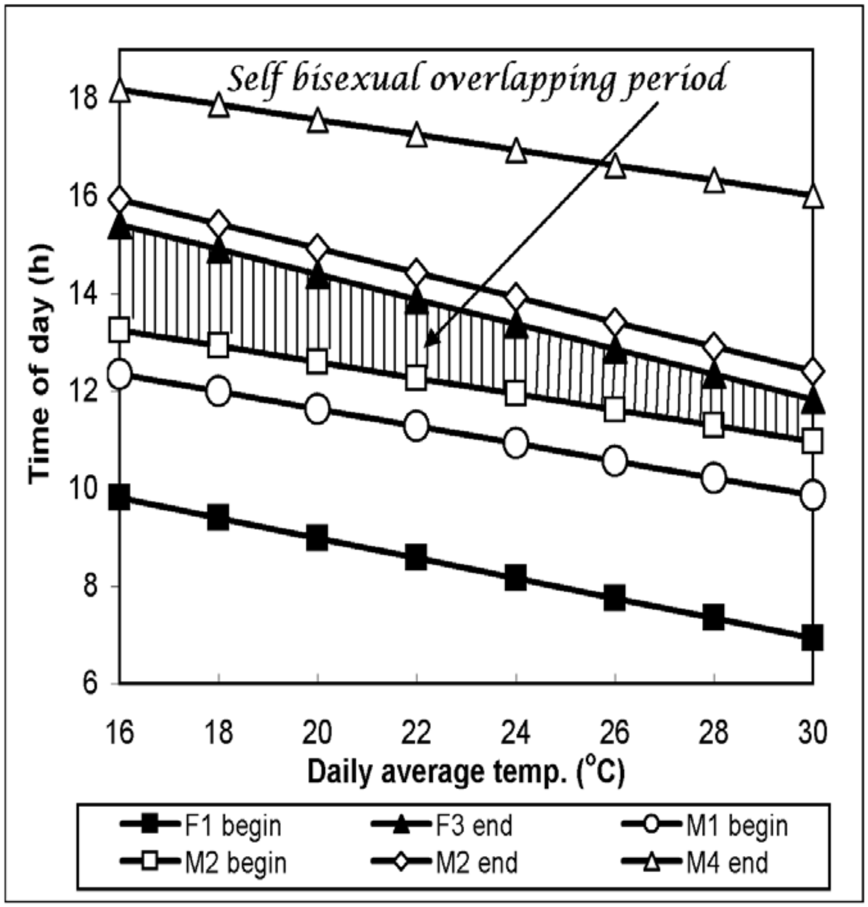

Figure 3: Ccorrelation between daily flowering course and temperature in Reed cultivar

