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Pollinating insects and the pollination of oil palms in Central America

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INTRODUCTION

The oil palm *Elaeis guineensis* is a monoic plant, which means it bears both male and female inflorescences, separated from one another on the same vegetative axis. This particular situation requires crossed pollination, as both inflorescences of the same plant are seldom simultaneously receptive. For some years, the idea of oil palm pollination by the sole action of winds prevailed (Turner & Gillbanks, 1974). Nevertheless, it was also known that rainfall levels as low as 2.5 mm/day, could considerably reduce the density of pollen in the air, to a figure below the acceptable minimum required to achieve an adequate pollination (Hardon, 1973; Turner & Gillbanks, 1974; Syed, 1978).During the 1978-1979 period, Syed (1978, 1979) conducted a series of observations in Cameroon and Malaysia, that ascertained the key role of insects in oil palm pollination.

The species *E. guineensis* is a native of West Africa, and there are many insects which are associated with the two types of inflorescences of this palm. At the time of the introduction of this plant to America and Asia, most of these insects were left behind, a situation which in turn led to serious pollination problems, due to the fact that any insect in the new environment was capable of effectively exploiting the new niche as an effective pollinator (Syed, 1978, 1979; Tan & Wahid, 1984). In Dominican Republic, for example, *E. guineensis* was introduced as a new crop, and before the introduction of *Elaeidobious subvittatus*, the fruit set value was as low as 20%.

Evers (1977), of United Fruit Co. in Central America, performed a series of valuable observations on insects associated with oil palm pollination in Costa Rica and Honduras. Among these reports, the possible pollination activity of a Nitidulidae *Mistrops costaricensis* was clearly pinpointed. The insect was found in large quantities around the male inflorescences of *Elaeis guineensis*, *Elaeis oleifera* and the interespecific hybrid (27.000-38.000 insects/inflorescence). The number of individuals around the female inflorescences was less than one percent of the number found around inflorescences of the opposite sex. Some 28-41% of the insects carried pollen mainly among their abdominal hairs and under their wings. The viability of this pollen reached almost a 70% in some of the samples. The activity of the insect was basically crepuscular, as 92% of the visits to *E. guineensis* palms occurred between 4-6 pm., in spite of the presence of rains.

Evers also evaluated the transference of pollen, by wind, from the male inflorescences to the female, by arranging microscope slides smeared with vaseline at varying distances from the male

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inflorescence. In 8 year old palms, the concentration of pollen was very high, even at a distance of 13 meters from the emitting source, and, more important yet, a larger concentration of pollen was found in slides located at only 5 cm from the female inflorescence, where the activity of *M. costaricensis* was being observed.

How the Curculionidae *E. subvittatus* came to America, is not yet known; it was supposedly introduced by way of pollen samples obtained someplace in West Africa (Luchini & Morin, 1984; Genty et al. 1986). *E. subvittatus* was found by Evers in Honduras in 1978.

The most important pollinators in West Africa belong to the Curculionidae family. In Cameroon, there are six species of the genus *Elaeidobious*, that visit both male and female inflorescences; *Elaeidobious kamerunicus* is the predominant species and it represents, in general, 75% of the individuals present. *E. subvittatus* represents approximately a 6% of the population (Syed, 1984a). Visits made by *Elaeidobious* spp. and other pollinators to the female inflorescences are probably by error, as the insects are attracted by an aroma similar to that expelled by the male inflorescences.

In West Africa, pollination has always been acceptable, not so in Southeast Asia, where *E. guineensis* was introduced and it was necessary to recur to assisted pollination (Hardon, 1973). In 1981, *E. kamerunicus* was introduced to this region of the world and was later brought to America: Colombia and Ecuador (1984-1986), Costa Rica (March, 1986) and Honduras (1986). Brazil introduced four species of *Elaeidobious* (Corrado, 1985). In general terms, the impact of the introduction of the species *E. kamerunicus* in Southeast Asia has been highly favorable (Corrado, 1985; Donough & Law, 1987; Wahid et al., 1987).

Observations prior to the introduction of *E. kamerunicus* in America indicated that, in some plantations, there existed the possibility of improving fruit set by means of bringing another pollinating insect (Corrado, 1985; Syed, 1985, 1986b). Observations carried out by Syed in Costa Rica and Honduras (Syed, 1985) brought him to recommend the importation of *E. kamerunicus* by these countries, in order to complement the labor carried out by *M. costaricensis* and *E. subvittatus*. In Colombia and Central America, it was determined that, in various plantations, fruit set was very similar, some months of the year, to that observed in Malaysia during the period prior to the introduction of *E. kamerunicus.*

In spite of low fruit set values present sometimes during the year, assisted pollination was never really considered necessary in Central America. It is also interesting to note that, even in Cameroon, where there are several species of pollinators, including *E. kamerunicus* and *E. subvittatus*, pollination values as low as 40% have been registered during some periods.

The introduction of *E. kamerunicus* in America would mean the confrontation of this species with *E. subvittatus* and *M. costaricensis*. The rencounter with the first of these species did not offer greater apparent risks, as both species coexisted with another four more of the genus *Elaeidobious* in Africa. On the other hand, nothing of the new interaction between *E. kamerunicus* and *M. costaricensis* under natural conditions was known.

Prior to the introduction of *E. kamerunicus* in Malaysia and America, detailed studies of the risk implied by the arrival of this insect at its new environmental niche were carried out. Based on these studies, it was concluded that this species maintains a very high specific relationship with *E. guineensis* and did not imply a risk to other crops.

The following observations refer in part to the situation of the pollinators in Costa Rica and Honduras prior to the introduction of *E. kamerunicus* in 1986, and the posterior effect this insect has had on fruit set, and over the other two pollinators already present*: E. subvittatus* and *M. costaricensis*. An evaluation of the methodology used for evaluating these changes is also presented.

MATERIALS AND METHODS

Relationship between the number of insects per spikelet in samples of 9 and 18 spikelets and the total inventory of the inflorescence

The chosen procedure consisted of a variation of the one suggested by Chiu et al., 1986 and Syed & Saleh, 1987. Samples of 9 and 18 spikelets were obtained from inflorescences between the 5th and 6th state of anthesis. The spikelets were collected in individual plastic bags during the first hours of the morning, and were then transferred to paper bags to dry at 35ºC overnight. The pollen was separated by screening, and the mixture of insects and floral parts was separated using 70 alcohol. The insects were again dried (35ºC x 4 hours) and separated into species using wire sieves.

After carefully collecting the selected spikelets, the rest of the inflorescence was bagged and cut off from the palm. After killing the insects with an insecticide, the species were separated. As counting all the insects proved to be difficult, a sample was taken from each inflorescence, (generally 1 gram for *E. kamerunicus* and 0.1 gram for *M. costaricensis*) (insects dried 18 hours at 35ºC). These observations were performed on inflorescences collected from adult palms (10 years and older) and from a 5 year old lot.

Seasonal variation of pollinating insect populations and fruit set

The observations here summarized were carried out on the Palma Tica oil palm plantations in Costa Rica (Coto and Quepos) and Tela Railroad Co. in Honduras (San Alejo, Atlántida)

The methodology suggested originally in 1985 for estimating pollinator populations in Central America (Syed, 1985) has been questioned (Chiu et al., 1986; Syed & Saleh, 1987). In spite of this, the procedures have been maintained to allow a continuity of the observations and to be able to compare them. A similar situation has also occurred concerning fruit set.

Following the recommendations by Syed (1985, 1986b), fruit set was estimated by drawing a stripe or band approximately 5 cm in width along the bunch periphery, including both the external region and the area that makes contact with the trunk. The marked spikelets on each bunch were separated and the normal fruits (pollinated flowers), the parthenocarpic ones, and the flowers that did not bear any fruit were then counted. Fruit set was estimated as the ratio of the total normal fruits, divided by the total number of fruits in the bunch, expressed as a percentage. A total of 15 bunches were examined per lot of approximately 70 ha., in strategic places that represented crops of different ages in the plantation.

The precision of this methodology was evaluated only once in each location by counting, in a sample of bunches, the total number of normal fruits and the non-pollinated flowers, and comparing the results with those obtained from the analysis of a band of the same bunch.

The number of insects per spikelet was estimated by counting the total insects in nine spikelets, three of each one of the parts (base, center and apex) of 10 male inflorescences in anthesis, from each one of the harvesting lots in which fruit set was determined. The spikelet samples were dried in an oven, in paper bags, for approximately 18 hours at 35ºC, and the insects present for each one of the species were then counted. If the number of insects was too high, the total was estimated from a sample. In Coto and Quepos, 5 and 12 harvesting lots were sampled, respectively. In Honduras five lots were originally chosen, but two of these had to be replanted: thus, one more was included in April 1986. During the first months, observations were carried out monthly, but it was then necessary to space them out to once every two months.

Number of pollinating insects per area and per male inflorescence

Three male inflorescences in each one of the seven anthesis stages (Chiu, et al, 1986) were bagged and cut off early in the morning. Prior to their bagging, three spikelets from each one of the parts (base, center and apex) and from the internal and external areas of the inflorescence (in relation to the trunk), were taken to make a total of 18 spikelets per inflorescence.

The number of insects in the sample of spikelets was individually counted and the total of insects per inflorescence was estimated by weight. The estimate of the total insects per area was obtained counting all the male inflorescences in each stage of anthesis in two areas of Tenera (Deli x AVROS) palms, 4 and 11 years old. A first sample was obtained during the month of March (dry period) and the procedure was repeated during the month of July, early in the rainy season, and in the month of October, when the maximum rainfall levels are reached in Coto.

The estimate of the number of insects per area in March and July was made using the average value estimated per spikelet (for inflorescences in each one of the stages of anthesis), the number of male inflorescences in each stage of anthesis per unit of area, the average number of spikelets per male inflorescence in each stage of anthesis, and the average number of spikelets per inflorescence in each age group of palms, as a base. During the month of October, the insect population drastically declined, which made it possible to count the total number of insects in each inflorescence.

Comparison between populations of pollinating insects in four types of germplasm

Male inflorescences from *E. guineensis* (DxP), *E. oleifera*, an OxG hybrid, and a compact material (OxG backcrossed to *E. guineensis*, all of which were planted in Coto, were collected. The gathering of the samples (18 spikelets per inflorescence) and their processing was affected following the same procedures described previously.

Pattern of pollinator visits to female inflorescences in anthesis

Six female inflorescences in DxP palms were located and marked before entering anthesis. During the anthesis period, these inflorescences were visited every 15 minutes to count the insects trapped in a glued transparent plastic tape (3 x 30 cm). The observations were repeated in Coto and Quepos for six year old palms.

Amount and viability of the pollen transported by the pollinating insects

Female inflorescences in anthesis were visited during the peak hours of activity for each one of the pollinators. The *M. costaricensis* adults that were flying over the inflorescences were captured with the aid of an entomological net (11 cm in diameter). The insects (a mixture of both sexes) were placed in groups of 10 individuals each, in a small vial with 0.5 ml of water, to which Tween 20 had been added. For the capture of *E. kamerunicus* adults, the inflorescence was covered with a white cloth. The individuals that arrived were trapped and placed in groups of 10 insects in vials with 0.5 ml of water.

The pollen grain count was performed adding some drops of a saffranine solution to the samples, and then observing each insect individually under a stereoscopic microscope. In order to count all the pollen grains carried, the wings were carefully separated from the body with the aid of fine point forceps or tweezers. The rest of the pollen loosened in the water was counted separately and added in proportional form to the total adhered to each insect. To estimate the viability of the transported pollen, some insects that were flying over the female inflorescences in anthesis were collected. Samples of the pollen obtained from the insects were placed directly in agar solution with sucrose 11%, or else in water with sucrose 0.5 and 10%. All the pollen samples from the insects were placed to germinate in agar with sucrose 11% at 35ºC for at least one and a half hours. Each pollen sample was run with a control sample (obtained from an inflorescence) and from which the germination was determined before and after the viability test for the pollen carried by insects.

RESULTS AND DISCUSSION

Relationship between the estimated number of insects per spikelet in samples of 9 to 18 spikelets, and the total inventory from the male inflorescence

In both 5 and 17 year old palms, the number of *M. costaricensis* per spikelet, estimated from a sample of 9 spikelets, was similar to the results obtained after the total analysis of the inflorescence. For *E. kamerunicus*, in the sample of 9 spikelets the actual pollinator population per spikelet was consistently underestimated. In 5 year old palms, the actual average number of *E. kamerunicus* per spikelet, in an inventory of the complete inflorescence, was 2.08 times greater than the number estimated in the 9 spikelet sample. In the adult palm, almost four times more insects were obtained per spikelet from the analysis of the whole inflorescence. These differences are due in part to the migration of insects from the spikelets towards the stalk of the inflorescences, when they were disturbed during the gathering. All of these insects were "harvested" the moment the whole inflorescence was cutoff. In the case of *M. costaricensis*, they seem to displace themselves less when disturbed; thus, the relatively accurate estimate of the actual average population per spikelet in the 9 spikelet sample. Due to the typical crepuscular habits of this insect in particular, it does not tend to abandon the inflorescence, as is the case of *E. kamerunicus*, when the spikelets were collected before 8 am.

According to Syed and Saleh (1987), the distribution of the adult insects in the inflorescences tends to be irregular; thus, the sample of 9 spikelets may be inappropriate for *E. kamerunicus* population estimation purposes. According to these authors, in order to skip this difficulty, all the insects present in all of the spikelets of a sample of inflorescences must be counted, and also the number of male inflorescences in anthesis per unit of area. The analysis of

15 inflorescences, three per stage of anthesis, is considered appropriate (Syed & Saleh, 1987). To complement the data, the number of male inflorescences in 500 palms should also be counted, in order to estimate the number per unit of area.

The hour of the day in which the samples are collected has also been designated as an important factor that exerts great influence over pollinator population estimates. This influence is no doubt stronger for *E. subvittatus* and *E. kamerunicus* than *for M. costaricensis,* as the greater part of the activity of the *Elaeidobious* species takes place during the hours of more sunshine.

A sample of 18 spikelets per inflorescence also underestimated the average number *of E. kamerunicus* per spikelet, but in a lesser degree. The value in the number of insects per spikelet obtained from the analysis of the whole inflorescence was 1.53 and 2.19 times higher, than the one estimated parting from the sample of 18 spikelets in 4 and 11 year old palms, respectively.

For *M. costaricensis*, this relation was similar in 4 year old palms, but in 11 year-old, the values of insects per spikelet obtained from the sample of 18 spikelets and from the whole inflorescence were very similar. It is therefore concluded that, as the number of spikelets sampled is augmented from 9 to 18 per inflorescence, no considerable increase in precision is obtained, where the estimates of average numbers of *M. costaricensis* per spikelet are concerned. In the case of *E. kamerunicus*, the difference between the "true" value and the "estimated" value is reduced in the 18 spikelet sample.

In any case, when populations are being compared, whether or not the extra effort needed to perform the gathering of the 18 spikelets (as much from the internal part as from the external part of the inflorescence) is justified, is indeed a questionable matter.

As a general rule, the spikelets collected from the external part of the inflorescence (opposite the trunk) contained more individuals of *E. kamerunicus* than the internal spikelets. This tendency was not clear in *M. costaricensis*.

Seasonal variation of pollinator insect populations and fruit set

The pollinator *E. kamerunicus* was introduced in Costa Rica in February 1986 and released in Coto and Quepos in May that same year. In Honduras, the liberation was performed in the San Alejo plantation in July 1986. Until mid-1987, a very defined relationship could be observed between the average *E. subvittatus* population and the average level of fruit set in both Costa Rica and Honduras. The largest populations of this insect were present in San Alejo, Honduras (Fig. 1) and the highest values of fruit set were obtained from this area also.

Coto had the lowest average fruit set values throughout the year, and also the lowest population of *E. subvittatus*. Quepos, with intermediate populations of the pollinator, had intermediate fruit set values, between the Coto and San Alejo estimates.

The other pollinator, *M. costaricensis* had a maximum population in Coto and minimum in San Alejo (Fig. 2). Based on this information, it could be concluded that the activities of this insect were not especially contributing to keep up the level of pollination in Central America. The humble role of this insect as a pollinator was also noted by Syed, 1984b and Genty et al., 1986. According to the latter authors, *E. subvittatus* is a more efficient pollinator than *M. costaricensis* due to a greater capacity for the transportation of pollen, and to the fact that *E. subvittatus* remains active more hours per day than *M. costaricensis.*

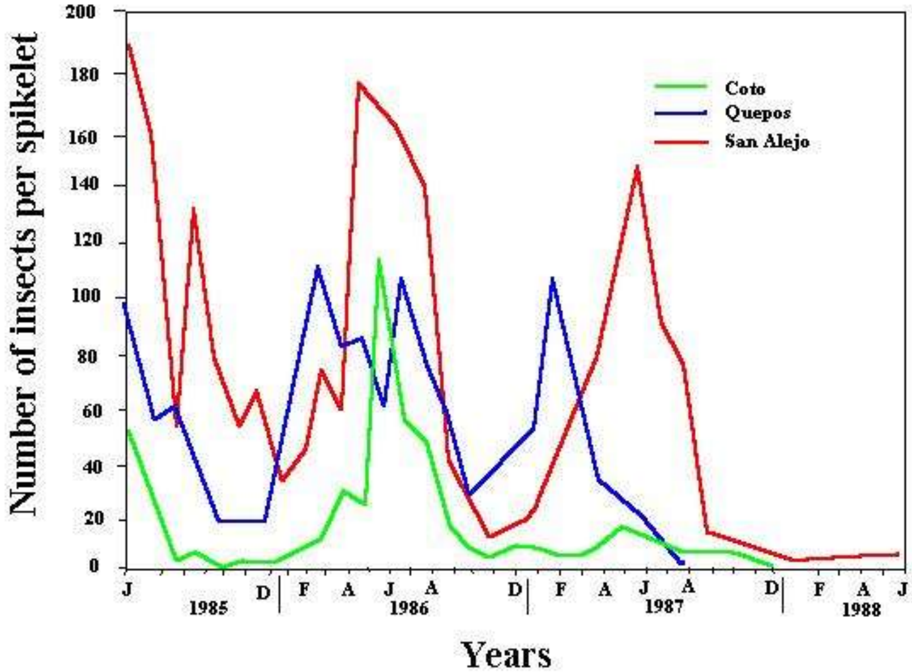

Fig 1. Seasonal variation of the *E. subvitatus* population in three different location

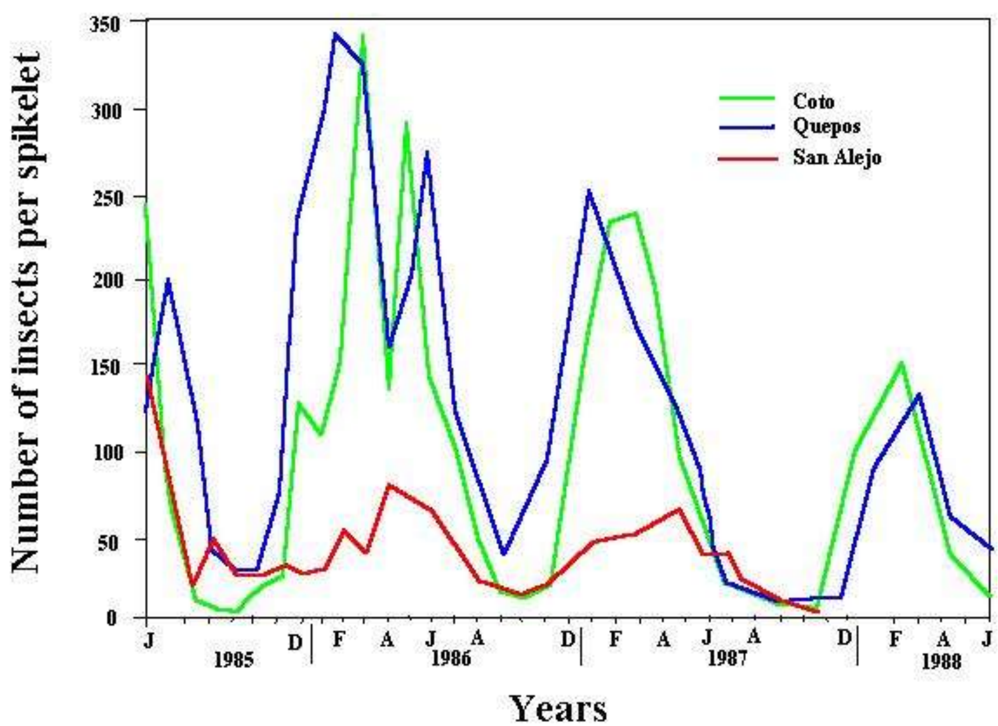

Fig. 2. Seasonal variation of the *M. costarricensis* population in three different locations

Coto Estate, South Pacific, Costa Rica

The estimated population of *E. subvittatus* per male spikelet, during the period prior to the introduction of *E. kamerunicus*, was low throughout the greater part of the year, in the Coto and Quepos Estates. The lowest levels observed in Coto (Fig. 3), occurred during the period comprising August-February. It was clear that the establishment of the rainy period (Fig. 4) exerted a detrimental effect, over the insect population, that extended itself well into the dry season. The reason for this type of behavior may has been due in part, to an increase in the population of natural enemies of the insect during the rainy season, as was observed in other studies (Zenner de Polania, 1986; Baylac, 1987). The apparent recovery of the population in the period comprising March through August of the year 1986, probably reflects the usual behavior of the insect population without the influence represented by *E. kamerunicus*in the following years.

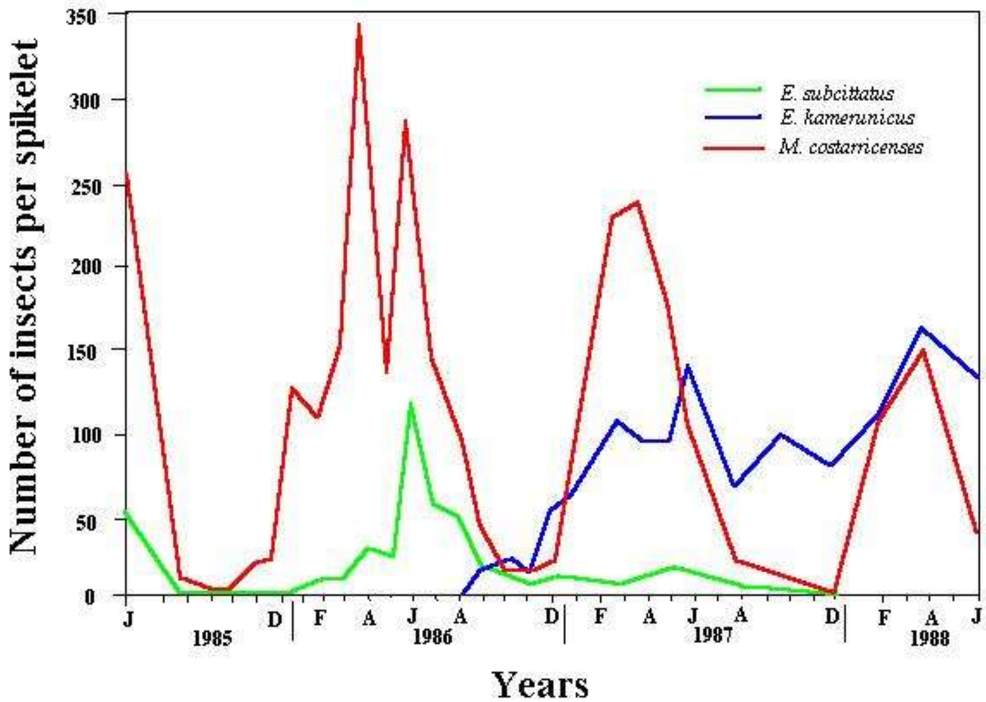

Fig. 3. Seasonal variation of the pollinator insects in Coto, Costa Rica

During 1987, the population of *E. kamerunicus* began to rise notoriously starting November (Fig. 3), which is associated with the incapability of *E. subvittatus* to increase its population to the levels observed the previous years. The antagonist effect of *E. kamerunicus* over the other species was clearly obvious in Coto, when it was not possible to find in the samples one single *E. subvittatus* individual starting October 1987. It is very possible that this situation be definite, since no individuals of this species could be found during the 1987-88 dry season, nor in the period comprising June-July, which were the months were the highest population values of *E. subvittatus* were observed in the past (Fig. 3).

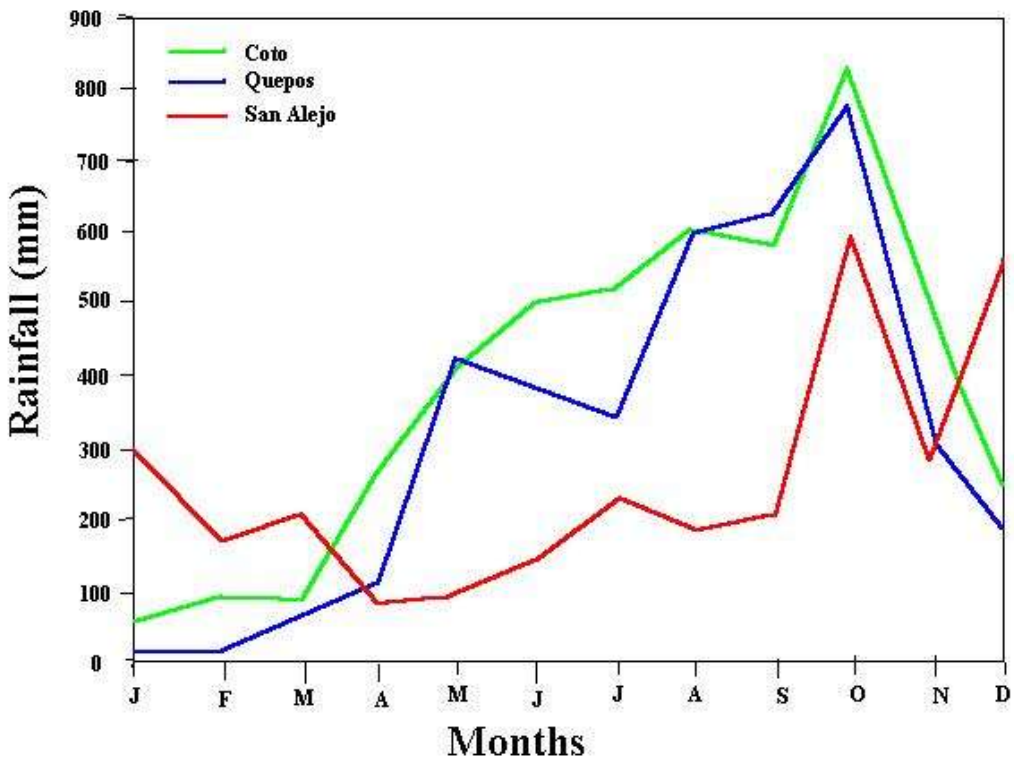

Fig. 4. Monthly rainfall in Coto & Quepos, Costa Rica and San Alejo, Honduras. Average of the years 1985 to 1988

The effect that the disappearance of *E. subvittatus* may have over the level of pollination is going to be very difficult to evaluate, but it is clear that, if there had been some negative effect, it would be minimized, and probably amply compensated by the large populations of *E. kamerunicus* that have developed. This latter insect has also been adversely affected by the prolonged rainy periods, but not as much as *E. subvittatus*.

According to the observations by Syed (1978), *E. kamerunicus* is a better pollinator insect than *E. subvittatus* in Africa, due to a greater capacity of pollen cartage. Nevertheless, the expected interaction between these two species was not one of antagonism but of complement, to achieve a more stabilized pollination throughout the year. According to Syed (1984a, 1986) in Central America both species would have the capacity of coexisting and would complement each other's pollinating activities; the expectative was that the population of *E. subvittatus* would maintain its high levels during the dry season and *E. kamerunicus* would therefore predominate during the rainiest months of the year. This conclusion came forth basically from the fact that these two species, plus other four belonging to the genus *Elaeidobious*, have co-evolutionated for thousands of years in West Africa, associated to *E. guineensis* (Syed, 1984a).

The reasons for the displacement of *E. subvittatus* by *E. kamerunicus* are not yet clear; according to Syed (1984) this situation should not be occurring as a consequence of a competition for food, but as a consequence of a competition for places for oviposition and larvae development. In Cameroon, the basal part of the male spikelets seem to be the sites preferred by *E. kamerunicus* for egg laying, whilst the distal part is clearly favored by *E. subvittatus* (Syed, 1984). Nevertheless, the establishment of *E. kamerunicus* in Colombia was accompanied by a considerable reduction of *Elaeidobious subvittatus* population levels and also for *M. costaricensis* (Mariau & Genty, 1987). The situations in Colombia and Central America could be explained in part, assuming that the site preferred by *E. subvittatus* for egg laying is also the basal part of the spikelets, although the presence of *E. kamerunicus* considerably reduces its chance of occupying those places (Zenner de Polania, 1986). On the other hand, the highest level of egg laying *for E. subvittatus* occurs at the end of the anthesis period of the male inflorescences (Genty et al., 1987). The egg laying activity of *E. kamerunicus* starts at the recently opened inflorescences, wherefore, when this insect is found in elevated population levels like the ones observed in Central America, it easily occupies all of the available sites for the development of *E. subvittatus* larvae.

The *M. costaricensis* population followed the pattern of rain distribution a little closer. At the beginning of the dry season (Fig. 3), its population recovered more rapidly than that of *E. subvittatus*. The largest populations per spikelet of *M. costaricensis* maintained themselves since the middle of the dry period (January), whereas the peak of the population of *E. subvittatus* was reached until well into the rainy period (May-June).

At the same time, the *E. kamerunicus* population has been increasing in Coto, the population peaks of *M. costaricensis* have come to be of a lesser magnitude (Fig.1). The apparent antagonic effect of *E. kamerunicus* and *M. costaricensis*, is expected to be maintained at a level similar to the present. Both species have very different behavior habits and do not directly compete for food, nor for sites for the development of their pupae, even if they do compete for larvae development sites (Genty et al., 1986).

In any case, the utility of *M. costaricensis* as an efficient pollinator for *E. guineensis* has been questioned (Syed, 1986a; Genty et al., 1986). This insect has a very reduced activity period and a low capacity to carry pollen (Syed, 1984b, 1986a; Genty et al., 1986; Mariau & Genty, 1987). Nevertheless, some races of this species possess a more extended activity period and have therefore greater potential as pollinators (Mariau and Genty, 1987).

After its liberation in Coto in May 1986, the *E. kamerunicus* population increased in a consistent manner until it reached figures between 75 and 130 insects per spikelet (Fig. 3). In general terms, the seasonal variation of the *E. kamerunicus* population in Central America, is similar to that observed in South America and West Africa (Syed, 1984; Genty et al., 1986). The fall of the population during the rainiest months of the year has not been as pronounced as it had been observed in the past for *E. subvittatus* and *M. costaricensis*. This means that, a greater and more stable level of pollination may be expected throughout the year.

The original estimates for *E. kamerunicus* populations in Cameroon came to 23-120 insects per male spikelet. In Malaysia, the population reached similar levels, wherefore it was accepted that these numbers were able to guarantee a fruit set value of at least 60% (Syed, 1984). Accordingly, a minimum of 30 adults per spikelet was considered acceptable in a new site after the introduction of the pollinator (Syed & Saleh, 1987). Assuming the methods of sampling were comparable, in each one of the studied sites (Coto, Quepos and San Alejo) the *E. kamerunicus* population per spikelet throughout the greater part of the year, was highly satisfactory for the purpose of achieving a higher value of fruit set. Some problems may emerge during the period September-November in Coto, when the heavy rains may severely reduce the population.

In general terms, fruit set has been higher in older palms, but these differences with younger palms tended to increase with the establishment of *E. kamerunicus*, and the younger palms were the ones that proportionately responded less to the activities of the pollinator (Fig. 5). The lowest values of fruit set in young palms could be associated sometimes to a larger sex ratio, but this was not always related to a considerably reduced amount of insects per male spikelet. According to Syed (1978, 1984b), the population of *E. kamerunicus* does not seem to be influenced directly by plant age, but by male inflorescence density per area. The accumulated data show a tendency concerning the development of greater populations of *E. kamerunicus* in younger palms as much in Coto as in Quepos.

