

Pollination and breeding system of a neotropical palm *Astrocaryum vulgare* in Guyana: a test of the predictability of syndromes

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ABSTRACT. A pollination and breeding system study was conducted on a neotropical palm, *Astrocaryum vulgare*, in Guyana, South America, to better understand its reproductive character evolution, and test the predictability of pollination syndromes. The pollination syndrome approach was used because it integrates characteristics of flowers and their pollinators into an evolutionary framework that allowed experimental testing of predictions. The flowers of *A. vulgare* displayed traits that were typical of both beetle and wind pollination syndromes. The protogynous inflorescences produced heat and odour during nocturnal anthesis, had numerous stamens with copious, light pollen, and were visited by hordes of beetles that used the inflorescences as feeding, mating and oviposition sites. In contrast, some of these features, such as numerous stamens with copious, light pollen, a high pollen to ovule ratio, and no obvious production of visitor rewards, were also typical of the wind pollination syndrome. However, floral rewards appeared to be tissues of the fleshy staminate petals and pollen that were readily devoured by the beetles. In addition to the Coleoptera, insect visitors to *A. vulgare* inflorescences included several species of Hymenoptera, Diptera and Orthoptera. However, only Nitidulidae and Curculionidae beetles were effective insect pollinators. Pollination treatments showed that wind pollination was possible, but fruit set was significantly higher for female flowers visited by beetles. Although a pollen/ovule ratio of 50 000:1 and outcrossing index confirmed an outcrossing breeding system, pollination experiments suggested that *A. vulgare* had the potential for self pollination. Therefore, the breeding system might be best classified as facultatively xenogamous (cross fertilizing). The predictive value of potential pollinator agents for *A. vulgare* was inadequate because its floral traits were indicative of both cantharophilous and anemophilous pollination syndromes.

KEY WORDS: anemophilous palm, cantharophilous palm, Coleoptera, Curculionidae, Nitidulidae, outcrossing index, pollination syndrome, xenogamous breeding system

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INTRODUCTION

The elucidation of relationships between major pollinators of a plant species and certain structural and functional floral features has led biologists to define pollination syndromes that serve to predict potential pollinators based on floral traits (Faegri & van der Pijl 1979, Herrera 1996, Howe & Wesley 1988, Johnson & Steiner 2000). Pollination syndromes are suites of flower traits, such as morphology, colour, nectar, relative amounts and type of pollen, and odour, that attract specific pollinators to particular flowers, permitting those pollinators to forage at the exclusion of other visitors that would usurp floral resources without effecting pollination (Faegri & van der Pijl 1979, Howe & Wesley 1988, Johnson & Steiner 2000, Proctor *et al.* 1996). Pollination syndromes imply specialization between plants and pollinators, but the match between pollinator and floral characteristics is often loose and not so specific as to exclude other agents or animal taxa from visiting and pollinating the flowers (Herrera 1996, Howe & Wesley 1988, Johnson & Steiner 2000, Waser *et al.* 1996).

Few pollination systems are so specialized that only one pollinator can effect fertilization (Faegri & van der Pijl 1979, Howe & Wesley 1988, Johnson & Steiner 2000, Waser *et al.* 1996). Thus, caution must be taken in extrapolating probable pollinators for plants based solely on the knowledge of blossom classes and floral traits (Johnson & Steiner 2000, Ollerton 1998, Pauw 1998, Wyatt 1983). Recently, pollination syndromes have attracted rigorous scrutiny because they might be unreliable tools for inferring the current pollinators of plant species in the absence of empirical data (Fishbein & Venable 1996, Herrera 1996, Johnson & Steiner 2000, Ollerton 1998, Ollerton & Watts *in press*, Waser *et al.* 1996). Moderate generalization in pollination for angiosperms appears to be the rule, with many species pollinated by a range of animal taxa (Herrera 1996, Johnson & Steiner 2000, Ollerton 1996, Renner & Feil 1983, Waser 1983). Additionally, the range of pollinators may vary over the course of a species' flowering period or between seasons (Fishbein & Venable 1996, Herrera 1996, Waser *et al.* 1996).