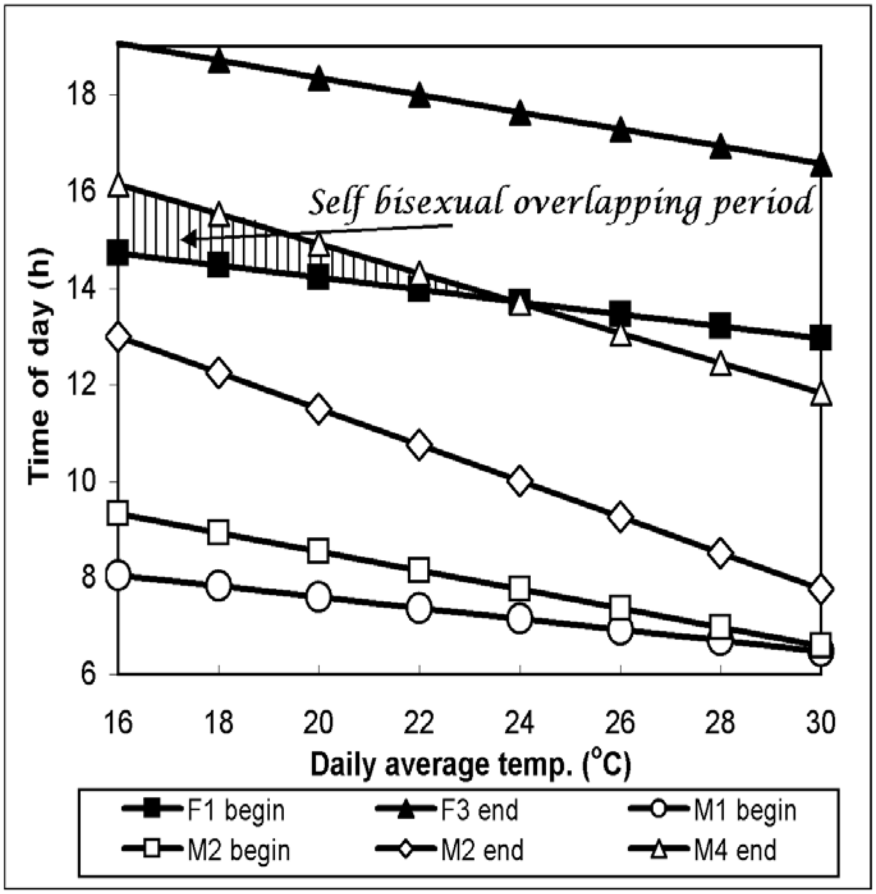

Figure 4: Correlation between daily flowering course and temperature in the Ndabal cultivar

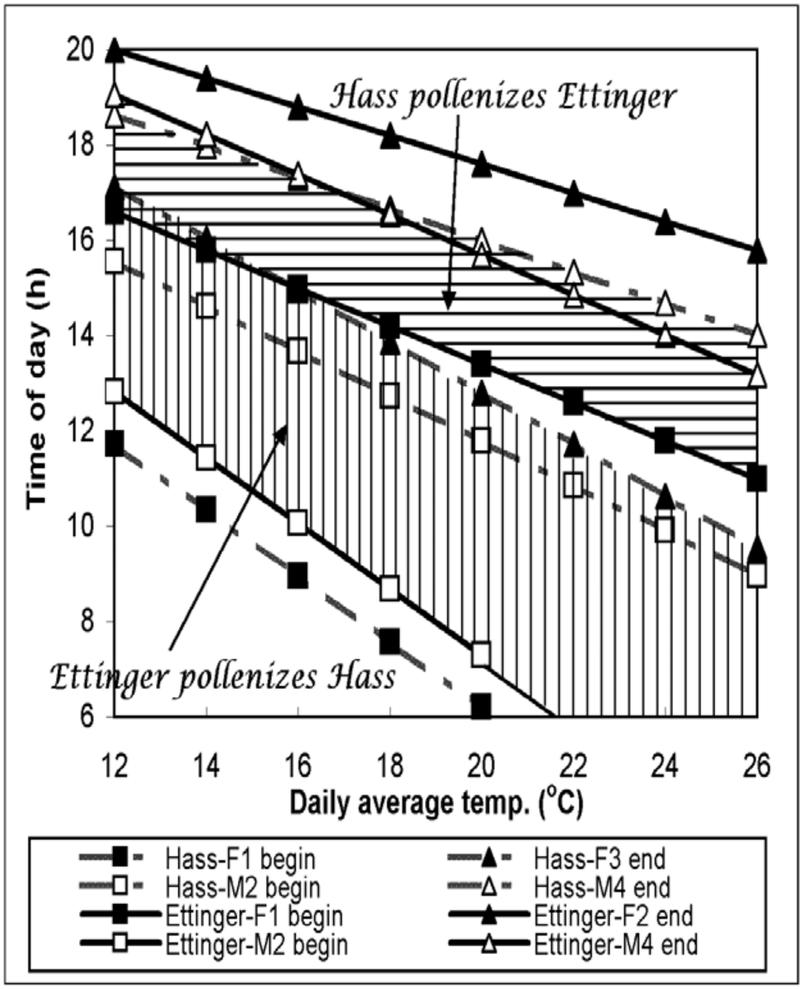

Figure 5: Daily cross bisexual overlapping periods in the early bloomers of the Hass and Ettinger cultivars

