

POLLINATION ECOLOGY OF MANGO (*Mangifera indica* L.) (ANACARDIACEAE)
IN THE NEOTROPIC REGION¹ /

L. F. JIRON*
I. HEDSTRÖM**

Resumen

Fueron realizadas observaciones sobre la interacción entre *Mangifera indica* L. (Anacardiaceae) y sus insectos visitantes, en la Estación Experimental "Fabio Baudrit", La Garita, Provincia de Alajuela, Costa Rica y otras localidades. Las observaciones se llevaron a cabo entre noviembre 1984 y febrero 1985, encontrándose que los visitantes de la flor del mango son principalmente dípteros ciclórrafos. Los insectos portadores del polen fueron en su mayoría moscas, sirfidas, califóridas y algunas moscas parasitoides de la familia Tachinidae. El polen es transportado por los insectos adherido a las patas, tórax y abdomen, y a la parte ventral de la cabeza. El polen transportado entra en contacto con el estigma cuando el insecto camina sobre la flor. Las flores cubiertas con bolsas no lograron producir fruto, lo que indica que la capacidad de autogamia es muy baja o no existe. *M. indica*, al igual que muchas plantas también introducidas en la región neotropical, no posee ningún insecto visitante perfectamente adaptado. Más bien la presencia de una determinada especie de visitante depende principalmente de la mayor o menor abundancia relativa de éste en la región, o de la disponibilidad de recursos alimentarios para ellos. Algunos de los dípteros encontrados en estrecha relación con la flor de *M. indica* poseen formas acuáticas, subacuáticas o de ambientes muy húmedos. Esto último sugiere que un cuerpo de agua suficientemente cerca de una plantación de mango podría incrementar la formación de frutos en el árbol.

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* Museo de Insectos, Facultad de Agronomía, Universidad de Costa Rica

** Department of Zoology, Section of Entomology, Uppsala University, Box 561, S-751 22 Uppsala, Sweden.

Introduction

The mango, *Mangifera indica* L. (Anacardiaceae) probably originated in the Indo-Burma region and grows wild in the forests of India, especially in hilly areas in the north-east (11). *M. indica* has been taken to many parts of the world and has nowadays a wide distribution throughout the tropical and subtropical regions. The plant was brought to Brazil by the Portuguese in the beginning of the 18th century. In Latin America there are more than 40 varieties of *M. indica*, of which some are of important commercial value for the exporting countries.

The main part of most studies on *M. indica* has been focused on the development of new varieties,

technical aspects of their culture and chemical control of insect pest and disease. Although *M. indica* is an introduced plant in the Neotropics, it is often very successful and gives a relatively high yield of crops. This seems to be one of the reasons why anthecological information on *M. indica* is so fragmentary: that part of the plants life has apparently not been looked at as very urgent to be studied.

The greenish-white and strongly scented inflorescences of *M. indica* develop in large, widely branched terminal panicles with thousands of staminate and hermaphroditic flowers of which the former has five stamens inserted on the outer margin of the disc and mostly one single pistil (Figure 1). Of the five stamens around the outer edge of the disc, usually only one or two are fertile (11); fertile stamens are longer than sterile ones. The pistil has probably been aborted in the staminate (male) flowers: the pink anthers turn purple at anthesis (4). Singh (13) has reported that pollination is essential for fruit setting and that stigma appears to be immediately receptive when the flowers open early in the morning. The same author found that the anthesis generally was complete in the forenoon, with a maximum opening between 9:00 and 10:00 a.m. Dehiscence takes place after the flowers open and the receptivity of the

stigma has been found to continue up to two days after the opening of the flowers, although the best receptivity was noted on the first day (13).

Experiments in bagging flowers have shown that there is no fruit set when panicles are bagged (11, 13). This suggests that cross-pollination is the rule of *M. indica*.

Singh (13) also mentioned that pollination is inadequate in *M. indica* and that 50% or more of the flowers remained unpollinated in nature. He suggested that more adequate pollination may result in a better fruit set. However, a larger quantity of young fruits does not necessarily represent a better crop. Too many fruits growing on a same tree do not reach an adequate size. Anyhow, after fruit setting there is a percentage of loss due to wind stress, too many units on a same bunch and disease.