Palms (Arecaceae) are an ancient group of flowering plants with primarily tropical distributions, and the family includes adaptations to pollination by wind, beetles, bees, flies, other insects and bats (Cunningham 1995, Ervik *et al.* 1999, Henderson 1986, Silberbauer-Gottsberger 1990, Whitmore 1993). Despite their economic and ecological significance, the pollination and reproductive biologies of only a few of the 2780 species of palms (Whitmore 1993) have been studied (Henderson 1986, Silberbauer-Gottsberger 1990). For more than a century, palms were considered primarily wind pollinated because they fit the anemophilous pollination syndrome – production of numerous, small flowers with copious amounts of light pollen, few ovules per flower, and flowers exposed beyond bracts (Henderson 1986, Schmid 1970a, b; Silberbauer-Gottsberger 1990). Now insect pollination is considered widespread in palms, even though most palm pollination studies have been entirely observational,

lacking any experimental tests for wind or self pollination (Beach 1982, 1984; Bullock 1981, Essig 1971, Henderson 1986, Listabarth 1996, Schmid 1970a, b). Many palms are visited by a diversity of insect taxa including bees and flies, but several species appear specialized for pollination by beetles (Anderson *et al.* 1988, Burquez *et al.* 1987, Henderson 1986, Silberbauer-Gottsberger 1990). The cantharophilous (beetle) pollination syndrome is typified by relatively large, mechanically strong flowers that emit heat and odour, are protogynous and have numerous stamens, fibrous pistillate structures and fleshy staminate petals (Gottsberger 1990, Henderson 1986, Silberbauer-Gottsberger 1990, Uhl & Moore 1977).

Astrocaryum vulgare Martius is a neotropical palm that is a good candidate for plantation cultivation to supply edible and industrial oils for Guyana, South America (N. Chandarpal, *pers. comm.*). However, nothing is known about its pollination or breeding systems. Thus, as part of a goal to understand the ecological interactions of the biota of white-sand environments (expansive deposits of the eroded and leached sands from the Pakaraima Mountains that cover 25 800 km² or 12% of Guyana's surface to depths of 80 m; Bernard 1999), a pollination and breeding system study of *A. vulgare* was conducted in coastal Guyana. In this study, we employed the pollination syndrome approach to test the aforementioned expectations of the cantharophilous and anemophilous pollination syndromes to evaluate the usefulness of syndrome classification as a predictor of specific categories of pollinator agents. Observational and experimental methods were also used to investigate the breeding system and test the effectiveness of pollinator agents.

STUDY SPECIES

Astrocaryum vulgare (Arecoideae: Cocoeae; Uhl & Dransfield 1987) is a neotropical monoecious palm distributed from Mexico south to Brazil and Bolivia, but it is absent from the West Indies except on Trinidad (Uhl & Dransfield 1987). The Guyanese name for *A. vulgare* is awarra or ocherie, while tucuma is used in other parts of northern South America (Kahn & Millan 1992). *Astrocaryum* is ecologically varied, with species occurring from the undergrowth of primary lowland forest, to light-demanding secondary forests or forest margins (Uhl & Dransfield 1987). In Guyana *A. vulgare* was frequently found in white sand savanna communities and in disturbed lowland forests or near human settlements (Kahn & Millan 1992, G. R. Bourne *pers. obs.*). *Astrocaryum vulgare* is a medium-sized palm, occurring in clusters of a few to several stems, reaching a height of 9 m, and armed with numerous unequal, flattened black spines up to 12 cm in length (Boer 1965). The palm's inflorescence consists of a rachis about 1 m long, bearing approximately 30 000 staminate flowers and 600 pistillate flowers enclosed in bud by a large, heavily spined bract (Figure 1). Each inflorescence bears about 200 rachillae up to 25 cm in length, and each rachilla produces about 150 staminate flowers, 3–4 mm long, on the distal half of a

rachilla, and two to four pistillate flowers, 1.2–1.5 cm long, on the proximal half of the rachilla (Boer 1965, Henderson 1995, Kahn & Millan 1992; Figure 1). The stigmas are at their maximum receptivity when they are creamy-white and covered by fluid droplets (Essig 1971, Henderson 1984, Scariot *et al.* 1991). After the stigmas become brown and withered they are no longer receptive (Essig 1971, Henderson 1984, Scariot *et al.* 1991).

