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Pollination Ecology of the *Manicaria saccifera* (ARECACEAE): A Rare Case of Pollinator Exclusion

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Additional information is available at the end of the chapter

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Abstract

We studied the reproductive biology and pollination ecology of the palm cabecinegro (*Manicaria saccifera*) in very wet tropical forest, in the Chocó, Pacific region of Colombia. We present data about the phenology, floral morphology, floral biology, reproductive system, and pollination. *M. saccifera* is monoecious, self-incompatible, lacks apomixis and has dichogamy in the form of protogyny. Flowering occurs all year round with a peak between April and May. A single individual may produce up to five inflorescences in its reproductive period. Each inflorescence has unisexual flowers grouped in dyads and triads; anthesis is diurnal and the flowers may be receptive for 72 h. Flowers are visited by 10 species of insects. The inflorescences in the female-phase do not offer reward and insects are attracted by olfactory mimicry; in the male-phase flowers reward visitors with pollen and a place to oviposit. The most efficient pollinator is *Mystrosp cercus* (Nitidulidae), the only visitor arriving in abundance during the female-phase. Other insects do not enter the flower because the peduncular bract and the petals act as barriers, blocking the entrance of insects greater than 2 mm. Having one exclusive pollinator which in turn depends on the palm for its survival is an example of extreme specialization and mutual dependence.

Keywords: Arecaceae, beetle pollination, *Mystrops cercus*, neotropical palm, phenology

1. Introduction

Palms are one of the most important plant families because they are a food source for wildlife [1]; they provide a variety of products that rural peoples use for construction, food, medicine and handicraft purposes [2, 3]; they are a source of raw materials for a great variety of products that communities exploit commercially at small or large scales, always in an extractive

way [3, 4], and finally, palms are culturally important because many species are essential to the cultural development of local peoples [5].

Due to this importance, studies on their reproductive biology have increased in the last decades [6]. Initially, most studies focused on cultivated palms or on widely used species [1, 7]; however, recent works have focused on a wider range of palms [8–10].

Research on the reproductive biology of this plant family has increased our knowledge on the great variety of pollination strategies and mechanisms found in plants and on the strong dependence and intimate association that most palm species share with the insects that pollinate them, mainly species of coleoptera belonging to the families Nitidulidae and Curculionidae [9–11]. Due to palms economic, ecologic and cultural importance, studies on palms reproductive biology are essential for their sustainable use, conservation and future domestication [10].

Manicaria saccifera is a widely distributed species [12], of ecological importance [1, 13] and great economic potential [14, 15]. It ranks among the most utilized and economically valuable palms for the Afro-American and indigenous communities of the Chocó biogeographic region: [16] reported 36 different uses for this species, evidencing its versatility as a non-timber forest product. The most significant uses of *M. saccifera* in the Pacific region of Colombia include: the use of the peduncular bract as a source of fiber for crafts and textiles [15–17]; weaving the leaf veins for basketry [15]; the use of unexpanded leaves for brooms; the leaves for thatch houses; the immature fruits filled with a liquid resembling coconut water are consumed while working in the forest. Additionally, fruits are sold in local markets for medicinal purposes [16]. In Venezuela the Warao Indians use *M. saccifera* for construction, sailing, food, medicine, and for crafting bags and hats [18, 19].

M. saccifera is a little studied palm in terms of its reproductive biology [20], who mentions the possibilities of auto-pollination and the great quantity of larvae inside the flowers. On the other hand, [21] reported several visiting insects, with *Mystrops cercus* and *Mystrops erviki* (Nitidulidae: Coleoptera) being frequent visitors. The most important aspect to highlight in this species is that, contrary to most species in the family, anthesis and all remaining reproductive mechanisms occur “hidden” within the interior of the peduncular bract, without opening or exposing the male and female flowers. This aspect makes an understanding of the species reproductive strategy even the more intriguing.

Our work constitutes the first significant contribution detailing the principal aspects of the reproductive biology and pollination ecology of one of the most important palms for the inhabitants of the Pacific region of Colombia and a key species of tropical pluvial rainforests. In this work we evaluate the periods of flower and fruit production, the reproductive system, floral biology, flower visitors and we quantify the role each visitor has in the pollination of the palm.

2. Materials and methods

2.1. Study area

Our study was conducted in the Quibdó municipality, Pacific coast of Colombia, in an area adjacent to the road leading from Quibdó to the Atrato municipality, at 5° 39' N, 76° 38' W

(Figure 1), and 90 m of elevation. With a mean annual temperature of 28° C, a relative humidity of 89% and a mean annual precipitation of 5000–7000 mm, this area is classified under very wet tropical forests in the Holdrige life zone system [22].

2.2. Study species

Manicaria saccifera Gaertn., known as “cabecinegro” in the Colombian Pacific (Galeano and Bernal [13]) is a monoecious palm that grows in swampy inundated areas, preferably near the edge of rivers and creeks. Its individuals are medium sized, solitary or cespitose, with large regularly pinnatisect or simple leaves and with a dentate margin. The inflorescences are interfoliar and solitary [13]. It is distributed in Central America, in the Pacific littoral of Colombia southwards to northern Ecuador, and in the Orinoco and Amazon basin of Colombia, Brazil and Venezuela [12].