The primary purpose of the present paper is to show the most important groups of insect visitors on the flowers of *M. indica* in the Neotropics and their efficiency as pollen carriers of the plant. Attention has also been paid to the anthecological *status* of the major flower visitors and some other ecological conditions, which might influence the number of fruit-set by *M. indica*.

Materials and methods

Field observations during daytime were made at the Experimental Field Station "Fabio Baudrit" of the University of Costa Rica, in La Garita, Province of Alajuela, and Finca San Luis, Ciudad Colón, Province of San José, Costa Rica. Flower visitors were observed and collected in La Garita on November 17 and during the flowering peak season of *M. indica* on December 22 and 28, 1984, from 7:00 till 18:00 hours, and on February 8, 1985, from 10:00 till 11:00. Nocturnal field observations were carried out at the campus of the University of Costa Rica (UCR), San Pedro de Montes de Oca, Province of San José, on January 7, 1985, from 19:00 till 19:45 hours, and at the campus of the National University in Heredia (UNA), Province of Heredia, on February 4 from 18:30 till 19:30 hours. Some observations of visiting insects on *M. indica* were also made in the surroundings of the Omar Torrijos International Airport in Panama on February 24, 1985, at 15:00 hours.

Visiting insects on the flower of *M. indica* were identified (at family level) and counted during periods of 30 minutes, at 08:00, 09:00, 12:00, 14:00 and 16:00 hours on December 29, 1984. Special attention was given to the visitors' behaviour in order to evaluate their potential as pollinators.

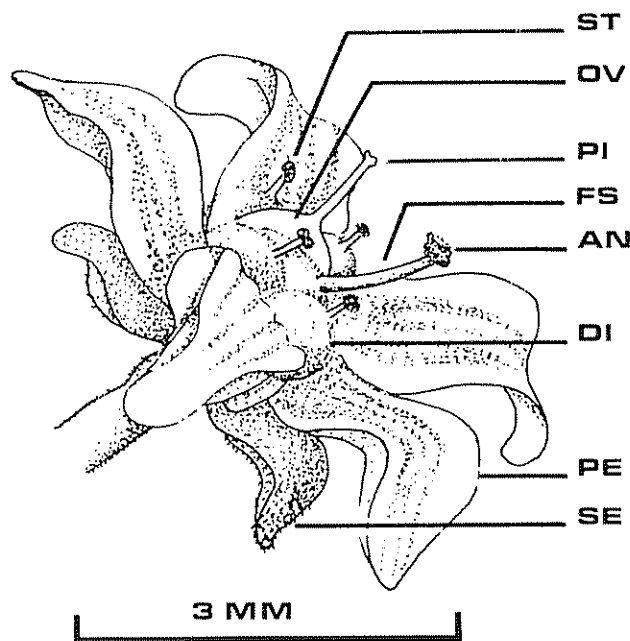


Fig. 1 The floral morphology in hermaphrodite flower of mango, *Mangifera indica* L. in La Garita, Costa Rica. —AN: anther, DI: disc, FS: fertile stamen, OV: ovary, PE: petal, PI: pistil, SE: sepal and ST: sterile stamen.

Experiments on autogamy were carried out in La Garita with panicles of *M. indica* isolated in muslin bags. Fruit set was observed two weeks later. To calculate fruit set of one single panicle, the number of flowers on one panicle was counted, and the result was compared with the number of small fruits on another panicle of relatively the same size.

Results and discussion

Scent

The flower of *M. indica* is rather strongly scented and the sweetish odor is easily detected against the wind by humans at a distance of 2-4 meters from the inflorescences. The scent is clearly of an ecological nature since a great number of insect species seem to be attracted by it, especially cyclorrhaphan Diptera.

Nectar and pollen

Comparatively easily reached nectar is produced by the flowers' sepal glands, which are located on the outer margin of the disc, inbetween the petals and the proper disc (Figure 1). We observed that nectar was utilized both by short-tongued and labellated insects, such as Diptera and Coleoptera. It was also visited by insects with a comparatively long proboscis, such as Lepidoptera species.

Produced pollen was utilized by some of the visiting insects on *M. indica*. New pollen, which was exposed in the morning remained probably on the anthers until the next day. Of the five stamens around the outer edge of the disc of observed hermaphrodite flowers ($n = 100$), the majority (96%) had only one well developed stamen, which produced pollen. Only 4% of all observed hermaphrodite flowers had two fertile stamens.

Flower visitors

Observed diurnal visiting insects on *M. indica* in the study site of La Garita, 474 individuals, were members of four different orders: Diptera, Lepidoptera, Coleoptera and Hymenoptera. Diptera and Lepidoptera predominated with 51.6% and 33.0% respectively (Figure 2). Minor proportions consisted of coleopterans (11.6%) and hymenopterans (3.6%); of Diptera, hover flies (Syrphidae), blow flies (Calliphoridae) and root gnats (Sciaridae), and of Lepidoptera, fritillaries (Nymphalidae) and hair streaks (Lycaenidae). Members of the Syrphidae group (Diptera) were the most frequent of all flower visitors on *M. indica* (20.9%).

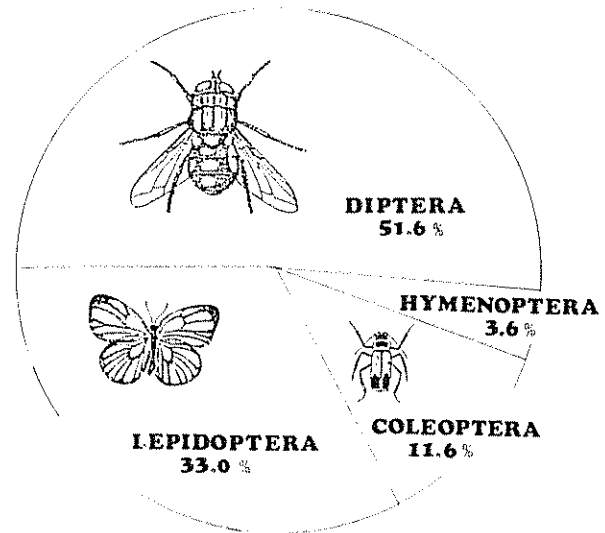


Fig. 2. Frequency in percent of total flower visits made by Diptera, Lepidoptera, Coleoptera and Hymenoptera on *Mangifera indica* L. in La Garita, Costa Rica, on December 29, 1984, from 07:30 until 17:00 hours.

In the inflorescences of *M. indica* we often observed hunting spiders. On one occasion a member of Salticidae was found together with a freshly killed *Chrysomya rufifascies* (Calliphoridae). Colonies of at least one unidentified species of Coccoidea (Homoptera), assisted by ants, inhabited the inflorescences of *M. indica*. We also observed some membracid nymphs (Homoptera) associated with the panicle stem of *M. indica*. Both membracids and coccoids are sap feeders and did not take part in the pollination processes of the mango tree.

Visiting activities started about 07:30 in the morning, with a low number of insects, and lasted throughout the day, with a visiting peak between 08:00 and 15:00 hours (Figure 3).

It was observed in the Central Valley of Costa Rica (Jirón unpubl. data) that the activity of muscoid species increased with sunny weather and at high relative humidity; during cloudy and windy mornings muscoid activity was very low. We observed the same phenomenon for visiting dipterans on *M. indica* in La Garita.

Observed flower visitors on *M. indica* in La Garita could be divided into two main groups: a) Nectar and/or pollen feeders, such as Syrphidae, Calliphoridae, Sciaridae (Diptera), Vespidae, Apidae (Hymenoptera), Nymphalidae, Heliconiidae, Lycaenidae (Lepidoptera) and Scarabaeidae, Cantharidae (Coleoptera), b) Predators of flower visitors, such as Asi-

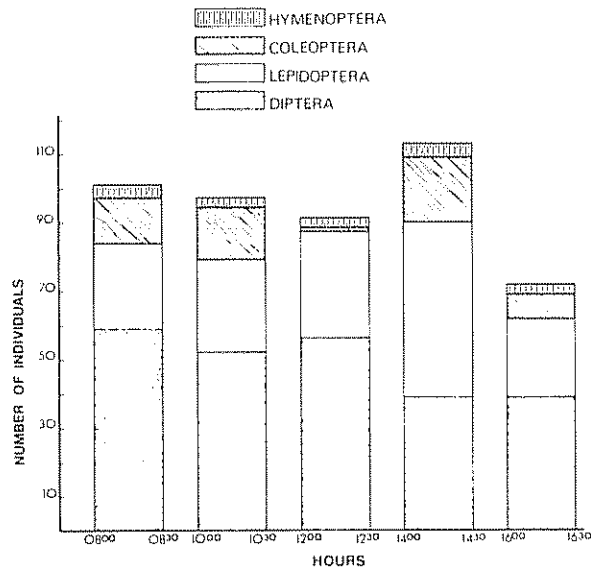


Fig. 3 Frequency of total flower visits made by different insect groups (grouped as Diptera, Lepidoptera, Coleoptera and Hymenoptera) to *Mangifera indica* L. in La Garita, Costa Rica, December 29, 1984, from 08:00 till 16:30 hours. A total of 474 insect visits were observed that day.