Astrocaryum vulgare is similar in morphology to *A. aculeatum* (Boer 1965), and the two species are connected by morphological intermediates thought to be the result of hybridization (Boer 1965, Uhl & Dransfield 1987). At our study site *A. vulgare*, *A. aculeatum* and a hybrid locally known as areapipi were present. These palms bloom in February–March (end of the short dry season) and again in May–July (during the long wet season) in Guyana (G. R. Bourne, *pers. obs.*).

STUDY SITE

The pollination biology of *A. vulgare* was studied from 15 May to 20 August 1997 on a population located approximately 1 km east of CEIBA Biological Center, Inc. (06°29'57"N, 58°13'06"W), on the Soesdyke-Linden Highway, Guyana. The 2-ha study site was an abandoned slash-and-burn farm on white podsolized sands with a stand of *A. vulgare*, *A. aculeatum* and their hybrids covering about 1.25 ha. The study plot was bordered by a seasonally flooded *Mora excelsa* rain forest and dry muri scrub habitat (Hughes 1947). Detailed

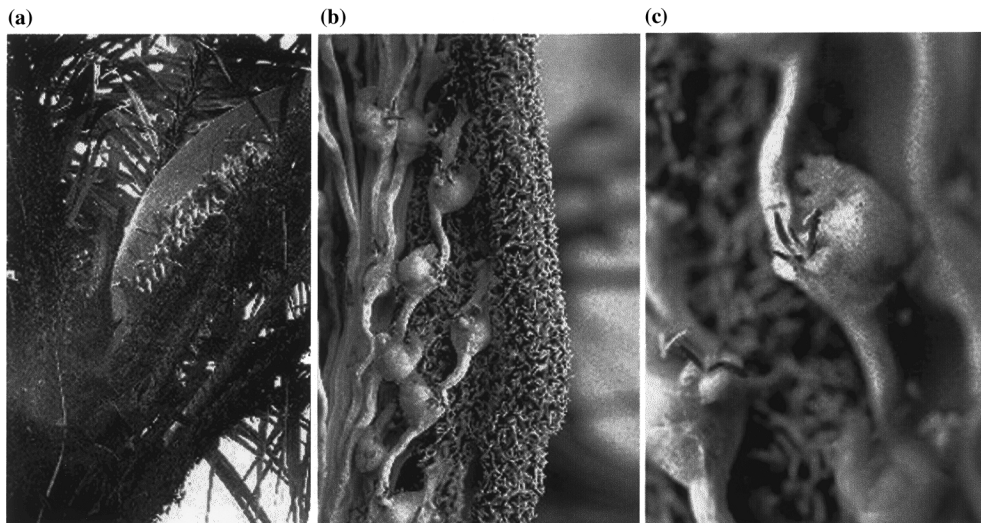


Figure 1. (a) Newly opened inflorescence of *Astrocaryum vulgare* showing its relationship to leaf petioles. At this time female (pistillate) flowers were receptive to pollen but male (staminate) flowers were not releasing pollen; (b) spatial relationship of the proximately attached pistillate (foreground) to the distally located staminate flowers during the second day of anthesis. The staminate flowers were liberating pollen, while pistillate flowers were unreceptive to pollen; (c) close-up of a receptive pistillate flower with its swollen ovary in the background. From colour slides by Godfrey R. Bourne.

descriptions of climate, geology, and flora and fauna of coastal locations in Guyana are available in Hughes (1947), Snyder (1966), and ter Steege (1993).

METHODS

Floral morphology and phenology

Thirty mature *A. vulgare* individuals were marked with numbered aluminium tags; detailed observations were made on 18 of these palms over the entire study period. Inflorescences were accessed by a 7.6-m extending ladder that was secured to the stem of the palm with rope. Daily observations were made in the morning, afternoon and on some nights. Time of bract opening, period of stigma receptivity, period of pollen liberation, odour diffusion, heat production, abscission of flowers, and qualitative changes in colour and presence/absence of droplets of fluid exudates on stigmas were noted. Pollen liberation was tested by dusting anthers with a number one watercolour brush and through qualitative direct observation of the amounts of pollen carried on insect visitors' bodies. Three plant voucher specimens of *A. vulgare* were made by TKC and deposited in the Missouri Botanical Garden (MO), the Smithsonian Institution (US) and the National Herbarium of Guyana (BRG).