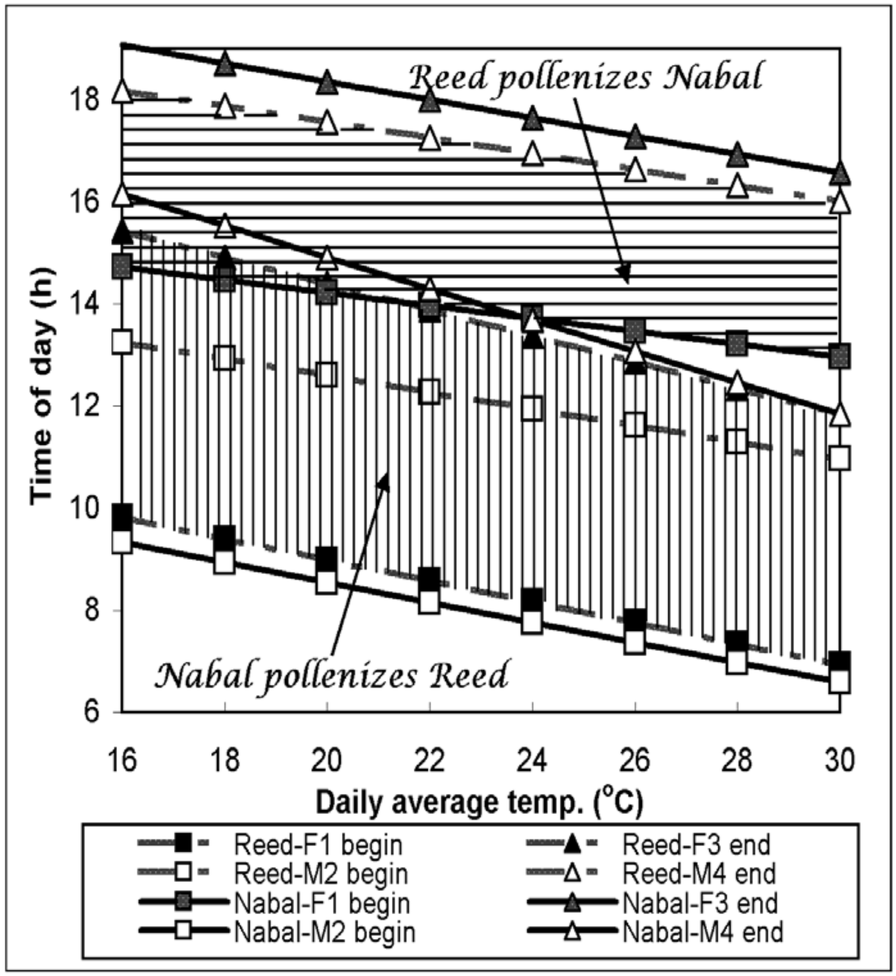

Figure 6: Daily cross bisexual overlapping periods in the late bloomers of the Reed and Nabal cultivars