lidae, Dolichopodidae (Diptera), Chrysopidae (Neuroptera), Reduviidae (Hemiptera), Salticidae (Araneae) and various families of Odonata.

Observed active nocturnal visitors on the flowers of *M. indica* at the campus of UCR and UNA included both males and females of *Culex* spp. (Diptera: Culicidae) and some unidentified species of Noctuidae (Lepidoptera). We also observed that some diurnal visitors passed overnight motionless on the inflorescences of *M. indica* at the same study sites.

Species of *Rhynchosciara* (Diptera: Sciaridae) were observed spending the night on the flowers of *M. indica*, possibly until the next nectar production period of the flowers, early in the morning (2). Observed resting insects at this time a day also included species of Tipulidae (Diptera), *Strigoderma rutelina* Bates (Scarabaeidae) and *Chauliognathus* sp. (Cantharidae) (Figure 4), coleopterans.

In spite of a fairly strong wind near the international airport of Panama, a number of individuals of *Ornidia* and Calliphoridae were observed visiting the flowers of one solitary adult tree of *M. indica*.

All observed visitors on *M. indica* at all study sites in Costa Rica carried pollen on the body, except species of Lepidoptera, Tipulidae (Diptera) and



Fig. 4 Species of *Chauliognathus* (Cantharidae, Coleoptera) feeding on flower of *M. indica* in La Garita, Costa Rica.

Synocca septentrionalis (Hymenoptera). Individuals of stingless bees, *Trigona* (Apidae) were recorded in a very low number (less than 1%).

The greatest number of pollen was found on species of Syrphidae, Calliphoridae and Tachinidae, all dipterans. We never found attached pollen grains on the second most frequent nectar feeders (Lepidoptera) while some of the less frequent feeders carried comparatively much pollen.

Species of Syrphidae and Calliphoridae seemed to be the most important pollen carriers of *M. indica* in La Garita. According to Proctor and Yeo (10), Syrphidae "is the most important family of flower visitors among Diptera". In addition, some of the dipterans such as Syrphidae, Calliphoridae and Sciaridae have been observed in the Central Valley of Costa Rica exploiting nectar from native species of Compositae common in secondary growth (Jirón, unpubl.).

It is well known that the relationship between plants and flower pollinators usually is mutualistic, and involves a coevolutionary process. As *M. indica* was introduced into the Neotropical region less

than 250 years ago, there has not been sufficient time for such a process to take place. The small open flowers of *M. indica* did not seem to restrict the access to any of the species of the wide range of groups that we found visiting the flowers of the tree. Also the absence of a dominating group of insects among insect visitors suggests a low anthecological specialization of the flower, if any at all. Visiting pollen and/or nectar feeders on *M. indica* are therefore probably "opportunists", which utilize pollen and/or nectar from the plant as an alternative energy resource.

Behaviour of visiting insects

In all, 245 individuals of seven different families of Diptera were observed on the flower of *M. indica* in La Garita (Table 1). The three most abundant individuals of Diptera ($n = 183$) belonged to the following families: Syrphidae (61.2%), Sciaridae (21.3%) and Calliphoridae (17.5%) (Figure 5). The most abundant genera was Syrphidae, represented by *Ornidia*. They stocky individuals of *Ornidia obesa* (Fabr.) arrived flying, in their hovering manner, and alighted either on the flowers or on other parts of the inflorescence and then explored the flowers in search of nectar. When *Ornidia* flies moved about on the



Fig. 5. Species of Calliphoridae exploiting nectar on *M. indica* in La Garita.

Table 1. Two-winged visitors (Diptera) recorded on the flowers of *Mangifera indica* and the presence of depositions of pollen on the insect.