Cruden's (1977) method was applied to *A. vulgare* by making direct counts of pollen from vouchers of three stamens from three different male flowers on one rachilla. The mean number of pollen grains per stamen was then estimated (Boer 1965), and used to calculate the total number of pollen grains for one rachilla. Ovaries of *Astrocaryum* species contain three ovules (Uhl & Dransfield 1987), and each rachilla bears two to four female flowers (Boer 1965, T. K. Consiglio & G. R. Bourne, *pers. obs.*; Figure 1). Therefore, a conservative approach was taken and the total number of ovules per rachilla was determined by multiplying the number of ovules per female flower by four. The pollen/ovule ratio (Cruden 1977) was then determined by dividing the estimated number of pollen grains by the number of ovules for one rachilla.

Thermogenesis, or heat production, was measured for four inflorescences just prior to and immediately following opening of the bract, and again the following morning when pollen was available. Temperatures were recorded by a Reotemp digital TM99-A thermometer (Reotemp Instrument Company, San Diego, California) through three small holes drilled into the boat-shaped bract just prior to its opening. Ambient air temperature was recorded immediately after the bract measurements. Temperatures of individual female and male flowers were also measured during receptivity and anthesis by touching the thermometer probe against them. Statistical comparisons for the differences between flower temperatures and corresponding ambient air temperatures were made using paired t-tests (Sokal & Rohlf 1995). Mean differences between flower temperature and air temperature for each floral stage were compared using a single factor analysis of variance (ANOVA) model, and the

contrasts for the means by the Tukey test (Sokal & Rohlf 1995). Descriptive statistics are given as mean \pm 1 SD in the Results section.

Floral visitors

Flower visitors were observed on 23 inflorescences 1-d-old to 4-d-old. Direct observations of visitor activity were made at least three times daily on 1-d-old to 3-d-old inflorescences ($n = 20$ d). These observations were made at 04h00–06h00, 09h00–12h00, 14h00–16h00 and on five occasions at 18h00–03h00. A red-filtered high-beam flashlight was used during nightly observations to minimize disturbance of insect visitors. Voucher specimens of insect visitors were taken from most of the inflorescences and stored in 95% ethanol, with the exception of Hymenoptera and Diptera, which were preserved in cresol. Voucher specimens of insects were made by TKC and deposited in the Natural History Collection of the University of Missouri-St. Louis. After 3 y we still await expert identifications of the beetle and other unidentified insect visitors to *A. vulgare*.

Numbers of beetle visitors were categorically estimated as ‘low’ (1000–10 000 beetles), ‘medium’ (11 000–21 000 beetles), and ‘high’ (22 000–30 000 beetles) during each observation block, because their immense numbers precluded any direct counting without disturbance. These categorical estimates were based on a reference standard established when we counted 15 000 beetles on a 2-d-old open inflorescence that was bagged at 07h30. This number was then used as an estimate for medium density. Direct counts provided estimates for Hymenoptera and Diptera during each observational block, because they occurred in much lower numbers. In addition, records were made of the type of activity, position on the inflorescence, and flower parts visited for all types of visitors during each observation period. These observational data were then associated with different receptivity stages of the inflorescences.

Pollination treatments

In May and June 1997, eight large but still closed inflorescences on eight different palms were randomly chosen and each covered with a long paper bag with a clear plastic window. The micro-perforated paper bags permitted gas exchange, and the plastic window allowed light to reach inflorescences but excluded all invertebrate visitors, thereby preventing contamination prior to pollination treatments. Insect visitors prior to treatment contaminated two of the inflorescences and another was used exclusively for voucher specimens of flower parts and visitors.

A randomized block design (Sokal & Rohlf 1995) was used to apply four different treatments to each inflorescence, using four flowers per treatment. Since thousands of insects congregated on the paper bags that enclosed each newly opened bud, we wiped off the paper bags with Vaseline and applied our treatments while the insects were dispersed. The number of flowers/treatment was limited by our ability to treat and bag individual pistillate flowers before