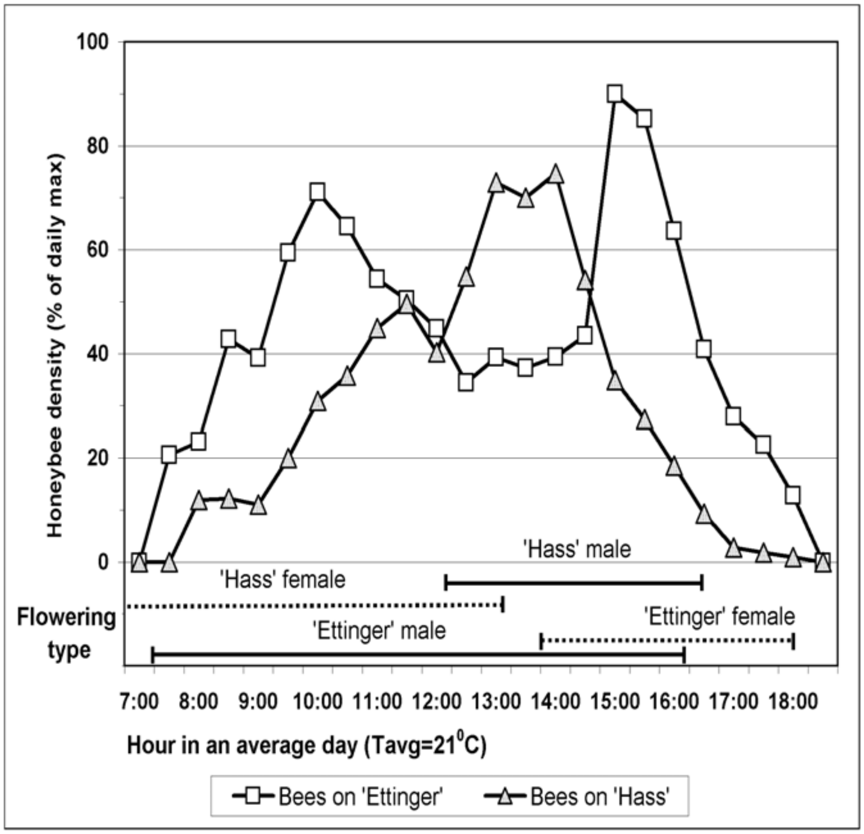

Figure 7: Hass and Ettinger cultivars average daily honebee activity

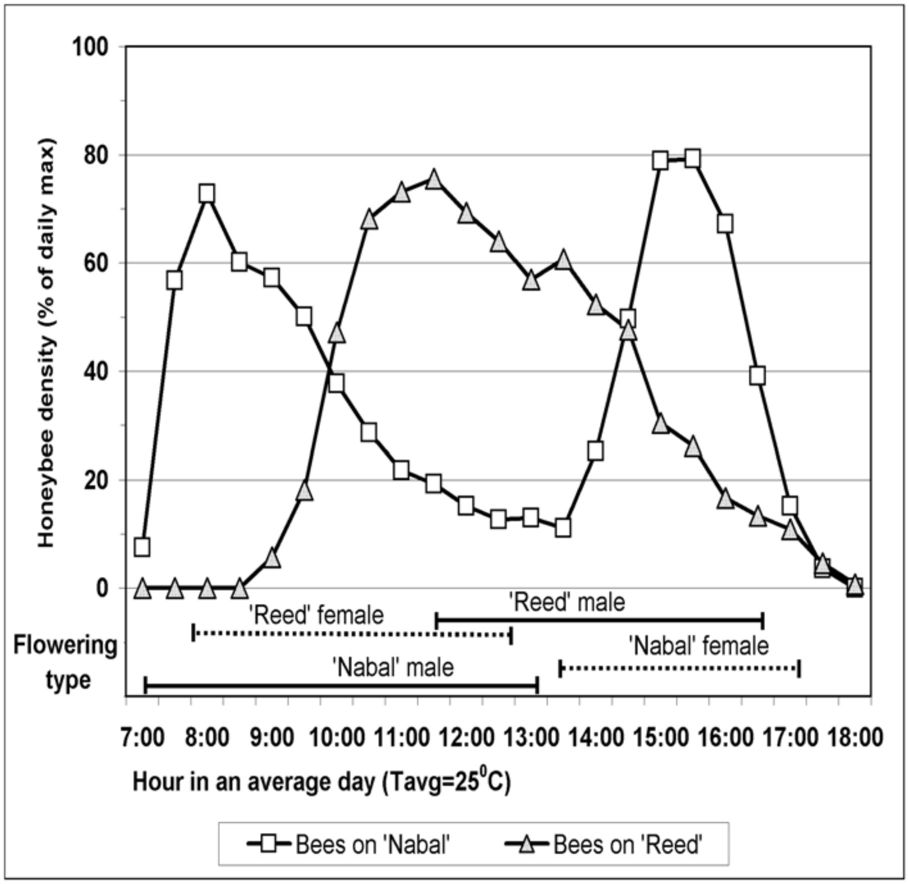

Figure 8: Reed and Nabal cultivars average daily honeybee activity