2.3. Inflorescence morphology

A morphological description of the inflorescence was performed based on 20 inflorescences of *M. saccifera*. We (i) recorded the height at which the inflorescences are found, (ii) measured the length of the inflorescence, rachillae and flowers; (iii) counted the number of rachillae, of female and male flowers per rachillae and of female and male flowers per inflorescence; and (iv) determined the position of the flowers in the rachillae, the number and shape of the

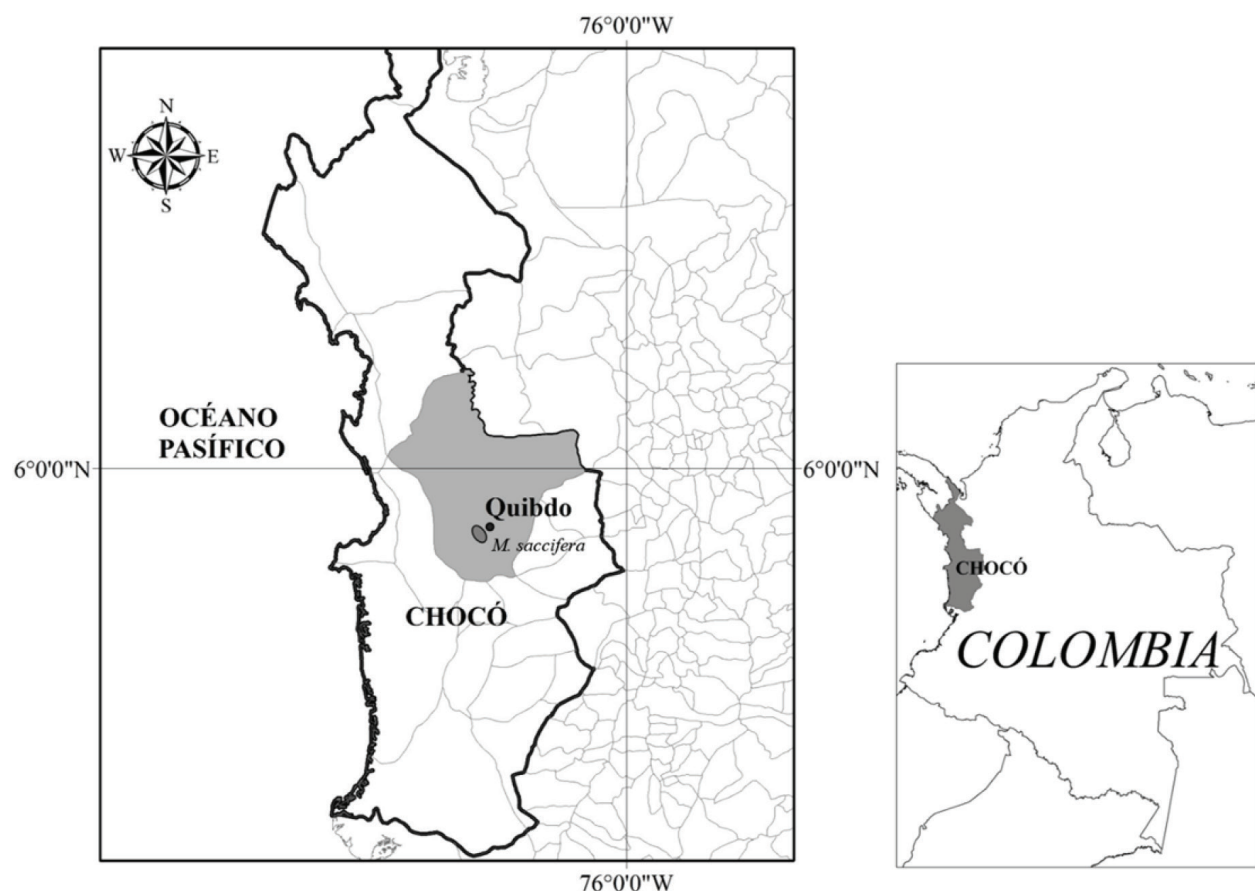


Figure 1. Study zone.

stigmas and the number of anthers. To estimate the number of flowers per inflorescence, we multiplied the total number of flowers of each rachillae by the mean number of rachillae counted in 10 inflorescences.

2.4. Reproductive phenology

We recorded the reproductive phenology of 48 individuals of *M. saccifera* during a 12-month period, marking individuals along a pre-defined trail in the forest. Each week we revisited the study area during 3 days to register in each individual if flowering and fruiting occurred. We calculated the monthly percentage of flowering and determined the flowering synchrony. Following [23] we defined flowering events as being: (i) asynchronous, when less than 20% of the individuals are in flower; (ii) low synchrony, between 21 and 60%; and (iii) high synchrony when over 60% of individuals flower at the same time.