the dispersed clouds of insect visitors returned to the inflorescences. The following experimental treatments were performed: (1) cross-pollination (pollen from an inflorescence on a different palm was dusted on the stigmas of the female flowers), (2) self pollination (pollen from the same inflorescence was dusted on the stigmas of the female flowers), (3) wind pollination (pollen bags made of porous cloth that excluded insect visitors but permitted access of pollen grains were placed over pistillate flowers), and (4) insect pollination (natural pollination by insect visitors with no human manipulation of female flowers). Four female flowers received each treatment in each inflorescence (block), resulting in a sample size of 128 flowers (4 flowers \times 4 treatments \times 8 inflorescences). The block design was used to reduce the effects of environmental factors that might affect fruit set within individual stems. The pollination treatments were performed immediately after bract opening for each inflorescence (06h00–08h00), except for the self-pollination treatments, which were performed shortly after pollen liberation on the second morning (07h00–10h00). Fruit set was evaluated 14–21 d later. Apomixis was not tested, because Burquez *et al.* (1987) found that it did not occur in a congener, *A. mexicanum*.

Statistical comparisons of the pollination treatments were made by fitting a linear logistic regression model, and by the method of maximum likelihood (Cox & Snell 1989, Hosmer & Lemeshow 1989). Each treatment was classified as a univariate indicator variable, and proportional odds ratios were calculated. Wind pollination treatment was set as the reference variable in the model, because it resulted in the lowest fruit set. Thus, the odds ratios for the other three treatments have values > 1 relative to the wind pollination treatment (Cox & Snell 1989, Hosmer & Lemeshow 1989). The significance of an overall block effect was tested using the logistic regression model, but due to the constraint of small sample size the effects of treatment/block interactions could not be determined.

RESULTS

Floral biology

In 1997, flowering began in late April and extended through August. *Astrocaryum vulgare* individuals from our study population bore 1–4 inflorescences (mean = 2.17 ± 0.94 , $n = 24$ palms) during the 3-mo study period. Individual stems never had more than one actively flowering inflorescence at a time ($n = 30$ inflorescences). At the population level, flowering was continuous throughout the study period, because on average at least one inflorescence opened per day (0.96 ± 0.6 , $n = 31$ days).

Heat production was detected inside inflorescences just prior to opening, with elevations up to 14.4 °C above ambient air temperature (13.6 ± 0.6 °C, $n = 4$; Table 1). Pistillate receptivity in *A. vulgare* began early in the morning (Table 1) when the peduncular bract opened. Female flowers had higher than ambient air temperatures at this time (1.7 ± 0.7 °C, $n = 4$; Table 1) and a faint

musky odour was detected during the first 10 h after bract opening. Female flowers had stigmas that were creamy-white and dewy for a period of 16 h, after which they became increasingly dry and turned brown ($n = 18$ inflorescences).

Male flowers opened early in the morning (Table 1) of the second day, and released pollen; at this time female flowers were dry and yellowish-brown. Male flowers also had temperatures higher than ambient air during the first few hours of pollen liberation (2.9 ± 0.9 °C, $n = 4$; Table 1). Pollen liberation occurred primarily during the first 12 h after male flowers opened, with smaller quantities of pollen available up to 24 h later. Staminate flowers opened synchronously in less than 3 h. Male flowers began to abscise on the morning of the third day after the bract opened. All inflorescences showed a 3-d cycle in which receptive females were exposed during the morning of the first day of bract opening, male flowers opened and began releasing pollen during the morning of the second day, and male flowers began to drop to the ground on the morning of the third day. Male flowers continued dropping on the fourth and fifth days. Thus, on any given morning, flowering inflorescences were in one of two distinct phases, with either receptive female flowers and closed male flowers, or with mature male flowers that were liberating pollen. The overall difference between flower and air temperature for all three floral stages (immediately prior to bract opening, female anthesis and male anthesis) differed significantly from each other (ANOVA, $F = 318$, $P < 0.01$; Table 1).

One stamen produced about 500 ± 100 pollen grains ($n = 3$ stamens), thus with their six stamens, each male flower produced approximately 3000 pollen grains. There were 200 male flowers on one rachilla so we estimated 600 000 pollen grains per rachilla. The maximum number of ovules per rachilla was 12 (3 ovules \times 4 female flowers). Therefore, the pollen/ovule (P/O) ratio for *A. vulgare* was 50 000:1. An outcrossing index (OCI; Cruden 1977) was also determined from the sum of assigned values based on three characteristics of the flower: width of the corolla, temporal separation of anther dehiscence and stigma receptivity, and spatial separation of stigma and anthers. With regard to its OCI, corolla width of *A. vulgare* was 2–6 mm, it was protogynous, and the spatial relationship of its anthers and stigmas precluded contact.