Visitors	Populations			Pollen attached on body
	UCR	La Garita	Villa Colón	
Syrphidae (hover flies)				
<i>Ornidia obesa</i> (Fabricius)	X	X	X	X
<i>Palpada</i> spp.	X	X	X	X
<i>Meromacrus</i> new sp.	—	X	—	X
<i>Syrphidae</i> spp. (unidentified)	—	X	—	X
Tabanidae (horse flies)				
<i>Tabanus</i> L. sp.	—	X	X	X
Sciaridae (root gnats)				
<i>Rhynchosciara</i> spp.	X	X	X	X
Tachinidae (parasitoid flies)				
<i>Tachinidae</i> spp. (unidentified)	—	X	—	X
Calliphoridae (blow flies)				
<i>Phaenicia purpurescens</i>	—	X	—	X
<i>Chrysomya rufifascies</i> (Mag.)	X	X	X	X
<i>Cochliomyia macellaria</i> (Fabr.)	X	X	—	X
<i>Paralucilia wheeleri</i> (Hough)	X	X	—	X
Stratiomyidae (soldier flies)				
<i>Hermetia illucens</i> (L.)	X	X	—	X
Tipulidae				
<i>Tipulidae</i> spp. (unidentified)	X	X	—	—

flowers and while feeding, we observed that pollen grains became attached to the body setae (hairs) on the ventral and lateral side of the visiting insects. Later in the laboratory we observed pollen grains attached to the body of collected individuals of *Omidia*, although this genera carries a less amount of setae than other observed dipterans on *M. indica* in La Garita.

The typical copulatory-like movements of the *Omidia* flies after landing on the flower, suggests that once the flies have come into contact with the fertil stamens of the open flowers, the possibility for pollen to attach to the body of the visiting insect increases by their particular movement.

Cyclorrhaphan flies, which commonly visit decomposed organic material (Jirón, unpubl.) were frequently observed on *M. indica* in La Garita. Four species of Calliphoridae (Figure 5), and at least six species of the genus *Palpada* (Diptera) also arrived flying and alighted on the inflorescence of *M. indica* where they repeatedly rubbed the stigma and stamens of the flowers with body and wings (Figures 4, 5 and 6). The former two genera, along with the hairy *Tachinidae* flies, carried a greater number of setae on its body than did *Omidia* flies. In the laboratory we also observed that individuals of Calliphoridae, *Palpada* spp. and *Tachinidae* had more pollen grains attached to their bodies than did *Omidia*.



Fig. 6 *Tabanus* (horse fly) (Tabanidae, Diptera) feeding on flower of *M. indica* in La Garita, Costa Rica

In addition, during the mango season from March till August (1984) in La Garita, the authors observed a high number of Calliphoridae, as well as other muscoid flies, feeding on the secretions from wounds produced in the mango fruits by birds and wasps (Vespidae).

One hundred and fifty seven individuals of three different families of Lepidoptera were observed on the flowers of *M. indica* in La Garita (Table 2). The butterflies visited the flowers but they did not get pollen grains adhered to their bodies (Figure 7). In the laboratory we were not able to observe any pollen on the body of collected lepidopterans. Butterflies are normally rather unimportant as pollen carriers, except in certain butterfly-adapted plants (6). "Butterflies as a group may have evolved to occupy a parasitic mode of life as adults, feeding on the nectar of flowers without pollinating them" (15).

Observed main families of Coleoptera (Table 3) were Cantharidae (Figure 4) and Scarabaeidae; males and females of the last family, *Strigoderma rutelina*, were commonly seen on *M. indica*. While the female was chewing pollen grains from the flower of the plant the male stayed attached on to the back of the female mating with her. We observed a considerable amount of pollen on the mouthparts of collected males of this species in the laboratory. Although observed males did not carry any pollen grains at all on their bodies.

According to Morton (8) bees seldom work mango blossoms. In all only three individuals of

Table 2. Butterflies (Lepidoptera) visiting the flowers of *Mangifera indica* and the presence of pollen on the body of the insect.

Visitors	Population La Garita	Pollen attached on body
Nymphalidae		
<i>Megalura pelex</i>	x	—
<i>Metamorphia epaphus</i> (Latr.)	x	—
<i>Metamorphia stelenes</i> (L.)	x	—
<i>Marpesia petreus</i> Bates	x	—
Lycanidae		
<i>Thecla damo</i>	x	—
Unidentified spp.	x	—
Heliconidae		
<i>Dryas julia</i> Fab.	x	—
Ithomiidae		
Unidentified sp.	x	—

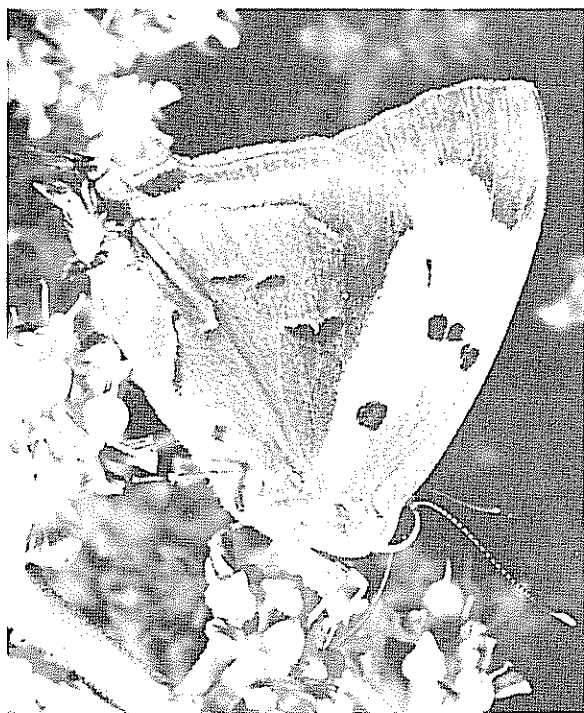


Fig. 7. Lycaenidae butterfly removing nectar from flower of *M. indica* in La Garita, Costa Rica

Table 3. Beetles (Coleoptera) recorded on the flowers of *Mangifera indica* and the presence of depositions of pollen on the insect.

Visitors	Study sites		Pollen attached on body
	UCR	La Garita	
Cantharidae (soldier beetles)			
<i>Chauliognathus</i> Hentz sp	x	x	x
Scarabaeidae			
<i>Strigoderma rutclina</i> Bates	x	x	x

Trigona bees were found visiting *M. indica* in La Garita (Table 4). Few pollen was observed in the laboratory on collected specimens of *Trigona*. In spite of the fact that the plantation of mango in La Garita is located close to a number of bee-hives of *Apis mellifera* L. (Apidae) we did not observe any individuals of *A. mellifera* on the flowers of *M. indica*. (In June-July 1984 at the same study site we observed a high number of *A. mellifera* feeding on fallen, overripened mango fruits). However, in Cacao de Alajuela, Costa Rica, a high number of *A. mellifera* was observed while feeding pollen from the flower of

Table 4. Wasps and bees (Hymenoptera) recorded on the flowers of *Mangifera indica* and the presence of depositions of pollen on the insect.

Visitors	Study sites		Pollen attached on body
	La Garita	Villa Colón	
Apidae			
<i>Trigona</i> sp	x	x	x
<i>Trigona fulviventris</i>	x		x
Vespidae (vulture wasps)			
<i>Synovca septentrionalis</i>	x		

M. indica, which apparently became a primary resource for the bees during a period of food stress (S. Salas pers. comm.).

Fruit set

The vegetative and reproductive phases of *M. indica* are normally distinct events (3); some meristems produce determinate flowering systems at one time of the year while vegetative meristems are active at other times. New leaf growth also occurs in "off years", i.e. when the trees do not yield fruits, between flowering periods (4). Periods of flowering, setting fruits and even leaf growth is very "costly" for the plant: it requires a high carbon/nitrogen ratio (12), which seems to be one of the reasons why few flowers, even if fertilized, make mature fruits; and these may be aborted at all stages (4). The percentage of fruit set in some species is also closely related to the application of fertilizers prior to flowering period. In the Neotropics there is no quantified information on this concerning *M. indica*.

The inflorescences of one single panicle of *M. indica*, of 10-60 cm in length, may have between 1 000-6 000 flowers (12). In the *M. indica* plantation in La Garita we counted the number of flowers and fruit sets, respectively, of two panicles of the estimated same size from one individual of *M. indica*: the former panicle carried only flowers, while the latter had mainly small fruits. We found 5 620 flowers and 474 small fruits, respectively. When we compared the number of flowers and fruits of these two panicles the fruit set was found to be 8.4% at this early stage of the development of the fruits. This apparently low fruit set was later on to be even more reduced by factors such as: a) Strong wind, which normally occurs in the Central Valley of Costa Rica during the maturation period of *M. indica* from November to January; b) Abortion of fruits at all stages due to the lack of minor elements, such as zinc (E. Vargas,

pers. comm.); c) Fruit fly attacks, mainly of the genus *Anastrepha* Schiner (Tephritidae), which according to Baraona-Cockrell (1) is the most important pest in the country (Costa Rica), and occasionally by *Ceratitis capitata* (Wied.) (Diptera: Tephritidae) (5); d) Other minor pests (1).

On the other hand, as described by Skutch (14), "one compensation for a severe dry season is a heavy crop of mangos. Mango flowers do not endure wetting."

According to R. L. Hernández (pers. comm.) the average fruit set of one single adult individual tree of *M. indica*, at the study site in La Garita, usually is between 2 000 to 2 500 ripen mango fruits. Purselove (12) reported that 65-85% of the flowers of *M. indica* normally remained unpollinated and that only 0.10 to 0.25% of the flowers reached the harvesting stages. In addition, bagged flowers did not produce any fruits, which indicated that the flowers of the plant probably do not have the capacity of being autogamous.

Conclusions

Insect pollination involves not only the transport of pollen grains between two conspecific individuals of plants by an insect vector (10). To be able to evaluate such an ecological process various areas of ecology, such as population dynamics of visiting insect species and coevolutionary relationships between the plant and its pollinators, should be understood.

Some of the most common flower visitors on *M. indica*, such as *Ornidia obesa*, *Cochliomyia macellaria*, *Tabanus* sp., *Palpada* spp. and *Hermetia illucens*, all dipterans, are normally associated, in their immature stages, with aquatic, subaquatic or very wet substrates, and in many cases in heavily polluted waters. It suggests that water bodies near plantations of *M. indica* may increase fruit set of the tree. However, a larger quantity of fruits does not necessarily represent a higher fruit yield, as discussed earlier.

In our principal study site in La Garita, anthesis matched well with the circumstances concerning the presence of pollinating insects, i.e. the population fluctuation dynamics in visiting insect species. In studies on Diptera population density, carried out in the Central Valley of Costa Rica, it was observed that some muscoid species fluctuated remarkably in number throughout the year (Jirón & Marin unpubl.). E.g. the *Chrysomya rufifascies* Macq. (Calliphoridae), recently introduced into Costa Rica (7), which was frequently seen on *M. indica* in La Garita, reached dense populations from mid November to the end

of February, with peaks in mid December and end of January. Instead, *Cochliomyia macellaria* Fabr. (Calliphoridae), in the same study, showed low population numbers throughout the year. Few individuals of the last species were also seen on the flowers of *M. indica* in La Garita during our study.

Hence the probability of the presence of any given species, in this case flower visitors on *M. indica*, may depend primarily on the population fluctuation of that particular insect species and not necessarily on the phenology of the visited plant species. Although, like in other introduced plants, we did not find any clear signs of any co-evolutionary adaptation between *M. indica* and its pollinators.

Summary

Interactions between *Mangifera indica* L. (Anacardiaceae) and anthophilous insects were observed at the Experimental Field Station "Fabio Baudrit" in La Garita, Province of Alajuela, Costa Rica, during November 1984 till February 1985. Additional observations were made in Panama and in the provinces of San José and Heredia, Costa Rica. The most common visitors were Diptera. The pollen carriers were mainly hover flies (Syrphidae), blow flies (Calliphoridae) and parasitoid flies (Tachinidae). The pollen was carried on the legs and on the ventral side of head, thorax and abdomen of visiting insects. It came into contact with the stigma of the flower when the pollen vectors walked about on the inflorescences of the tree. Bagged flowers of *M. indica* did not set fruit, which indicated no capacity for being autogamous. *M. indica* is an introduced plant into the neotropical region and it is suggested that the presence of any given flower visitor may depend more on the population fluctuation of the visiting vectors than on the phenology of the plant. Some dipterans, which were found to be associated with the flowers of *M. indica*, are often found in aquatic, subaquatic and other wet habitats. It is suggested that water bodies near plantations may increase fruit set of the tree.

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