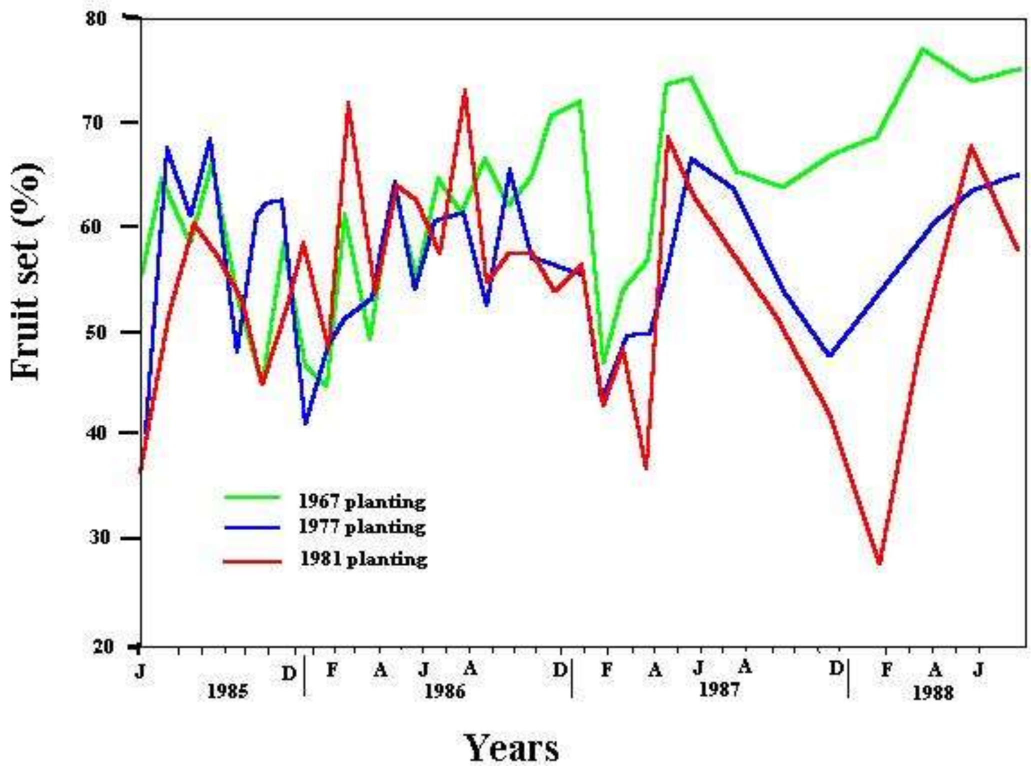

Fig. 5. Fruit set (%) in palms of three different age groups in Coto, Costa Rica

A better appreciation of the global change in fruit set value that has occurred since 1985, is observed in Fig. 6. The category of bunches with a fruit set less than 40% had been considerably reduced from 19.64% in 1985 to a 2.68% in June 1988. On the other hand, the category of bunches with a fruit set between 60 and 80% was observed to rise from 32.74% in 1985 to 61.36% in June 1988. Due to the age groups to which the majority of evaluated lots belong, these changes cannot be ascribed to an increase in pollination related to the change in age; from the five lots evaluated, two of them were planted in 1967, one in 1971 and another in 1977. The number of male inflorescences per area in each one of the lots being studied has been similar during the evaluation period.

The fruit set value was estimated sampling a band painted along the periphery of the mature bunch. When comparing the data with the value obtained from the analysis of the complete bunch, it was found that both numbers could differ in several perceptual units. The painted band method may underestimate the actual value of fruit set up to 5% in a particular age group. In general terms, fruit set values estimated with the help of the painted band method may be considered in reality 2-3% lower than the actual values.

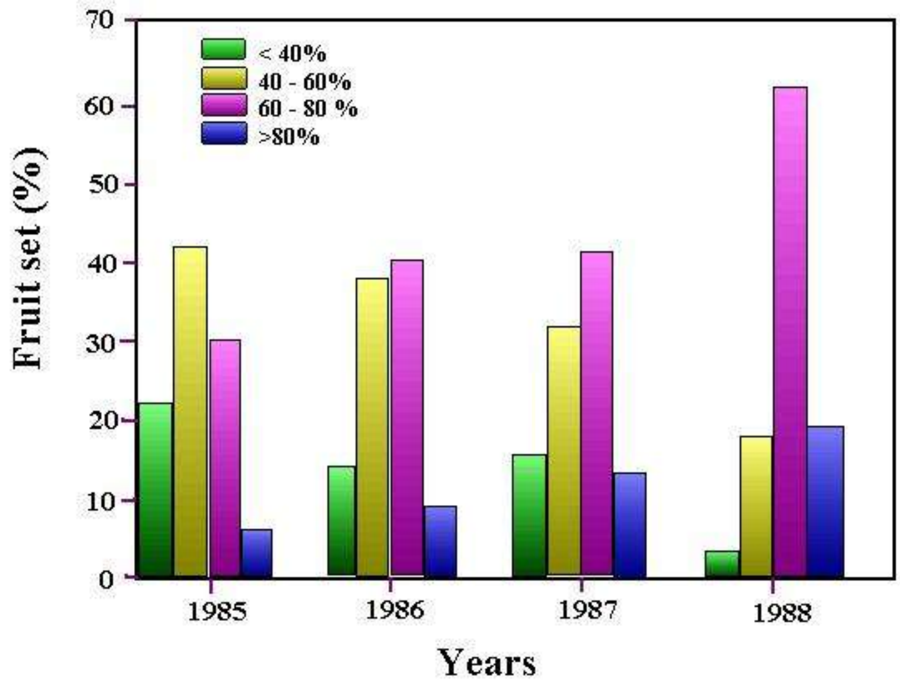

Fig. 6. Classification of bunches by categories of fruit set.

The relation between the number of male inflorescences per area and pollinator population was not always clear, but a larger number of insects in periods of greater male inflorescence density may be expected. However the inflorescence density did not follow a definite seasonal pattern. These changes, in sex ratio of the plant, is normal, and responds to changing climatic conditions even in old palms.

Quepos Estate, Central Pacific, Costa Rica

The behavior of *E. subvittatus* and *M. costaricensis* throughout the year in Quepos was similar to that observed in Coto, regarding the response of the populations to rainfall fluctuations (Fig. 7). The maximum populations were observed during the February-July period. With the establishment of the dry season, the recovery of the *M. costaricensis* population occurred more rapidly than for *E. subvittatus*. Nevertheless, in this Estate, the *E. subvittatus* population was recovering quicker and kept itself higher for a greater number of months per year than in Coto (Fig. 1).

The highest fruit set values during the months of July-November in 1986 and 1987 corresponded fairly well with the larger populations of *E. subvittatus* and *M. costaricensis* 5-6 months before (February-June) (Fig. 7 and Fig. 8). In general terms, the low insect population during the rainiest months (August through November in 1986 and 1987) were related to the low values of fruit set obtained during the months of January through April the following year.

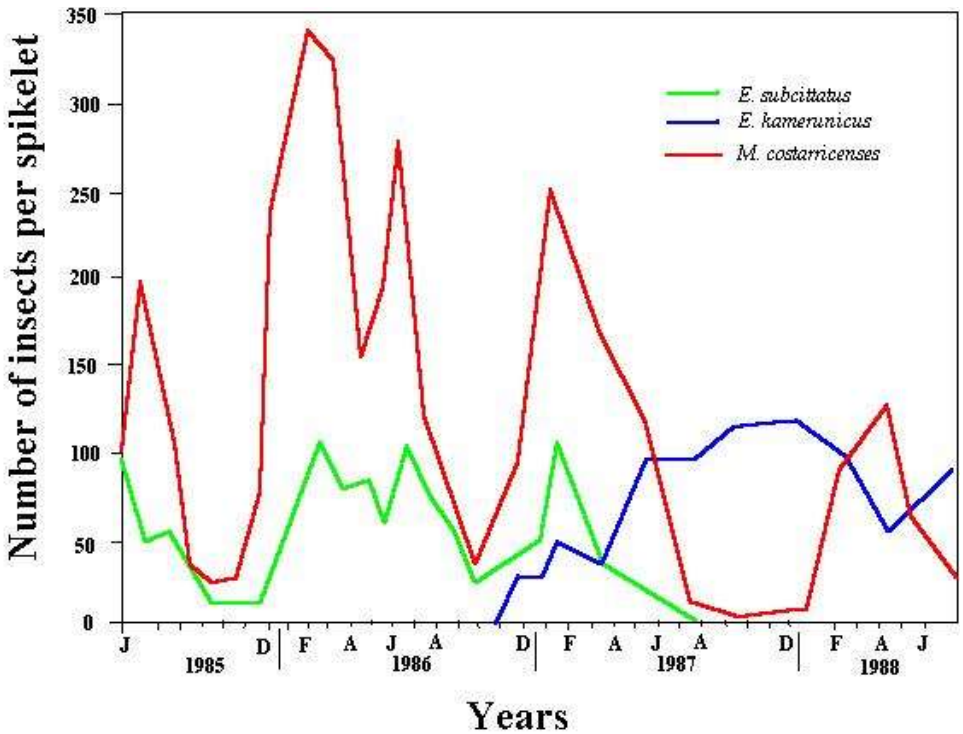

Fig. 7. Seasonal variation of the insect population in Quepos, Costa Rica.

From February 1987, the number of *E. subvittatus* per spikelet started to decrease considerably until it disappeared during the August sampling. Due to the fact that the disappearance of this species occurred within the months were its population was at its peak in the past, it is considered, to any practical effect, that *E. subvittatus* does not exist in Quepos either.

The decrease in the *E. subvittatus* and *M. costaricensis* populations was directly related with the establishment of *E. kamerunicus*, the population of which rose in a consistent manner since April 1987, and has stabilized itself around 50-100 insects per spikelet.

The negative effect that highly rainy periods have over *E. kamerunicus* is definitely less drastic than the effect those periods had over the other two pollinator species, whereas a continuous increase of the average value of fruit set has also been observed within this Estate, which is also noted to have been most notorious in older palms (Fig. 8).

San Alejo Estate: North Atlantic Coast, Honduras

If both of the Costa Rican Estates have suffered the fate of having the *E. subvittatus* population adversely affected by the establishment of *E. kamerunicus*, the Honduras Estate has been no exception. This situation was unexpected in Honduras since, *E. subvittatus* populations here were very large and thus, it was believed that this species was well adapted in this region, and that it could compete under better conditions against *E. kamerunicus*. The other pollinator present in San Alejo, *M. costaricensis*, had a much lower population than the one found in Quepos and especially in Coto (Fig. 1 and Fig. 2).

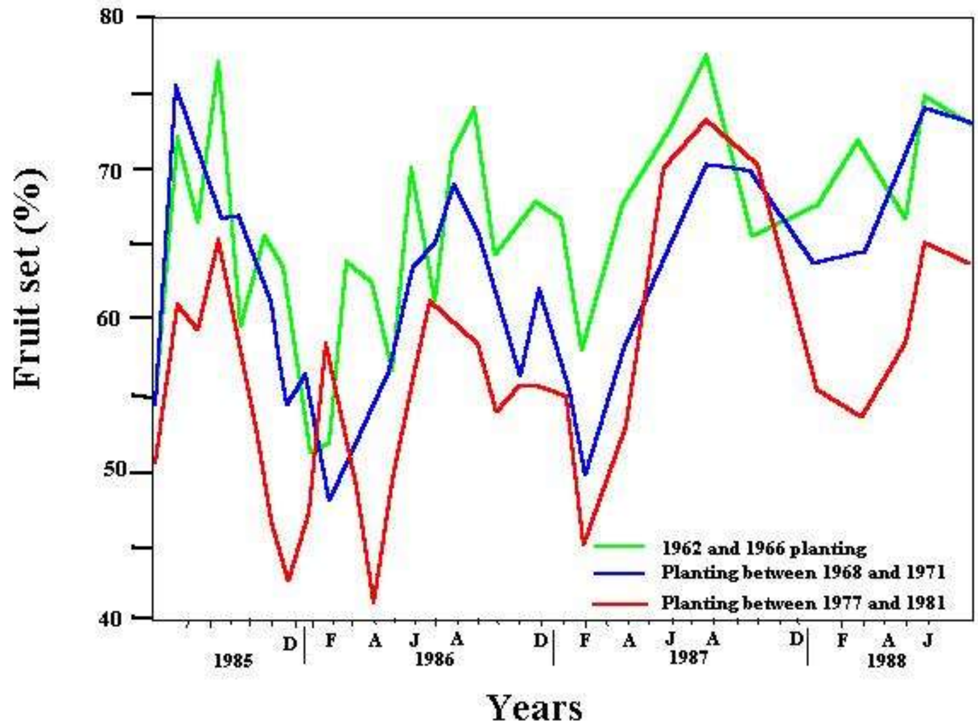

Fig. 8. Fruit set in three age groups of palms from the Quepos state.

The responses of *E. subvittatus* and *M. costaricensis* to annual rainfall variations were similar to those observed in Costa Rica. The population peaks occurred during the driest months of the year. The average fruit set in Honduras oscillated between 60 and 70% during the greater part of the year, even before the introduction of *E. kamerunicus*, and it has a tendency towards an improvement with the establishment of the pollinator.

Number of pollinator insects per area and per male inflorescence

These observations were carried out in Coto during the dry season (March), early in the rainy season (July) and during the period of heaviest rainfall in October. A similar methodology to that suggested by Chiu et al. (1986) was followed, taking a sample of 18 spikelets from three inflorescences in each one of the seven stages of anthesis. During the October sampling, the insect population was very low in four year old palms, wherefore the insects were individually counted in the 21 inflorescences.

During routine (insects per spikelet) sampling in Coto, it was already determined that the insect population reached a maximum at the end of the dry period, which extended itself well into the month of June (Fig. 3). The *M. costaricensis* population tended always to recover more rapidly during the dry season, and this seemed to occur most evidently in 11 year old palms.

The number of *E. kamerunicus* adults present per hectare during March (dry period) was inferior to the value observed during the month of June (early rainy period). In spite of this, the number of insects per hectare in March and June was highly satisfactory and it indicated that the number of insects present had the potential to guarantee a high fruit set value (Table 1).

Table 1. Number of insects per male inflorescences in different stages of anthesis and estimated number of pollinator insects per area in three different months of the year (Coto). (Average of three inflorescences in each stage of anthesis)

Stage of anthesis	Inflorescences per hectare in each stage			**March**				**June**				**October**			
				Insects /Inflores.		Insects / ha		Insects /Inflores.		Insects / ha		Insects /Inflores.		Insects / ha	
	Mar	Jun	Oct	M.c	E.k	M.c	E.k	M.c	E.k	M.c	E.k	M.c	E.k	M.c	E.k
							4 years old palms								
1	0.9	2.2	2.3	0	0	0	0	0	0	0	0	0	0	0	
2	0.9	2.2	3.6	518	658	464	590	336	1690	753	3789	0.7	541	2.4	1967
3	3.1	2.2	0.9	1630	1776	5115	5574	6831	19113	15316	42854	8.3	1517	7.5	1379
4	1.3	3.6	2.7	1968	4402	2647	5922	10971	20677	39358	74177	8.0	1980	21.8	5400
5	1.6	1.8	0.5	3808	3540	5122	4762	5612	28244	10066	50662	3.3	1186	1.5	539
6	2.7	3.1	2.3	10855	5188	29206	13958	11546	7061	36243	22165	13.0	712	29.5	1618
7	0.4	0.4	0.9	7225	2678	3240	1200	8832	5198	3960	2231	2.0	616	1.8	560
Total				26004	18242	45794	32006	44128	81983	105696	195978	35.3	6552	65	11463
							11 years old palms								
1	0.6	1.7	1.2	0	0	0	0	0	0	0	0	0	0	0	0
2	4.3	1.4	0.5	1642	3720	1766	1368	348	4154	475	5671	51	4030	24.0	1919
3	1.2	3.1	0.7	10266	7976	26384	6770	4703	16671	14446	51208	47	3178	33.6	2270
4	1.9	1.4	1.2	48656	52748	72141	29097	2342	43005	3197	58710	120	3900	143.0	4643
5	0.6	2.0	0.7	18684	38003	14448	11329	6496	27413	13302	56136	80	6188	57.0	4420
6	3.7	1.7	1.0	25049	36206	83503	44861	2708	6679	4621	11398	71	4185	68.0	3986
7	3.7	1.7	-	16801	19185	135109	50924	1373	439	2341	749	-	-	-	-
Total				121098	157868	333350	144349	17969	98361	38382	183872	369	21481	32.6	17238

M.c. = *Mystrops costarricenses*. E.k = *Elaeidobious kamerunicus*. Stage of anthesis: see text

According to Syed and Saleh (1987), a population of 20.000 *E. kamerunicus* adults per hectare would be in a capacity to guarantee an acceptable fruit set value of at least 60%. The situation in the month of October was very different, and in young palms it was estimated that there existed only 65 individuals of *M. costaricensis* per hectare and only 11.463 *E. kamerunicus*, Therefore, the fruit set values could be expected to be low for the period comprising January through March. There is no data available, that permits to estimate the minimum population of *M. costaricensis* that can guarantee an adequate pollination level, and this number will obviously vary with the type of race or subspecies present of this pollinator (Genty et al., 1986).

Comparison of pollinator insect population in four types of germplasm

A sample of six inflorescences was examined in ten year old palms, in each one of four types of germplasm. *E. oleifera* attracted a lower number of insects of both species (Table 2). Very few individuals of *E. kamerunicus* visited the flowers of these plants. A similar behavior had been observed by Syed (1984).

The hybrid OxG was more attractive to *E. kamerunicus* than *E. oleifera*, but even so, the number of insects of this species and the number of *M. costaricensis* were comparatively low in the hybrid. Both the commercial material DxP (Deli x AVROS) and the compact (OxG backcrossed to *E. guineensis*) presented the highest number of insects from both species. It is interesting to note that, in spite of the low *E. kamerunicus* population values in OxG and *E. oleifera* materials, none of the samples had *E. subvittatus* individuals.

Table 2. Comparison of the population of insects in four types of palm germplasm (April, 88)

Type of palm*	Spikes per inflorescence	Insects per spike		Total of insects per inflorescence	
		M.c.	E.k.	M.c.	E.k
Compact	255	267.1	28.0	68108	7129
	239	111.6	144.2	26684	34472
	243	108.2	103.9	26303	25252
	272	158.7	68.9	43178	18744
	316	148.0	108.8	46782	34385
	143	49.0	99.9	7013	14288
Mean	245	140.0	92.3	36344	22378
Total				218069	134272
Hybrid (OxG)	238	83.2	26.6	19810	6321
	280	45.8	42.8	12814	11997
	174	17.2	-	3002	78
	203	13.8	15.6	2804	3172
	241	70.6	7.3	17018	1763
	211	2.3	5.7	488	1206
Mean	224	38.8	19.6	9322	4089
Total				55937	24538
E. oleifera	181	100.9	0.2	18260	46
	152	80.0	0.0	12285	2
	133	160.0	0.5	21284	61
	154	61.8	0.3	9369	50
	192	39.0	0.4	7497	72
	194	39.9	0.3	7740	50
Mean	168	80.4	0.3	12739	46
Total				76437	281
E.guineensis	204	238.5	258.6	48655	52748
	199	93.9	191.1	18684	38033
	235	106.6	154.1	25049	36206
	168	100.0	114.2	16801	19184
Mean	201.5	134.8	179.5	27297	36542
Total				109190	146171

* Ten years old palms except *E. guineensis* which was eleven years old. Inflorescences around the 5th and 6th days of anthesis

Pattern of visits of the pollinators to female inflorescences in anthesis

The population per spikelet of *M. costaricensis* was a maximum in the Coto Estate (Fig. 2). The number of individuals that visited female inflorescences in anthesis was likewise found to be higher in Coto than in Quepos during July, 1988. Approximately three individuals of *M. costaricensis* visited female inflorescences in anthesis per individual of *E. kamerunicus*. In Quepos, this ratio was of 1.7 *M. costaricensis* per *E. kamerunicus* individual (Table 3).

E. kamerunicus adults only visited female inflorescences during the hours of the day with a lot of sunshine (Fig. 9). This type of behavior creates a limitation for the species in Coto, where it is generally very cloudy during the rainy season. Throughout the observation period in July (mid rainy season), the insect did not show any activity during those hours that were cloudy or rainy. The greatest activity occurred between 10 a.m. and 1.0 p.m., when the 83% and the 71% of the total of the visits on the first and second day of anthesis where carried out, respectively. This period of maximum activity of the insect is probably more extended under conditions of more hours of sunshine, during the dry spells throughout the year. The basic patterns of this particular insect's activity were determined in Africa by Syed (1978, 1979, 1984b) and they conform, in general, to the observations made in Central America.

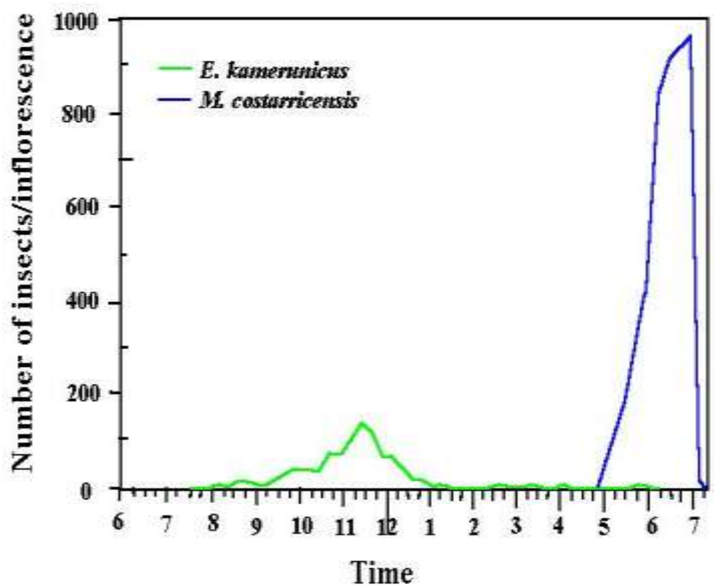

Fig. 9. Pattern of visits of *E. kamerunicus* and *M. costarricensis* to female inflorescences in anthesis (Coto).

The other species of insect studied (*M. costaricensis*) has crepuscular habits, as was observed in this and other studies (Genty et al. 1986). Only a few individuals visited the female inflorescences between 6 and 8:30 a.m. In Coto; the greatest number of visits occurred after 6:00 p.m. and were kept high until 7:45 p.m. with a peak at 6:45 p.m. At the Quepos Estate a similar behavior was observed; nevertheless, the greatest activity was initiated one hour earlier than in Coto, but also ceased one hour earlier, at 7 p.m.

The short period of activity of *M. costaricensis* is an impediment for the execution of an adequate pollination of an inflorescence, which is receptive only 40-52 hours and where not all the flowers of the inflorescence are simultaneously receptive. Nevertheless, there apparently exist some races or subspecies of *M. costaricensis* in some regions of America, that have longer activity periods and are capable of guaranteeing an adequate fruit set. The population of these races is also maintained more stable during the rainiest periods of the year (Genty et al., 1986). The daytime behavior of *E. kamerunicus* in Quepos was similar in Coto, wherefore its greatest activity was initiated at 9:15 a.m. and notoriously decreased after 12:30 p.m.

During the two days of the period of anthesis in Coto (mid- May, 1988), it was determined that 3,189 individuals of *M. costaricensis* and 1026 adults of *E. kamerunicus* were trapped on the adhesive tapes (90 cm2) (Table 3). The sex ratio observed for *E. kamerunicus* was of approximately 78% females and 22% males. These values are similar to those observed by Syed in Cameroon (Syed, 1978). In the case of *M. costaricensis*, it was found that the individuals that visited the inflorescences were 60% females. The great attraction that the female inflorescences exerted over the female of *E. kamerunicus* is unfortunate from the pollination point of view, as the females carry a much more reduced quantity of pollen.

Table 3. Number of visits of *E. kamerunicus* and *M. costarricensis* to female inflorescenses of *E. guineensis* in anthesis in two different zones in Costa Rica

Inflores-cence	Coto				Quepos			
	First day of anthesis*		Second day of anthesis		First day of anthesis		Second day of anthesis	
	M.c.	E.k.	M.c.	E.k.	M.c.	E.k.	M.c.	E.k.
1	1613	82	1522	34	1658	818	243	191
2	1248	30	583	430	1636	191	121	81
3	329	139	3845	1925	1094	969	239	271
4	2614	176	1257	1355	367	57	437	438
5	1759	21	-	-	565	1107	140	124
6	762	-	-	-	-	144	166	338
Total	8325	448	7207	3744	1333	3268	1346	1443
Mean	1387	89.6	1802	936	1109	548	224	241

* Total number of insects collected on an adhesive tape 90 cm^2

Estimating the total female inflorescence area exposed, it was estimated that it could be visited by approximately 40,000 individuals of *M. costaricensis* and 12,000 *E. kamerunicus* within the two days of anthesis. Assuming that 78% of the individuals of the latter species were females, these insects would carry some 7.4 million pollen grains, that with a germination percentage as low as 4.8%; they would contribute 355,000 available grains to pollinate some 1,000-1,500 flowers in each inflorescence. It was also estimated, that each individual flower in the inflorescence had, in theory, the chance of being pollinated by a quantity of some 300 grains of pollen carried by *E. kamerunicus* individuals, plus some 60-75 grains carried by the total of *M. costaricensis* that visited the female inflorescence during its anthesis period.

The number of insects available per female inflorescence may actually vary amply from one time of the year to another, as it is concluded from the summarized data in Table 1. In four year old palms, during the month of March, it was estimated that there existed 4,758 available *E. kamerunicus* individuals per female inflorescence and in June, this figure had risen to 27,314. The period March-June generally marks the peak of the maximum population of the pollinators in Coto (Fig. 3). During the rainiest spells of the year, the insect populations were considerably reduced, and with them the number of visits to the female inflorescences, and the amount of viable pollen carried per insect. In October 1988, only 740 *E. kamerunicus* individuals were available per female inflorescence in the four year old palm.

Under certain environmental conditions that favor pollination, and with an adequate distribution of male inflorescences per area, it was estimated that 3,000 available *E. kamerunicus* adults per female receptive inflorescence, permitted a satisfactory fruit set (70%). The minimum acceptable level to achieve a 50% of fruit set was 1,500 available adults per female inflorescence (Syed, 1987).

Using these observations as basis, it seemed that the limiting factor in Coto for the achievement of higher fruit set values during the greater part of the year, was not the availability of pollen, nor of insects, but the prevalence of certain environmental factors (heavy rainfall and cloudiness) that act negatively upon the activity of the pollinators and upon their capacity to carry viable pollen. However, during the months of September and October, the main limiting factor has no doubt been the insect population that dramatically falls, particularly in October. The period of daytime activity for *E. kamerunicus* is reduced to a few hours in cloudy days, as it occurred during the month of May, in which these observations were carried out in Coto. Some samples of the pollen adhered to these insects had a germination percentage very near to zero, the same as some samples obtained from *M. costaricensis*.

Very prolonged periods without rainfall and a larger number of sunshine-hours per year in Quepos, and in San Alejo especially, could lead consistently to a greater fruit set value. More male inflorescences per area in San Alejo gave this plantation an extra advantage.

An important detail to be noted is that, after the *M. costaricensis* evening visits ceased, the insect continued moving around within the female inflorescence for several hours, while the mayor part of *E. kamerunicus* individuals did not remain within the inflorescence during the night, and the few that were left remained hidden among the flower bracts. It is possible that in young palms with an elevated sex ratio, the number of *M. costaricensis* individuals that remain within the female inflorescences during the night be considerable and, if not taken into account, the actual pollinator population per area is underestimated, when counting only the insects in the male inflorescences. It remains to be seen if the insects that have had their chance to pollinate the inflorescence, will again enter the potential pollinating population.

Quantity and viability of the pollen transported by the pollinator insects

E. kamerunicus was chosen by Syed (1986b) to be introduced in Malaysia and in America due, fundamentally, to its elevated capacity to transport pollen. According to this author, the male of the species carried an average of 235 grains of pollen per individual and the female 56 grains. *E. subvittatus*, also present in America, is considered in Cameroon less efficient as a pollinator, because, in spite of being more numerous around female inflorescences, it carried an inferior quantity of pollen: 15 grains average per individual. Some of these data were obtained examining a fairly low number of insects (Syed, 1978). *M. costaricensis* was considered an even poorer pollinator than *E. subvittatus*, as it was found that it carried an average of only 0.6 grains of pollen per individual (Genty et al., 1986).

E. kamerunicus individuals (male and female) that were examined in Coto and in Quepos, carried a considerably larger number of pollen grains than the amount determined by Syed (1978) in Cameroon. The males of this species were found to carry an average of 1078 grains of pollen and the females transported an average of 498 grains (Table 4).

Table 4. Number of pollen grains carried by *M. costarricensis* (M.c.) and *E. kamerunicus* (E.k.) adults collected from female inflorescences in anthesis in two different zones in Costa Rica

Group of insects[1]	Average number of pollen grains adhered to the body[2]				Grains easily loosened[3]				Estimated amount of pollen carried per insect[4]			
	Female		Male		Female		Male		Female		Male	
	M.c.	E.k.	M.c.	E.k.	M.c.	E.k.	M.c.	E.k.	M.c.	E.k.	M.c.	E.k.
Coto (may)												
1	3.9	349.3	3.6	152.2	11.9	381.4	10.8	166.2	15.8	730.7	14.4	318.4
2	3.1	121.1	3.5	2114.7	17.8	50.9	198.8	875.3	20.9	172.0	23.3	299.0
3	6.2	334.6	5.3	548.5	14.2	230.0	12.3	377.0	20.4	564.6	17.6	925.5
4	5.0	248.8	5.0	232.0	20.7	124.1	20.7	115.8	25.7	372.9	25.5	347.8
5	1.8	57.8	2.3	84.5	17.5	742.3	23.3	1086.2	19.7	800.1	25.6	1170.7
6	4.4	133.2	3.8	185.7	9.6	384.8	8.3	536.0	14.0	518.0	12.1	721.7
7	2.0	107.4	2.0	345.5	14.4	136.3	14.4	438.4	16.4	243.7	16.4	783.9
8	2.0	156.8	1.7	1025.0	8.1	170.4	6.7	1114.2	10.1	327.2	8.4	2139.2
9	1.9	128.2	2.5	-	6.1	317.6	9.5	-	8.0	445.8	12.0	-
10	2.4	136.0	2.4	298.0	8.9	149.5	8.8	327.4	11.3	285.5	11.2	625.4
Mean	3.3	177.3	3.2	554.0	12.9	268.7	13.4	559.6	16.2	446.0	16.6	1113.6
Quepos (July)												
	3.3	72.5	6.7	110.0	3.2	355.9	5.7	539.5	5.6	428.4	12.3	649.5
	2.9	91.1	3.7	92.0	3.2	650.6	4.3	656.7	6.1	741.7	8.0	748.7
	3.7	73.1	4.1	310.5	4.6	329.5	5.1	1400.5	8.3	402.6	9.2	1711.0
	-	102.0	-	154.0	-	501.4	-	757.5	-	603.4	-	911.5
	-	58.6	-	122.0	-	1511.9	-	1067.0	-	570.4	-	118.9
Mean	3.3	79.5		157.7	3.4	469.9	5.0	884.2	6.7	549.3	9.8	1041.9
Mean										498		1078.0

1. Each group consists of 10 insects of each species placed in approximately 0.5 ml of water, males and females together. In the case of Quepos, 50 *M. costarricensis* were placed in all three groups.
2. The majority of the grains were found under the wings.
3. The total pollen loosened from the body and recovered in the water was assigned to each insect in proportion to the quantity that remained adhered to the body.
4. Sum of the grains of pollen adhered the body plus the grain recovered from the water

In the case of *M. costaricensis*, the values found were also greater than the ones observed by Genty et al. (1986). The females of this species transported an average of 11.4 grains and the males 13.2 grains. Around 32% of the insects, (both sexes), transported between 9 and 11 grains of pollen. The maximum number of grains found on an insect was 25 and the majority carried only 4 grains.

For the other species of insect examined, *E. subvittatus*, the individuals were obtained in Honduras and no separation was made between sexes. The average number of pollen grains in several groups of insects examined varied from 46 to 64 grains per individual.

Due to the fact that *E. subvittatus* lays most its eggs at the end of the period of anthesis of the male inflorescences, many insects that have just emerged may visit female flowers without carrying viable pollen. The maximum viability of the pollen is observed in those insects that abandon male flowers during the period of maximum anthesis (Genty et al, 1986).

In the case of *M. costaricensis*, the pupa stage occurs outside the male inflorescence, which implies that the adult, upon emerging, carries no pollen and the visit of one of these adults directly to a female flower is useless from the pollination point of view (Genty et al., 1986).

These observations explain in part, why there was a better fruit set in San Alejo when the species *E. subvittatus* was more numerous in that particular plantation, than in Coto or Quepos. The observations made in several countries in America pointed out that *M. costaricensis* predominates in drier areas (Syed, 1984b; Genty et al., 1986; Mariau & Genty, 1987). As important as the number of grains of pollen carried by the insects is the viability of this pollen. The viability of the pollen transported by *E. kamerunicus* and *M. costaricensis* was comparatively low during the period in which these observations were carried out in Coto and Quepos.

A study on viability of the pollen was performed in the month of July, during the rainy season. It is expected that the viability of the pollen carried by insects improve during the dry season, during which the pollen remains humid less time and preserves its germination capacity longer (Ekaratne & Senathirajhah, 1983).

The *E. kamerunicus* adults collected flying around female inflorescences in anthesis, transported pollen that only germinated from 4.4% to 5.3% in several samples examined. This value may be compared to the control sample of male inflorescence pollen, which was set out to dry and from which was obtained a 55% of germination.

When the insects were captured over a female inflorescence that was on the same palm with a male inflorescence in anthesis, the pollen from these insects was found to have a germination of 12.3%. The percentage of germination of the pollen transported by *M. costaricensis* was greater (12.5%), than that found for *E. kamerunicus*.

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