Table 1. Flower and ambient air temperatures (mean \pm 1 SD) for four inflorescences taken immediately prior to bud opening, and at individual flowers at the beginning of female receptivity and male anthesis, CEIBA Biological Center, Guyana, 15–20 August 1997.

Phenology	Temperature (°C)		Time of day	Paired t-test
	Flower	Ambient air		
Inflorescence just before opening	36.5 \pm 3.3	22.9 \pm 3.8	05h00–06h00	46.1*
Female receptivity	24.5 \pm 4.0	22.9 \pm 3.8	04h00–06h00	4.99*
Male anthesis	25.3 \pm 2.4	22.4 \pm 0.6	03h00–05h00	6.16*

* $P < 0.01$.

Floral visitors

Table 2 lists the insect visitors to *A. vulgare*. During the morning when a bract opened, about 30 000 Nitidulidae (sap beetles) were present at an inflorescence. Nitidulidae were always present in high numbers on both first- and second-day inflorescences, and engaged in copulation. Coleoptera were common visitors to inflorescences (Table 2), and provided evidence of pollen transport because individuals obtained from flowering inflorescences deposited pollen on the walls of glass vials when placed in them. The highest density of beetles was on first-day inflorescences, immediately after bud opening at 06h00 until 12h00, and again after sundown at 18h00. Nitidulidae copulated on both male and female flowers, as well as fed and oviposited on male flowers during all periods of visitation. Low numbers (< 1000 per inflorescence) of Curculionidae (snout beetles) were present on stigmas and ate petals and pollen of male flowers in both first- and second-day inflorescences. Medium numbers (11 000 to 21 000) of Coleoptera were present breeding on the inflorescence for the first 2–3 h after pollen liberation on the second day. Beetle larvae were found in tissues of several male flowers not yet fallen on two 3-d-old inflorescences.

Minor visitors to inflorescences included a few (1–10) Diptera. These oviposited on the closed male flowers on first-day inflorescences, but were never observed on female flowers. Other minor visitors included Hymenoptera that foraged on male flowers in both first-day and second-day inflorescences. No insects ate female flowers, but fed on the inner surfaces of petals on closed male flowers. However, damage appeared superficial in most cases and did not appear to affect the subsequent opening of male flowers or release of pollen. About 50–100 Hymenoptera visited male flowers early on the morning of the second day (n = 23 inflorescences). Bees never came in contact with female flowers while carrying large pollen loads, and they were therefore pollen thieves. Bee activities were limited to foraging on male flower tissue and pollen. A few (1–5) wasps were observed foraging on pollen and inside male flowers

Table 2. Insect visitors and their relative abundance on *Astrocaryum vulgare* inflorescences growing on an abandoned slash-and-burn farm at CEIBA Biological Center, Guyana, May–August 1997.

Order	Family	Species	Relative abundance ²
Coleoptera	Nitidulidae	3 species ¹	Very common
	Curculionidae	1 species ¹	Common
	Chrysomelidae(?)	1 species	Rare
Hymenoptera	Apidae	<i>Trigonia fuscipennis</i>	Common
	Apidae	<i>Trigonia lurida</i>	Common
	Apidae	<i>Apis mellifera</i>	Common
	Vespidae	<i>Polybia</i> sp. ¹	Common
Diptera	Tephritidae(?)	1 species ¹	Rare
Orthoptera	Unknown	1 species ¹	Rare

(?) unsure about taxon.

¹ Unidentified.

² Very common = 1000s, common = 50–100, rare = < 20 individuals.

on inflorescences 1–3 d old. Ants were occasionally present on 1–4-d-old inflorescences, primarily foraging on closed male flowers and walking along the outside of the peduncular bract and along rachillae. Ants attacked Coleoptera, and inflorescences with ants had fewer than half as many Coleoptera visitors as those inflorescences without ants. Hymenoptera and Coleoptera continued to feed at the inflorescence until after dark on the second day. By the morning of the third day, only wasps were present, apparently foraging for beetle larvae in the not-yet-fallen male flowers. On the fourth day, inflorescences lost most of their male flowers and were visited by only a few wasps (2–6).

Pollination treatments

Results of the pollination treatments are summarized in Table 3. Fruit set was evident to the naked eye within 14 d. The joint effect of treatment on fruit set was statistically significant ($P = 0.04$). The joint effect of block on fruit set was also significant ($P < 0.01$); however, further elucidation of the relationship between block and treatment was constrained by small sample size (Table 3). The slope coefficient for insect pollinated flowers was significantly different from zero ($F_{1,31} = 6.34$, $P = 0.01$), and the slope coefficient for cross-pollinated flowers approached significance ($F_{1,31} = 3.08$, $P = 0.08$). However, slope coefficients for both wind-pollinated and self-pollinated flowers were not significantly different from zero ($F_{1,31} = 0.12$, $P = 0.72$; $F_{1,31} = 0.25$, $P = 0.62$, respectively). Nevertheless, 47% of wind-pollinated flowers and 53% of the self-pollinated flowers set fruit. Odds ratio estimates indicated that relative to wind pollination, self-pollinated, cross-pollinated and wind-plus-insect-pollinated flowers were 1.3, 2.5 and 4.0 times more likely to set fruit, respectively (Table 3).

Table 3. Percentage of *Astrocaryum vulgare* flowers that set fruit following experimental treatments ($n = 32$ flowers each) in coastal Guyana. Differences among treatments were revealed by linear logistic regression using the method of maximum likelihood. The 2 log L score was significant ($P = 0.04$) for the joint effect of treatments on fruit set. Since wind pollination produced the fewest fruit it was used as the reference variable. Thus, odds ratios were estimated relative to fruit set for wind pollination.

Pollination treatment	% fruit set	Wald Chi-Square	P	Odds ratio
Wind	47	0.13	0.72	–
Experimental Self	53	0.25	0.62	1.28
Experimental Cross	69	3.03	0.08	2.49
Beetle and wind	78	6.34	0.01	4.05

DISCUSSION

Floral biology of the beetle pollination syndrome

Flowers predominantly pollinated by beetles typically exhibit specialized characteristics defining the beetle pollination syndrome including cream-coloured flowers, protogyny, temperature elevation, musty odour and nocturnal staminate anthesis (Henderson 1986). For example, beetle-pollinated plants from diverse taxa such as *Philodendron selloum* (Araceae), *Carludovica palmata*

(Cyclanthaceae), the giant water lily, *Victoria amazonica* (Nymphaeaceae), and the lotus lily, *Nelumbo nucifera* (Nelumbonaceae), are nocturnally thermogenic, odoriferous, protogynous, produce numerous stamens, and have a 2-d anthesis (Armstrong & Irvine 1989, Gottsberger 1977, 1990; Seymour & Schultze-Motel 1997, Young 1986). Beetle pollination syndromes in *C. palmata*, *V. amazonica*, *Dieffenbachia longispatha* (Araceae), *Myristica insipida* (Myristicaceae), and *Cyclanthus bipartitus* (Cyclanthaceae) are also comparable in their nutritious rewards of petals, sepals, trichomes and pollen to their beetle visitors (Armstrong & Irvine 1989, Beach 1982, Gottsberger 1977, 1990; Young 1986). The floral biology of *A. vulgare* conformed to the beetle pollination syndrome: the inflorescences produced heat during nocturnal anthesis, were protogynous, odour was released at the beginning of anthesis, anthesis lasted 2 d, flowers were cream-coloured and numerous stamens were produced. Moreover, beetles used inflorescences as feeding and mating sites. Beetle larvae found in several male flowers on two inflorescences suggested that these visitors were also using inflorescences as oviposition sites.

Heat production in *A. vulgare* may have served to attract beetles to an open inflorescence through volatilization of floral odour during anthesis (Ervik *et al.* 1999, Knudsen *et al.* 1993, Pellmyr & Thien 1986, Schroeder 1978). We detected a faint musky odour up to 10 h after female anthesis. Thermogenesis may also play a role in maintaining high metabolic rates in beetle visitors, encouraging fast pollen deposition during the initial period of visitation that corresponds to the period of maximum stigma receptivity. Floral odour may work in a similar fashion by stimulating the sexual activities of the beetle visitors (Gottsberger 1977, