

Mixed mating strategies and pollination by insects and wind in coconut palm (*Cocos nucifera* L. (Arecaceae)): importance in production and selection

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- Abstract**
- 1 Coconut is one of the most important tropical crops. It is threatened by Lethal yellowing disease. Production and selection by breeding require pollination, yet little is known of the pollination requirements and breeding system of this palm.
 - 2 This study was carried out from 1999 to 2001 in coconut plantations represented by five coconut ecotypes commonly found in Mexico. It is the first study in the Neotropics on pollination and the breeding system of this palm.
 - 3 Hymenoptera were the most numerous and diverse visitors to coconut flowers. The greatest period of insect abundance occurred during the rainy season (July to October). Insect abundance on the flowers correlated highly and positively with precipitation.
 - 4 The abundance of visitors to pistillate flowers did not vary with season but there were significant differences between palm ecotypes; the most insect-visited flowers were of the Atlantic Tall ecotype.
 - 5 The introduced honeybee (*Apis mellifera*) had the most appropriate foraging behaviour, visiting both pistillate and staminate flowers. These insects were probably the most efficient pollinators as they carry pollen on their ventral surface. Ants were present on flowers day and night but had no effect on pollination.
 - 6 Pollination experiments indicated a mixed mating strategy: self-pollination by geitonogamy produced almost 19% of the fruit set, but cross-pollination (xenogamy) was the most important contribution (c. 30%). Anemophilous cross-pollination only accounted for 10% of fruit set, whereas entomophily became the most important pollination mechanism under Yucatan conditions.
 - 7 As coconut palm grows naturally on the oceanic strand in a wide variety of seasonal conditions of wind and rain, we suggest that they may have evolved pollination, breeding and mating systems that ensure fruit production under a wide variety of conditions, while maximizing the probability of cross-pollination.

Keywords *Apis mellifera*, coconut palm, mating strategy, Mexico, pollination, Yucatan.

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Introduction

Coconut palm (*Cocos nucifera* L. (Arecaceae)) is one of the most important crops throughout the tropics (Ohler, 1999). The geographical origins of this palm are unknown but Harries (1990) suggests the Indopacific region. Domestication probably started in South-east Asia, Malaysia and

Melanesia (Purseglove, 1972). It was introduced into Mexico during Spanish colonial times in the 16th Century (Zizumbo, 1996) by both Pacific and Atlantic routes. Recently, coconut plantations in Mexico have been devastated by Lethal yellowing, a phytoplasma disease vectored by *Myndus crudus* Van Duzze (Homoptera: Cixiidae) (Howard, 1983, 1995). Different levels of resistance to this disease have been found in Mexico (Zizumbo *et al.*, 1999) so there is potential to replant and re-establish coconut palms by creating hybrids with resistance combined with other desirable traits (Zizumbo, 1998). For this reason, and because little is known about the pollination requirements of *C. nucifera*, basic and applied studies in pollination biology are needed to produce hybrid seeds and ensure future crops.

Entomophily (pollination by insects) is thought to be the typical mode of pollination in palms, but pollination by different groups of insects and by the wind has arisen several times within the family Arecaceae (Silberbauer-Gottsberger, 1990). Wind pollination (anemophily) is considered a derived condition and is not common, whereas several kinds of entomophily are frequent. Entomophily in palms falls into three categories: bees (mellitophily), flies (myophily) and beetles (carantherophily) (Henderson, 1986). Coconut palms are monoecious; flowers are produced mostly in large inflorescences comprising a large number of unisexual flowers (thousands, mostly staminate) that offer insect pollinators pollen and nectar (staminate flowers) or nectar only (pistillate flowers) (Silberbauer-Gottsberger, 1990). The inflorescences of *C. nucifera* are protandrous, as in other mellitophilous palms, and pollen is shed and liberated before the pistillate flowers become receptive (Aldaba, 1921; McGregor, 1976; Free, 1993; Ashburner, 1995; Roubik, 1995; León, 2000). However, in most tall ecotypes there is an overlap between staminate and pistillate phases (Sholdt & Mitchell, 1967; Rognon, 1976).

In various parts of the world, principally in tropical Asia, various species of insects have been recorded as flower visitors to *C. nucifera* and most reports, including reviews, have considered, without experimental evidence, bees to be the principle pollinators (Aldaba, 1921; Sholdt, 1966; Sholdt & Mitchell, 1967; Jay, 1974; McGregor, 1976; Free, 1993; Macfarlane, 1995; Heard, 1999). *Apis* spp. and stingless bees (Meliponinae) have been reported in many countries (Burkill, 1919; Aldaba, 1921; Dammerman, 1929; McGregor, 1976; Engel & Dingemans-Bakels, 1980; Hedström, 1986; Pardede *et al.*, 1986; Kevan, 1989; Free, 1993). Other commonly encountered insects of the flowers of *C. nucifera* have been wasps, ants, flies, butterflies, black earwigs and beetles, but these have been discounted as important in pollination (Sholdt & Mitchell, 1967). It is particularly important to realise that the conclusions about insect pollination *per se*, and about the relative importance of various insects in pollination of *C. nucifera*, are based on observations of numbers of floral visitors and on anecdote rather than on experimentation. As far as we are aware, there are no studies that make inter-ecotype comparisons of insect visitation and behaviour on the flowers of *C. nucifera*, although there are likely to be differences in the ratios of staminate to pistillate flowers between

varieties, and differences in the phenologies of inflorescence and flower production (Ohler, 1999a) that could influence pollination.

Two previous experimental studies reached divergent conclusions. On strand-growing palms in the Maldivian Islands, Kevan (1993) concluded that anemophily was as important as insect pollination, but Ashburner *et al.* (2001) concluded that anemophily accounted for only c. 4% of the fruit set in Kerevat, New Britain (Papua New Guinea). The small islands of the Maldivian archipelago are continually windy because of the prevailing monsoon winds that average 15 km/h all year (Chawler, 1986), whereas the coconut plantation at Kerevat in Papua New Guinea is inland in an area that is often almost windless; winds average 2.8 km/h all year (McAlpine *et al.*, 1983). Thus, physical conditions (windiness) may explain, at least in part and perhaps combined with biotic differences between the palms of the two places, the differences in results from the two studies. We may therefore expect differences in the means of pollination and the relative importance of entomophily and anemophily for *C. nucifera* growing in different places and under different conditions.

The objectives of our comparative study on five commercially used ecotypes of coconut palm were: (1) to determine the diversity of the insect fauna that visits the staminate and pistillate flowers of *C. nucifera*; (2) to document their temporal variation diurnally and seasonally; (3) to examine the effects of environmental conditions on insect abundance at the flowers of *C. nucifera*; (4) to determine the pollination systems of *C. nucifera* by testing the relative importance of insect and wind pollination in cross- and self-pollination in plantations; and (5) to determine which flower-visiting insects, including ants, are pollinators and how effective they are.

Materials and methods

Study site

The study was done in experimental plantations that were established in 1991, to represent coconut palm populations in the principal production zones of Mexico. These plantations were near San Crisanto, Sinanche municipality (21°20' N, 89°09' W) on the north coast of Yucatan. The populations represented the ecotypes Atlantic Tall, with mixed characteristics of wild palms (unselected) and domesticated (selected) palms: Pacific Tall 1, Pacific Tall 2, Pacific Tall 3, and Yellow Malayan Dwarf (Zizumbo, 1998).

The vegetation around the plantations was typical of the coastal dunes, is dominated by species of grass (Poaceae), palms (Arecaceae), bromeliads (Bromeliaceae), composites (Asteraceae), legumes (Fabaceae), euphorbs (Euphorbiaceae) and cactus (Cactaceae) (Espejel, 1984). The soil was typically sandy. The climate in this region is warm tropical subhumid (Garcia, 1989) with relatively low rainfall and high atmospheric temperatures (Flores & Espejel, 1994). The total annual precipitation is 579.2 mm and the mean annual air temperature is about 26 °C (Garcia, 1989).

Flower-visiting insects and their seasonal variation

Between January and December 1999, observations and collections of insect visitors to coconut flowers were made 4 days a month on 48 total inflorescences of the five ecotypes within experimental plantations. Randomly chosen plants were observed from 9.00 to 13.00 hours, which includes the period of maximum insect activity at coconut flowers (Free, 1993). Observations and collections from the polleniferous staminate and receptive pistillate phases were alternated every 30 min. Insects were collected with nets, killed and kept individually in plastic vials in 70% ethanol for identification and pollen analyses. Specimens were deposited in the official insect collection (Entomological Collection of the Autonomous University of Yucatan, Mexico). Insects were classified as morphospecies for further quantitative analyses (Mayr & Ashlock, 1991).

Climatological data (temperature and precipitation) were obtained from the nearby National Commission for water in the state management office of Merida, Yucatan. Supplemental weather data were collected every 15 min on all days when insect observations and collections were made and included temperature and relative humidity (Oakton digital thermohygrometer), wind speed (Kestrel 2000 anemometer) and light intensity (by Foot candle/Lux Meter) (all from Forestry Suppliers, Inc., Jackson, MS, Catalogue 2001). Statistical analyses included ANOVA (one- and two-way), multiple comparisons (Bonferroni's method), linear and multiple linear regressions (Systat, 1997).

Flower-visiting insects to polleniferous staminate-phase and to receptive pistillate-phase inflorescences

The relative diversities and abundance of the insect visitors to the flowers of each sex and palm ecotypes was estimated and measured by the assemblage of floral visitors to each sex by the Sorensen coefficient (Krebs, 1999). Analyses with the chi-square test (χ^2) were made to determine whether the insects visit both staminate and pistillate phase of the inflorescences equally. Environmental conditions were simultaneously recorded and used in a two-way ANOVA with multiple comparisons (Bonferroni's method) for different seasons (Systat, 1997). Visitation rates per flower were not assessed because staminate flowers are so numerous (hundreds anthesing each day) that counting them was impractical; however, the pistillate flowers were counted. To assess the potential importance of insect visitors in pollen transfer to receptive pistillate flowers, specimens were examined microscopically for the presence of coconut pollen.

Diurnal and nocturnal activities of flower visitors and the contribution of ants to pollination

Diurnal and nocturnal activities of insects visiting receptive pistillate and polleniferous staminate flowers were made by direct observation and samples collected of insects over 2 days from 06.00 to 00.00 hours (6 and 19 May 1999). Four palms of Pacific Tall 1 were used each day and observations

and collections alternated between sexes of inflorescence each 30 min. To determine if there were differences between parts of the days' observations, three-hourly sets of data were combined and compared.

The effects of ants on coconut pollination were evaluated on 20 palms from August 2000 to March 2001. The palms studied were Pacific Tall 1, all of similar age and development. The treatments were: (1) natural pollination, with unrestricted access to the flowers by ants; or (2) natural pollination but ants were excluded from 60 receptive pistillate-phase inflorescences on 10 palms (six inflorescences/palm) using a Vaseline barrier at the base of each inflorescence. No artificial pollinations were made. Fruit set (fruit/pistillate flowers \times 100%) was assessed for each treatment 3 months later and the findings, after arc-sine transformation (Zar, 1999), tested by Mann-Whitney Rank Sum Test (Systat, 1997).

Wind vs. insect pollination, and allogamy (xenogamy) vs. autogamy (geitonogamy)

The mating system and the relative contributions of wind and insects to coconut pollination were assessed from August 2000 to March 2001. Mating systems are the result of different forms of pollen transfers and the patterns are referred as: autogamy, transfer within the same flower (selfing); allogamy, transfer between flowers; geitonogamy, allogamy on the same plant or between vegetative ramet (genetically identical) of the same parent plant (selfing) and xenogamy, allogamy between flowers of genetically different plants (genets) (out-crossing). One hundred and eight palms of Pacific Tall 1 (six inflorescence/palm) were subjected to the following treatments: (1) control, in which only the receptive pistillate-phase (emasculated inflorescence) were enclosed in canvas bags that prevented the entry of insects or wind-borne pollen; (2) anemophily 1 (xenogamy), in which only the receptive pistillate-phase (emasculated inflorescence) were enclosed in mesh bags (mesh *c.* 1 mm \times 0.5 mm) that prevented the entry of insects but allowed wind-borne pollen; (3) anemophily 2 (xenogamy + geitonogamy), as treatment 2 but with polleniferous staminate-phase flowers of the inflorescence included within the bag; (4) hand pollination (xenogamy), as treatment 1 but hand pollination was made with pollen from other palms; (5) open pollination (xenogamy + geitonogamy) with no treatment; (6) anemophily + entomophily (xenogamy), as treatment 5 but without polleniferous staminate-phase (emasculated inflorescence). After 3 months fruit-set was assessed by comparisons of fruit set using ANOVA followed by multiple comparison procedures (Bonferroni's method) (Systat, 1997), after arc-sine transformation (Zar, 1999).

Results

Flower-visiting insects and seasonal variation

A total of 3544 insects were collected, mostly in three orders, during this study (Table 1) and 83 morphospecies were identified. The most abundant order was the Hymenoptera,

including the western honeybee (*Apis mellifera* L. (Apidae) (africanized), wasps (Vespoidea, including *Polistes* spp. and the Braconidae) and ants (Formicidae). Much less abundant were native bees (Apidae and Halictidae), Hemiptera, Homoptera and Thysanoptera (Table 1).

Environmental conditions during the study clearly showed distinct seasons: dry (March to June), rainy (July to October), and 'nortes' (cooler with showers and winds from the North, November to February) ($F_{d.f.=2,9} = 15.3$, $P < 0.01$ and $F_{d.f.=2,9} = 22.5$, $P < 0.001$), mean monthly temperature and mean monthly rainfall, respectively) (Fig. 1). The total monthly precipitation ranged from 0 to 151 mm. The precipitation (total monthly) has an important effect on insect abundance with a high positive correlation ($r^2 = 0.60$, $P < 0.05$, $n = 12$). In general insect abundance peaked during the rainy period, was intermediate during the dry period, but was lowest during 'nortes' (Fig. 1), although the differences were minor ($F_{d.f.=2,9} = 4.14$, $P < 0.053$) but these differences were particularly marked for *Apis mellifera* over the course of the year ($F_{d.f.=2,9} = 24.7$, $P < 0.001$) (Fig. 1). However, it seems that daily temperature, light intensity and wind speed had little or no effect on insect abundance. Only relative humidity correlated positively with insect abundance on the flowers ($r^2 = 0.144$, $P < 0.05$, $n = 48$).

Flower-visiting insects to polleniferous staminate-phase and to receptive pistillate-phase inflorescences

The diversity of insects visiting the different sexual-phase inflorescences was similar (64%, Sorensen's coefficient), but the abundance of flower visitors, regardless of taxon, was much greater on staminate-phase inflorescences than on the receptive pistillate-phase ($\chi^2_{d.f.=6} = 74.9$, $P < 0.0001$) (Fig. 2). Even so, some taxonomic differences were evident. Wasps, ants and flies were relatively more abundant on pistillate-phase than were honeybees, but native bees were relatively less abundant than honeybees. Thus, relative abundances of flower visitors seemed to depend to a minor extent on the type of flower. *Apis mellifera* was at its lowest abundance from January to April (total monthly abundance), and greatest from May to December, but only when pistillate flowers were visited ($F_{d.f.=11,36} = 2.12$, $P < 0.05$) and not when staminate flowers were visited ($F_{d.f.=11,36} = 1.066$, $P = 0.1$). The abundance of wasps and ants did not change during the year for both pistillate ($F_{d.f.=11,36} = 1.59$, $P > 0.1$) and staminate ($F_{d.f.=11,36} = 1.24$, $P > 0.1$) flowers (Fig. 2). There were no correlations between the abundance of honeybees and wasps and ants ($r^2 = 0.2$, $n = 94$, $P > 0.1$ and $r^2 = 0.08$, $n = 94$, $P > 0.1$, for either staminate or pistillate flowers, respectively).

No effect of local and short-term microclimatic conditions (temperature, RH, wind, and light intensity) on insect visitation (as measured by abundance) was found to either staminate or pistillate phase of the inflorescences. A comparison of the total abundance of visitors to staminate inflorescences of the different ecotypes of palm indicated no inter-ecotype differences ($F_{d.f.=4,43} = 1.88$, $P > 0.1$).

Table 1 Relative abundance of insect visitor classes (order and common name) on *Cocos nucifera* flowers, from January to December 1999. $N = 3544$ individual insects collected on 96 coconut palms (one inflorescence per palm) in experimental plantations found in different ecotypes

Order/Common name	Number of species	Relative abundance (%)
Hymenoptera	44	89.8
Honey bee		59
Ants		8.7
Native bees		1.1
Diptera	20	4.9
Coleoptera	12	4.3
Homoptera	4	< 1
Hemiptera	2	< 1
Thysanoptera	1	< 1

However, when seasonality was considered, differences emerged ($F_{d.f.=2,45} = 5.67$, $P < 0.01$ for abundance) and were pronounced during the rainy period, but smaller during 'nortes' and the dry seasons (Table 2). General abundances of visitors to pistillate flowers did not vary with season ($F_{d.f.=2,45} = 2.11$, $P > 0.1$), but the ecotype of palm made a statistically significant difference ($F_{d.f.=4,43} = 4.50$, $P < 0.01$). The most visited flowers were those of Atlantic Tall, followed by Pacific Talls 1 and 3, with those of Pacific Tall 2 and Yellow Malayan Dwarf being the least visited (Table 3). The number of receptive pistillate flowers was found to vary on an inflorescence (Table 4) and was positively correlated with the abundance of visitors ($r^2 = 0.33$, $n = 48$, $P < 0.001$) (Fig. 3)

The pollen loads on the bodies of the most abundant insect taxa visiting coconut flowers were very different. *Apis mellifera* carried the highest quantity of pollen when they visited the staminate flowers (100s to 1000s of grains each), but moderate amounts (20–100 grains) when they visited pistillate flowers. Wasps carried moderate quantities from staminate flower and very few (1–20 grains) from pistillate flowers. Ants, beetles and flies carried only a few pollen grains from staminate flower and none from pistillate flowers.

Diurnal and nocturnal activities of flower visitors and the contribution of ants to pollination

Coconut inflorescences in either sexual phase are most visited by insects during daylight hours and mostly from 9.00 to 11.00 hours. Honeybees continued visiting the flowers until 18.00 hours, but showed an activity peak similar to that of other insects. The typical nocturnal insects were mostly two species of ant that visited the flowers of either sex from 18.00 to 23.00 hours (Figs 4a, b).

Ants did not have any effect on fruit production. Fruit production per 100 flowers on inflorescences from which ants were excluded was $29 \pm 2.6\%$, and control inflorescences was $33 \pm 3.1\%$ ($n = 60$ inflorescences at six per palm for each treatment) ($t = 3494$, $P > 0.1$).

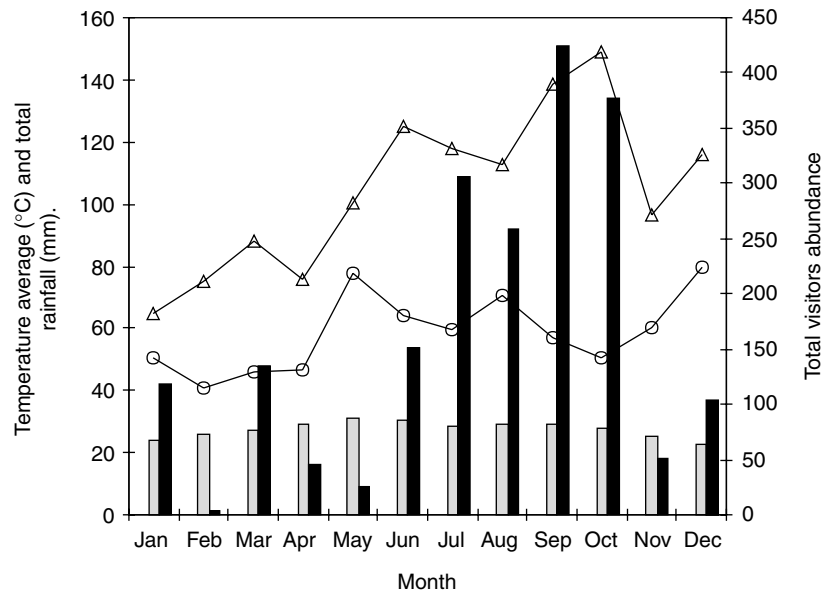


Figure 1 Monthly insect visitor abundance (all insects = Δ , *Apis mellifera* = \circ) in inflorescences of *Cocos nucifera* (five different ecotypes) during 1999. Monthly average temperature and precipitation indicated with light and dark bars, respectively. $N = 96$ individual palm trees (16 h per eight inflorescence per month).

Wind vs. insect pollination, and allogamy (xenogamy) vs. autogamy (geitonogamy)

Pacific Tall 1 ecotype showed significantly different insect and wind pollination effects ($F_{d.f. = 5,632} = 30.06, P < 0.0001$)

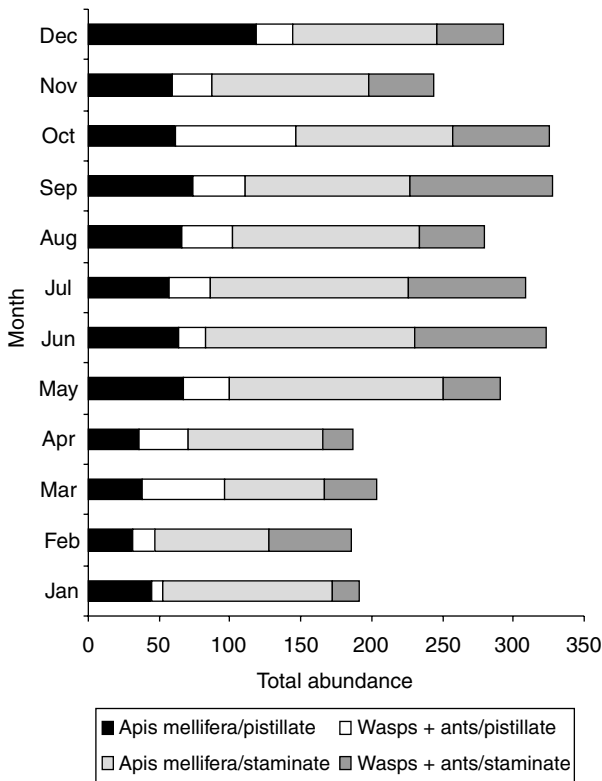


Figure 2 Monthly abundance of honey bees and wasps + ants in pistillate and staminate flowers during 1999 in *Cocos nucifera* experimental plantations. $N = 96$ palm trees. Each point represents 8 h of observation in four individual palm trees (one inflorescence per palm tree).

(Table 5). Wind averaged 5.4 km/h all year in the study area. Almost 10% of the fruit set was produced when flowers were pollinated only by wind (xenogamy). This figure for fruit set almost doubled when wind pollination was accompanied by self-pollination (19%) or manual pollination xenogamy (21%). Nevertheless, the greatest fruit sets (c. 30%) occurred when insect and wind pollination were allowed (xenogamy and geitonogamy) (Table 5).

Discussion

The pollination mechanisms in most palms are largely unknown (Silberbauer-Gottsberger, 1990). *Cocos nucifera* is pollinated by wind and insects (McGregor, 1976). Prior to the present research only two experimental studies had been made (Kevan, 1993; Ashburner *et al.* 2001).

Visitors to the flowers of coconut have been recorded from various countries. *Apis* spp. are known as visitors to coconut flowers in many places (McGregor, 1976; Free, 1993). Kevan & Blades (1989) list 52 species of visitors to coconut flowers in the Maldives, but note that only a few were found on receptive pistillate flowers. The genus *Apis* is absent from the Maldives (P. G. Kevan, pers. comm.). Ashburner *et al.* (2001) suggested that three species of bee,

Table 2 Average seasonal abundance of insect visitors on the staminate phase of inflorescences between January and December 1999, in experimental *Cocos nucifera* plantations. $N = 48$ coconut palms (2 h observations per day in one inflorescence per palm)

Season	Insect abundance (mean \pm se)*	$n =$ number of palms
Rainy	59.8 \pm 5.4 a	16
Dry	45.1 \pm 5.4 ab	16
Nortes	34.0 \pm 5.4 b	16

*Different letters indicate significant differences ($P < 0.05$).

Table 3 Average abundance of insect visitors on the pistillate phase of inflorescences, between January and December 1999 in different ecotypes. $N=48$ *Cocos nucifera* palms (2 h observations per day in one inflorescence per palm)

Ecotype (group of the population coconut palm)	Insect abundance (mean \pm se)*	n = number of palms
Atlantic Tall	41.1 \pm 4.3 a	7
Pacific Tall 1	26.7 \pm 2.8 b	19
Pacific Tall 2	21.0 \pm 3.5 b	13
Pacific Tall 3	21.0 \pm 5.4 b	5
Yellow Malayan Dwarf	18.5 \pm 6.1 c	4

*Different letters indicate significant differences ($P < 0.05$).

Homalictus spp. (Halictidae) are the principle pollinators in Kerevat, Papua New Guinea. In the Neotropics, Hedström (1986) indicates that five species of the stingless bee, *Trigona* spp. are potentially important as pollinators; *Apis mellifera* have lesser roles. He reports that in Ecuador, *A. mellifera* and various wasps (unidentified Vespidae) and Diptera are the most abundant flower visitors and pollinators. The importance of wind in coconut pollination is indicated from the Maldivian study (Kevan, 1993), and from earlier comments that both wind and insects are important (Hunger, 1920; Patel, 1938; Ohse *et al.*, 1961; Scholdt & Mitchell, 1967).

The present results are consistent with those of others in indicating that honeybees, *Apis* spp., are the most abundant flower visitors and probably the most important pollinators in Yucatan (Table 1) and that the flowers contain rewards (nectar or pollen or both) sought by insect pollinators. The centre of origin of *C. nucifera* is probably within the range of the various Asian species of *Apis*, i.e. South-east Asia (Ruttner, 1987) so the importance of this genus as flower visitors is not surprising. The genus *Apis*, and *A. mellifera* in particular, are considered to be generalist foragers in all parts of their ranges, although where congeners occur some separation of resource use is known (Appanah & Kevan, 1995). Similarly, it is suggested that the pan-tropical stingless bees (Meliponinae) had their ancestors in the Gondwana (Michener, 2000) and dispersed with drifting continents and so, as a subfamily of generalist foragers, may have an ancient association with coconut even though the species indigenous to the Americas may not have.

The present results show a marked monthly change in the abundance of visitors to coconut flowers (Figs 1 and 2). *Apis mellifera* abundance varied through on pistillate flowers but

not on staminate flowers. This may be explained, at least in part, by the presence of other flowers that may be more attractive, especially for their nectar. During 'nortes' and the dry season, two necatiferous and polleniferous plants bloom: *Viguiera dentata* (Compositae) in February and *Gymnopodium floribundum* (Polygonaceae) in April. Both are known to be important to honeybees (Flores, 1990) and casual observations near the study site (unpublished data) corroborate that view. Thus, if populations of honeybees and other pollinators are low, other flowers could detract from coconut's being pollinated. Correlations between the abundance of floral visitors and coconut and rainfall (positive) were noticed, but not with wind speed. Wind, especially if strong and gusty, inhibits flight by insects but rainfall may enhance nectar production and humidity reduces evaporation and so may encourage floral visitation.

Pollinators of coconut must visit both polleniferous staminate and receptive pistillate flowers and carry pollen from the former to the latter. This study confirms that *A. mellifera* has that capacity: all the honeybees we examined from both sexes of flowers carried coconut pollen dusted on their bodies so that it could be transferred to the stigmatic surfaces of pistillate flowers (i.e. on their ventral surface and not sequestered in corbiculae). Wasps, beetles and flies are not considered to be important pollinators of the coconut; insects collected from pistillate flowers had fewer pollen grains or none on their bodies. The number of pistillate flowers on an inflorescence, which varies between ecotypes, was positively influenced the abundance of flower visitors, presumably because of the concomitant amount of nectar present, and may be an important factor to take into account in pollination management and selective breeding.

Table 4 Average number of flowers of the pistillate phase of *Cocos nucifera* inflorescences in different ecotypes from January to December 1999. $N=48$ coconut palms (one inflorescence per palm)

Ecotype (group of the population coconut palm)	Number of flower/inflorescence (mean \pm se)	n = number of the palms (one inflorescence/palm)
Atlantic Tall	57.29 \pm 16.1	7
Pacific Tall 1	18.95 \pm 2.1	19
Pacific Tall 2	16.46 \pm 2.1	13
Pacific Tall 3	15.60 \pm 3.7	5
Yellow Malayan Dwarf	9.00 \pm 1.3	4

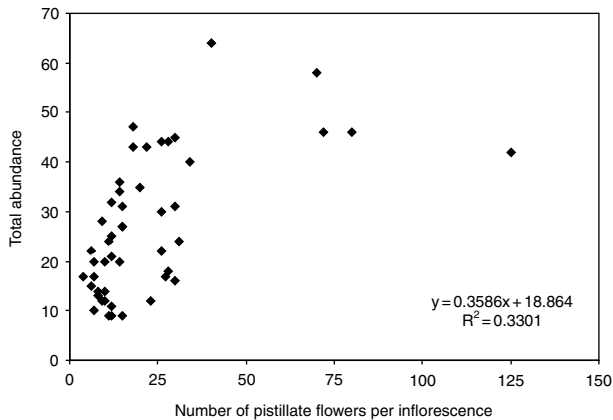


Figure 3 Relationship between insect abundance (2 h per point) and the amount of pistillate flowers per inflorescence of *Cocos nucifera* palm trees. $N = 48$ individual palm trees (one inflorescence per palm).

Over the period of 11 h of daylight, most visitation occurred from morning to early afternoon (Figs 4a, b), as has been noted by other studies (Jay, 1974). The visitation of ants was mostly early at night (Figs 4a, b), but it is unlikely that they carry pollen from staminate to pistillate flowers, even on the same inflorescences, and thus we agree with Huggins (1928) and Scholdt & Mitchell (1967) that ants are not pollinators of coconut. On a few occasions, ants have been noted to invade coconut inflorescences in large numbers during the day and, presumably, then could adversely affect pollination through interference with other flower visitors. Such extreme situations were observed in some palms in this study but their effects were not quantified. On the other hand, ants may be important biocontrol agents of pestiferous insects on coconut palms (Ohler, 1999b).

The relative importance of insect and wind pollination in coconuts seems to be regionally variable, but present results and those of Ashburner *et al.* (2001) and Kevan (1993) agree in that both entomophily and anemophily operate, a condition called ambophily by Stelleman & Meeuse, (1976). In open habitats, where coconuts naturally grow, wind pollination might be effected (cf. Faegri & van der Pijil, 1979; Whitehead, 1983) especially in places with strong to moderate breezes (e.g. many oceanic islands, Maldives) but insect pollination is not precluded except under exceptionally windy conditions (Roubik, 1989). On the other hand, some tropical coastal areas are noteworthy for long periods of calm weather when wind pollination would be impaired (e.g. Papua, Sabah, Kalimantan, Sarawak). In situations where cross-pollination is not assured, i.e. few insect pollinators and little wind, or in places of single seed colonization (founders on small islands, remote beaches, etc.) self-pollination with self-fertility would be an advantage, in accordance with Baker's Law (Stebbins, 1957). Results presented in Table 5 support the importance of allogamy with the capacity for geitonogamy even though incomplete protandry is always evident except in the highly derived (through artificial selection) Malaysian Dwarf cultivars,

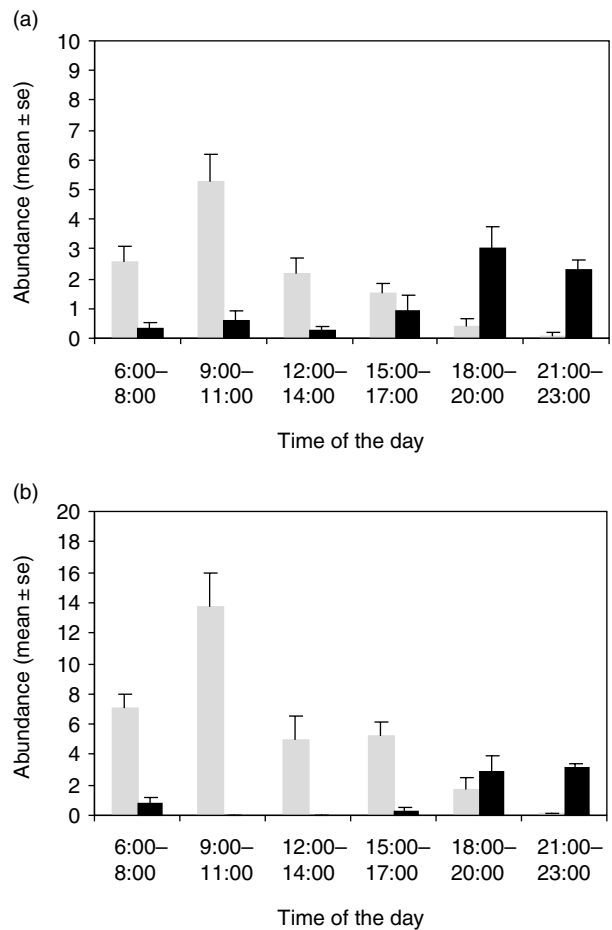


Figure 4 Abundance (mean \pm se) of insect visitors with typically diurnal (dark bar) and nocturnal (white bar) activity in the pistillate (a) and staminate (b) parts of *Cocos nucifera* inflorescences. In experimental plantation of Yucatan (6 and 19 May 1999). $N = 8$ palm trees (1.5 h per observation period).

which tend to be autogamous. Other studies (Sholdt & Mitchell, 1967; Ashburner, 1995) support these ideas. Thus, one can argue for ambophily and facultative geitonogamy as being important to a plant with powerful means of long-distance diffused dispersal in a wide geographical area with highly variable and seasonal wind conditions.

The capacity of coconut palms to take advantage of a wide variety of non-specific pollen vectors (wind and social bees) allows pollination under many environmental conditions. In plantations, extensive and even-aged stands of palms with a uniform canopy in thickness and height above the ground, wind speed would be reduced and pollen movement impeded (Di Giovanni & Kevan, 1991). Under such conditions, insect pollination would make an important contribution to crop production. In some places, native pollinators are recognized as the most important pollinators, e.g. in Central and South America (Hedström, 1986) and in New Guinea (Ashburner *et al.*, 2001). In other places, the introduced western honeybee (*A. mellifera*) is a well-known visitor for the flowers of coconut, e.g. Hawaii

Table 5 The contributions of wind and insects, average fruit set of *Cocos nucifera* inflorescences (fruit-set per flowers as percentages \pm se) with different pollination treatments by self-pollination (geitonogamy) and outcrossing (xenogamy), at the experimental plantations. $n = 108$ inflorescences per treatment (six inflorescences of 18 palm trees per treatment). (+) = yes (-) = no

Treatment	Mating strategy				Fruit set (%) (mean \pm se)
	Emasculation	Pollination vector	Self pollination	Outcrossing	
Control	+	-	-	-	0 a
Anemophily 1	+	Wind	-	+	9.50 \pm 1.46 b
Anemophily 2	-	Wind	+	+	18.59 \pm 1.92 c
Hand pollination	+	Hand	-	+	21.11 \pm 1.82 c
Open pollination	-	Insect + wind	+	+	29.14 \pm 2.32 d
Anemophily + entomophily	+	Insect + wind	-	+	28.41 \pm 2.25 d

*Different letters indicate significant differences ($P < 0.05$).

(Sholdt & Mitchell, 1967), Jamaica (Jay, 1974), Ecuador (Hedström, 1986) and Yucatan (this study). In Yucatan, the fauna of native bees is diverse (H. Delfin, pers. comm.) and important for crop pollination (Meléndez *et al.*, 2002). The fauna includes *Trigona fulviventris*, also noted as a potential pollinator of coconut in Costa Rica (Hedström, 1986). However, in Yucatan, stingless bees (Meliponinae) are found in their greatest abundances in the caducifolious forest rather than in the area of coastal dunes where nesting sites may be few. It may be that coconut monoculture does not provide the required diversity of floral resources for these bees. Nevertheless, there seem to be enough *A. mellifera* and other insect pollinators in the experimental plantations to effect 30% fruit-set. In this way, it is very important to conserve bee pollinators on the sites where coconut is cultivated. It is likely that this level of fruit set could be increased through management of honey bees or stingless bees, but there are other factors which may be involved (e.g. resources availability) and the natural level of floral abortion (Shouldt & Mitchell, 1967; Ohler, 1999a).

From the experimental research on coconut pollination (Kevan, 1993; Ashburner *et al.*, 2001, the present study), it seems that coconuts are ambophilous and sometimes geitonogamous, but there are great inter-regional and inter-ecotype differences in the relative importance of insects and wind in bringing about pollination, and in facultative and obligate out-crossing. These considerations need to be kept in mind by plant breeders who are developing new cultivars of coconut for various desirable traits, including disease resistance.

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