2.5. Floral biology

To view the reproductive structures and carry out our observations, a longitudinal slit was opened on the peduncular bract and was later covered with paper tape. Direct observation of the flowering buds and opened flowers were made at intervals of 6, 12, and 24 h in 10 inflorescences of 10 individuals. We registered the (i) hour of anthesis of the flowers, (ii) the daily rhythm of anthesis of the flowering buds, (iii) the presence and longevity of pollen, and (iv) the stigmatic receptivity. We used three methods to evaluate the stigmatic receptivity: (1) direct observation of the stigmas, noting changes in morphology, color and presence of exudates; (2) signs of peroxidase activity, using hydrogen peroxide tests [24]; (3) colorimetry tests, applying the Perex-Test solution by Merck [25]. Additionally, we registered the increase in temperature within the inflorescence using digital thermometers made by Cox Technologies Inc., with a range of temperature between -35 and 210°C . We performed measurements in five closed inflorescences of five individuals, introducing the thermometer's sensor to register the internal temperature of the inflorescence, which was compared with ambient temperature.

2.6. Reproductive system

We determined the reproductive system of *M. saccifera* by performing controlled pollinations on five inflorescences from different individuals using four different treatments: (i) Auto-pollination: we isolated inflorescences to avoid the entry of pollen; (ii) Open pollination: natural pollination without our intervention; (iii) Apomixis: without pollination; (iv) Allogamy: controlled pollinations using pollen from different individuals of *M. saccifera*. In all cases, the flowers were isolated with synthetic mesh at least 30 days. After each treatment we checked whether fruits were developing and recorded the percentage of fruits formed. The degree of genetic compatibility was evaluated using the self-incompatibility index proposed by [26].

2.7. Floral visitors and pollinators

The composition of floral visitors was studied in 10 inflorescences from 10 individuals. When the rate of visits was highest, inflorescences were covered with bags and shaken so insects would fall

inside the bags. This procedure was repeated three times each day during all the flowering phase. For each floral visitor we documented its (i) abundance, (ii) behavior and (iii) role in pollination. To document the behavior of floral visitors we performed observations on the female- and male-phase of each palm, noting: the hour of arrival and departure to the flower, the activity within the flower, the utilized resources, and the permanence in the flower, and the contact with the stigmas in the female-phase. Following [10] we calculated the pollinator importance value (PIV) and the pollinator relative importance value (PRI). The variables used to calculate these indices were: the relative abundance of insects in the female flowers (AB), pollen-transport capacity (PTC), fidelity (F), constancy (C), and pollen-transport efficiency (PTE). For details on each variable refer to [10]. To determine the CTP and ETP, we collected five insects of each species, preserved them in 70% alcohol and took them to the laboratory to conduct the pollen load analyses following the methods in [9]. To evaluate fidelity we compared the pollinators of *M. saccifera* with pollinators of the palms *Attalea allenii*, *Attalea cuatrecasana*, *Oenocarpus bataua*, *Oenocarpus minor*, *Socratea exorrhiza* and *Wettinia quinaria*, all of which are palms that grow in the study area together with *M. saccifera*.

3. Results

3.1. Inflorescence morphology

The inflorescences of *M. saccifera* are interfoliar and located at a mean of 1.89 ± 1.1 (SD, $n = 20$) meters above the ground (**Figure 2A**). An individual during the reproductive phase may produce 1–5 inflorescences ($n = 45$), which are found in different developing stages and which flower alternately. Each inflorescence can measure up to 1.50 m, including the peduncle, which measures 46 cm and the prophyll (35 cm). Each inflorescence is covered by a fibrous peduncular bract, which is closed without suture, is brown and has the shape of a long hood. Throughout all development phases of the inflorescence, the peduncular bract acts as a mesh or as a selective barrier to insect visitors (**Figure 2B** and **C**). The bract suffers changes in morphology and coloration at its exterior surface and thickening due to the development and growth of the fruits in the inner part. Inflorescence present a mean of 35 ± 19.5 (SD, $n = 10$) rachillae. The flowers in inflorescences are distributed in (i) triads, with a female flower in the center and two male flowers at the sides in the basal part; (ii) toward the apex as dyads, with two male flowers (**Figure 3**). This distribution of flowers distinguishes the subfamily Arecoideae from the other palm subfamilies. Generally, the last rachillae to develop contain only male flowers.

Each rachillae contains a mean of 2.88 ± 0.84 (SD, $n = 504$) female flowers and a mean of 218 ± 132 (SD, $n = 504$) male flowers so that each inflorescence can harbor 199 ± 32 (SD, $n = 10$) female flowers and $15,085 \pm 532$ (SD, $n = 10$) male flowers.

The flowers are of rigid texture, yellowish in color, and the female flowers are greater, measuring 0.7 ± 0.3 cm (SD, $n = 16$) in length, and with a laminar stigma in the shape of a pyramid (**Figure 2E**); each male flower measures 0.8 ± 0.3 cm (SD, $n = 16$) in length and has numerous stamens (mean of 35) (**Figure 2D**).

The fruits are spherical, 5 cm in diameter and covered with woody pyramidal or pointed projections; occasionally the fruits have the shape of two or three united spheres forming a

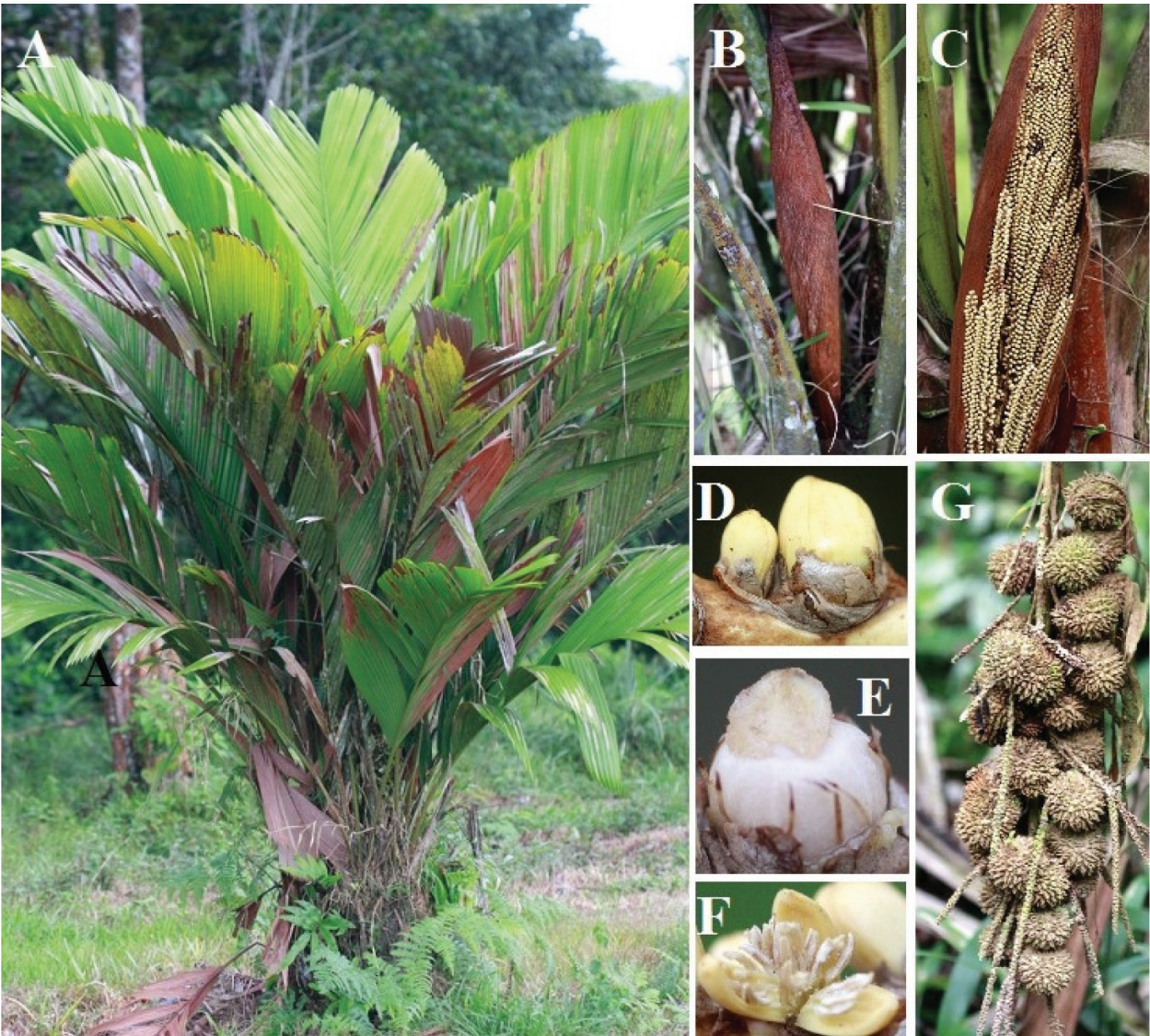


Figure 2. Morphology of *Manicaria saccifera*. (A) Habit. (B) and (C) inflorescence covered by the peduncular bract. (D) Flowers of *M. saccifera* in triads. (E) Receptive female flower. (F) Open male flower.

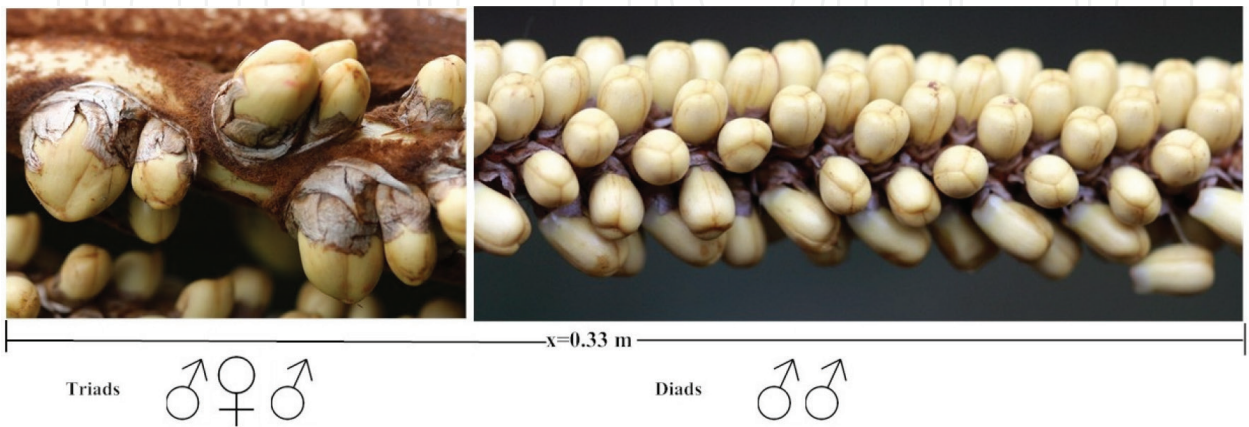


Figure 3. Distribution of the female- and male-flowers at the rachillae of *Manicaria saccifera*.

triangular structure. The seed is spherical, very hard, and is covered by a brownish or light purplish kernel of brittle texture (**Figure 2G**).

3.2. Reproductive phenology

M. saccifera flowered throughout the year (**Figure 4**), with a peak in inflorescence production in the month of May, when nearly 61% of individuals had one or two inflorescences; the remaining individuals flowered during the months of June until August. There was no relationship between flowering and precipitation, flowering being constant in months of low rainfall (February) and highest rainfall (November). The individuals of the studied population showed low synchrony in flowering, with 27% of the individuals flowering simultaneously. The fruiting period was relatively constant throughout the year (**Figure 4**).

3.3. Floral biology

The events that take place during floral biology can be summarized as: (1) flower buds emerge; (2) buds of pistillate flowers develop completely; (3) anthesis begins; in female flowers it occurs simultaneously whereas it is alternate in male flowers and lasts up to 2 days. During anthesis there is an increase in temperature above ambient temperature in female and male inflorescences of 4.0 and 4.7°C, respectively (both $n = 3$); (4) maximum stigmatic receptivity, evidenced by the white color of the stigmas covered by a hyaline-brilliant substance; (5) pollination, with subsequent loss of stigmatic receptivity evidenced

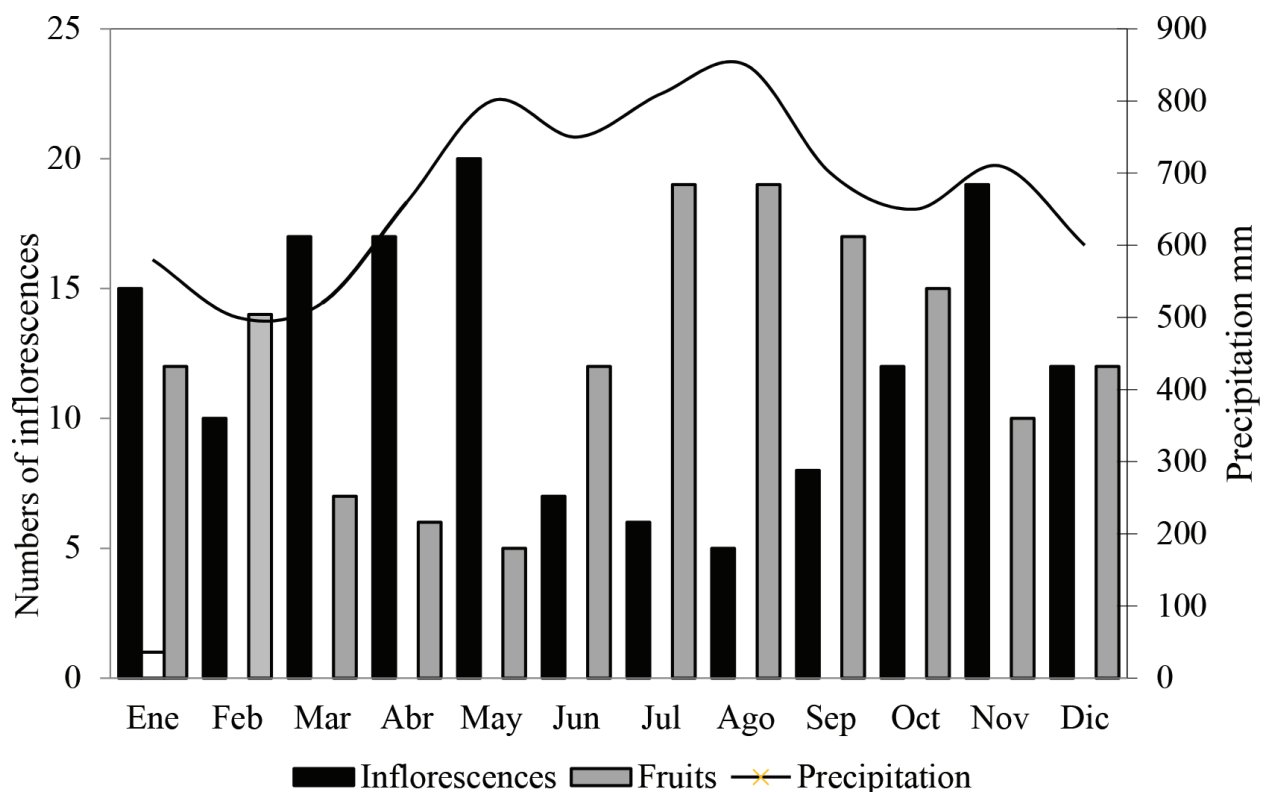


Figure 4. Monthly proportion of flowering and fruiting individuals of *Manicaria saccifera* compared with annual precipitation.

by a change of color from white to brown to black; (6) fruit formation, with maturation lasting approximately 15 months.

3.4. Reproductive system

Our controlled pollination treatments revealed that *M. saccifera* is strictly xenogamous. Thus, neither of the apomixis or auto-pollination treatments led to fruit formation. In contrast, with the open pollination and allogamy treatments the percentage of fruits (Table 1).

3.5. Floral visitors

The inflorescences of *M. saccifera* were visited by eight species of insects (Table 2), with a mean abundance of 716 ± 60 visitors per inflorescence ($n = 10$). *Mystrosp cercus* was the most abundant floral visitor and the only insect able to cross the two barriers imposed by the fibrous peduncular bract and the petals of the female flowers. It had the highest pollinator relative importance value, representing 99.9% of the pollination in *M. saccifera*. In contrast, the remaining species were occasional visitors with low abundances and were only present in the male-phase of the inflorescences. Among these frequent species were *Amazoncharis* sp.1 and *Xanthogypus* sp.1 (Staphylinidae).

Treatments	N° palms/ N°flowers	N° fruits/% set fruits
Apomixis(A)	5/410	0/0
Open pollination (OP)	5/410	225/62
Auto-pollination (AP)	5/410	0/0
Allogamy (AL)	5/410	220/53

Table 1. Percentage of fruits formed in *Manicaria saccifera* after four controlled pollination tests.

Floral visitors	AB	CTP	ETP	C	F	IVIP	IRIP
<i>Mystrops cercus</i>	560	1564	569	1	1	498,352,960	99.9
<i>Mystrops erviki</i>	12	156	234	0.25	1	109,512	0.021
<i>Trigona fulviventris</i>	23	669	245	0.05	0.5	94245.3	0.018
<i>Trigona ferricauda</i>	12	456	123	0.05	0.5	16826.4	0.003
<i>Derelomini</i> sp.1	12	123	12	0.25	0.33	1461.24	0.0002
<i>Xanthopygus</i>	34	167	32	1	0.33	59959.68	0.012
<i>Atheta</i> sp.1	12	23	12	1	0.33	1092.96	0.0002
<i>Amazoncharis</i> sp.1	123	12	12	1	0.33	5844.96	0.001
Total						498,641,903	100

AB: abundance in female phase, PTC: pollen-transport capacity in female phase, PTE: pollen-transport efficiency, C: constancy in the phase female, F: fidelity, PIV: pollinator importance value and PRI: pollinator relative importance value

Table 2. Role of visitor in the pollination of *Manicaria saccifera*.

4. Discussion

Results of the reproductive system indicate that self-pollination is unlikely because *M. saccifera* is a monoecious palm with unisexual flowers and anthesis time of the male and female phase do not match due to the type of protogynous dicogamia present. No fruit formation occurs via apomixis (**Table 1**), and the probability of geitonogamy is low due to the non-coincidence of two inflorescences in anthesis in the same individual; however, if the two inflorescences in anthesis manage to coincide, fertilization is prevented by the self-incompatibility found. And because the anthers and stigma remain covered avoiding pollen dispersion by wind anemophilia is unlikely to occur. Consequently, the non-presence of apomixis, the non-occurrence of self-pollination, the degree of self-incompatibility found and the fact that no wind pollination occurs, determine that *M. saccifera* should be considered a xenogamous palm, dependent on insects for pollination.

Cross pollination apparently works well in *M. saccifera* as open-pollination and allogamy testing showed 62 and 53% of fruit formation, respectively (**Table 1**), such efficiency indicates the importance of pollinators as carriers of pollen between individuals in the population, given the obligatory xenogamy of the palm. Cross-pollination is efficient despite that the pollination mechanism that occurs in *M. saccifera* is atypical to what usually happens in palms, in which visitors insects have full access to the flowers. In *M. saccifera* the peduncular bract keeps hidden and isolated male and female flowers, and only *Mystrops cercus* can cross the peduncular bract when the stigmas are receptive, the rest of the insects that are attracted at this time cannot enter; they do it in male phase when receptivity has passed and focus their activity in male phase.

The fact that the peduncular bract does not open preventing access to a group of insects, mainly larger than 2 mm, becomes a selective filter that limits free access of insects into the inflorescence at a critical moment in the reproduction of the palm. Large insects like bees (Apidae) or with larger sizes cannot cross the peduncular bract, while small insects or smaller than 2 mm, are the only ones who can access the flowers when they are receptive.

The peduncular bract acts as a barrier or selective filter that restricts access of large insects to female flowers at the most important time for fertilization, but is not the only one: those insects that may cross the first barrier are immediately faced with a second barrier and therefore a second filter, this time generated by the petals of the female flowers which do not open completely either and only two small slots of 1–2 mm are the space between the petals that insects may use to enter the flower, access the stigma and deposit the needed pollen to fertilize each flower of the inflorescence. Consequently, the bract that covers the inflorescence and the petals of the female flowers become two barriers that act as filters for selecting by size the type of pollinator in *M. saccifera* and only *Mystrops cercus* is the insect that passes through the filters and access the stigma that are hidden for the rest of the visitors.

Keep flowers hidden at the time of anthesis is a rare phenomenon in palms, presented only in other species of the genus *Pholydostachys* (personal observation), which have a fibrous small peduncular bract similar to *M. saccifera* and insects must pass through at the time of anthesis in a yet unknown mechanism. The closest thing to the selective filter imposed by the

peduncular bract occurs in some palms species of the genus *Attalea* in which as at the time of anthesis the peduncle bract leaves only a small slit that acts momentarily as a filter, but over time the bract exposes most of the flowers and insect access is complete [9].

In angiosperms the mechanism of pollination where flowers are not exposed and the androe-cium and gynoecium are hidden at the time of fertilization is rare but still occurs in several plant families and this type of pollination is called cleistogamy [27]. Cleistogamous plants are usually hermaphroditic, self-compatible and the release of pollen and stigmatic receptivity occurs at the same time therefore self-pollination and autogamy are predominant [28], freeing themselves from dependence on pollinators. Although *M. saccifera* reproductive structures remain hidden, cleistogamy is unlikely because the palm has unisexual flowers, with temporal phase separation and high values of self-incompatibility, therefore highly dependent on insects to fertilize the flowers.

The selective filter imposed by the peduncular bract of *M. saccifera* really influences the access of floral visitors as evidenced by the fact that the diversity of insects found within the inflorescence was low (only eight species). Comparing the rate of visitors to palms with characteristics similar to *M. saccifera* as size, rewards offered, type and location in the forest, these are visited by great diversity of visitors; for example, in *Oenocarpus bataua* [10] reported 81 species; *Phytelephas macrocarpa* is visited by 45 [29], as *P. seemanii*; and *Astrocaryum mexicanum* is visited on average by 35 species [30].

Therefore, the mechanism of isolating the reproductive structures and to have selective barriers can bring advantages and disadvantages for *M. saccifera*. Among the disadvantages, access by insects is limited and therefore the options of species that can act as pollinators is reduced, which may limit pollen flow with consequent pollination problem [31]. It has often been suggested that plants that display their flowers can attract more visitors and potential pollinators than those with few exposed flowers [32] and thus the pollination probabilities increase. Moreover, the filters presented in *M. saccifera* can bring advantage in the fact that there is a real selection of insects that prevents the entry of those who have little part in pollination, and thus an antagonist interaction with the palm, generating actions that directly or indirectly affect the reproductive success of the species. This phenomenon of insects that are not involved in pollination of palms is very common and widely reported for other species, where only a small number of visitors is actively involved in pollination and most visitors focus their activities exclusively on male stage or male flowers [9, 10, 33–35].

The low diversity of visitors generated by the selective filters in *M. saccifera* is balanced by an intimate and exclusive association of the palm with its main pollinator *Mystrops cercus*, which has easy access to the inflorescence through the selective filters and deposits pollen with efficiency values reaching 99% of the pollen transported and used for fertilization of the flowers of the palm (**Table 2**), ensuring fertilization of flowers and thus a constant fruit production. The pollination mechanism present in *M. saccifera* with *M. cercus* as main pollinator is summarized in a general model of pollination (**Figure 5**).

Because *Mystrops cercus* depends *M. saccifera* flowers as an ideal environment for feeding with pollen, protection (isolated flowers) and an ideal microenvironment to develop part of their life cycle due to the thermogenesis of the flowers, such association entails the

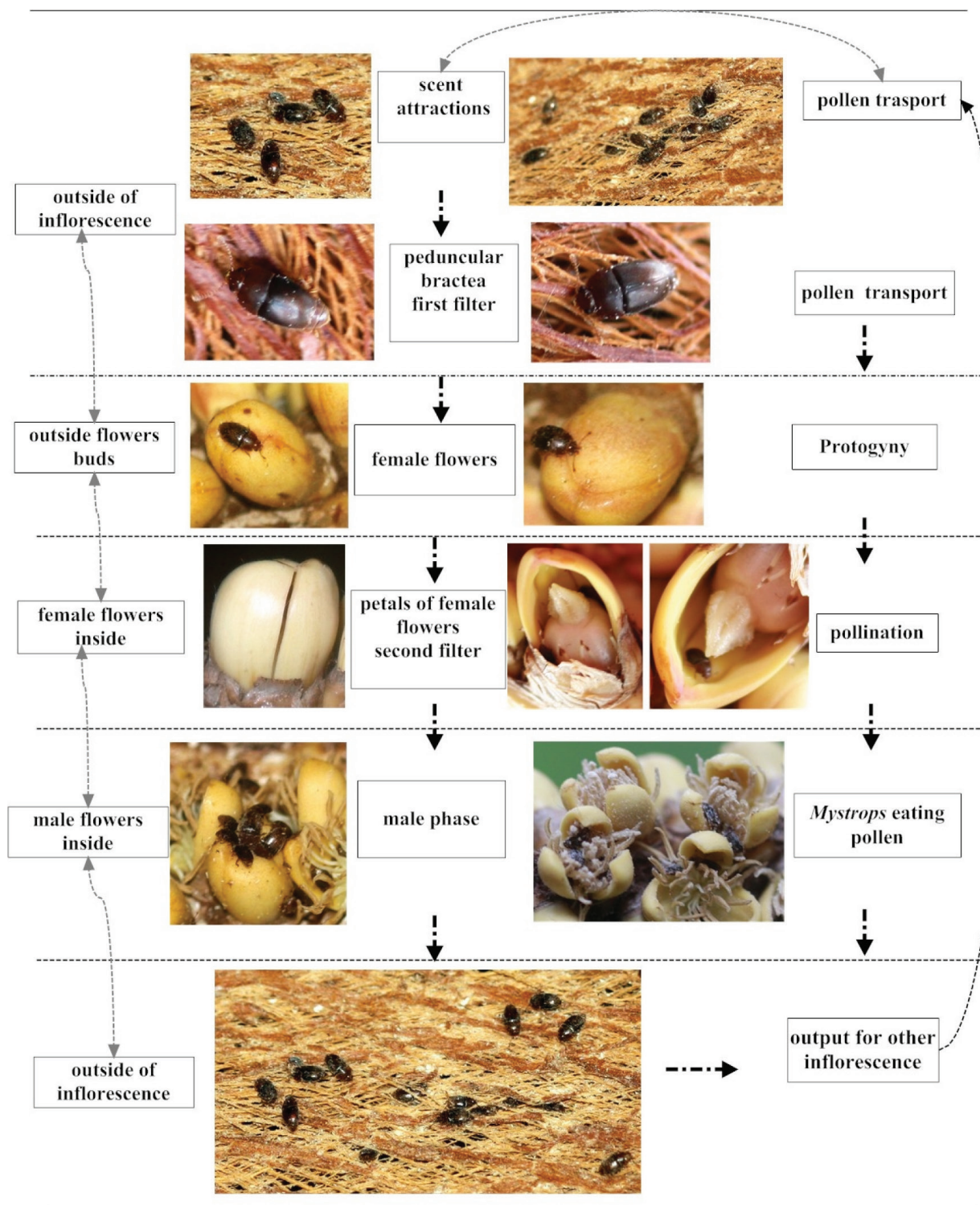


Figure 5. Pollination of *Manicaria saccifera* by *Mystrops cercus*.

establishment of a relationship of mutual dependence or obligatory mutualism between the palm and its pollinator. In that mutualism, pollinators need the palm they host for food, find a mate, make their life cycle; while for the palm the benefit of having a close relationship with the pollinator ensuring their loyalty, perseverance and efficiency in pollen transfer necessary to achieve reproduction.

Obligate mutualisms *Mystrops* - *Palmae* are more and more recognized, sometimes in one-to-one relations as in *Attalea allenii* [9, 36, 37]; or a *Mystrops* species associated with several species of the same genus of palms as with *Mystrops rotundula* and *Mystrops pulcra*, which pollinate seven species of the genus *Ceroxylon* [36]. The mutual dependency between *Mystrops cercus* and *M. saccifera* ensures reproductive success of the palm and the permanence of pollinators through the coordination of several mechanisms of association including attraction, maintenance and fertilization of flowers by their primary pollinator *Mystrops cercus*, this leads us to suggest that a high degree of specialization exists between *Mystrops cercus* and *Manicaria saccifera*, which has also been reported in other palm species pollinated by *Mystrops* species [1, 7–9, 21, 36, 38]. Likewise, two additional evidences can support the degree of specialization found and suggested in this paper: specificity and distribution of interaction.

Regarding specificity [36] conducted a comparative study of *Mystrops* species in at least 80 species of palms including *Mystrops* species visiting and pollinating flowers of palms found in the Chocó (*Attalea allenii*, *Attalea cuatrecasana*, *Oenocarpus bataua*, *O. minor*, *Socratea exorrhiza*, *Wettinia quinaria* and *M. saccifera*), and found that species of pollinators are not shared: each palm has its own association with a particular *Mystrops* species. In terms of distribution, we have found *Mystrops cercus* in five additional locations to our study area.

Participation of the genus *Mystrops* in the pollination of palms has been amply demonstrated, whether acting as principal pollinators, secondary or co-pollinators [9, 30, 34]. However, to the extent that detailed reproduction studies of tropical palms increase, species of the genus *Mystrops* are showing greater relevance and importance as pollinators of palms: one or more species of *Mystrops* are the most important pollinators, and in some cases, are the solely responsible for the movement of pollen in a particular palm species, e.g., *Mystrops* sp. nov. 1 in *Attalea allenii* and *Mystrops* sp. nov. 2 in *Wettinia quinaria* [9], *Mystrops* sp. in *Mauritia flexuosa* [37], *Mystrops* sp.15 in *Wettinia praemorsa*, and *Mystrops* sp. nov. 22 in *Cryosophila kalbreyeri* (Núñez [36]) *Mystrops* in *Wettinia kalbreyeri* [39].

In synthesis, *M. saccifera* presents a specialized pollination system with morphological barriers that blocks access of floral visitors when the stigmas are receptive, and is closely associated with *Mystrops cercus*, a kind of small beetle that, in an exclusive way, visits and pollinates the flowers of this important palm with morphological constraints. The most striking examples of highly specific mutualism relationships and close interdependence between plants and pollinating insects are given in cases where the flower morphology limits the visitor access to reproductive or floral rewards structures and consequently the possibilities of pollination are minimal, *M. saccifera* is a clear example.

We recommend further studies, mainly focused on evaluating features like the changes in time and if this mutual dependence is maintained throughout the disjunctive distribution of the palm.

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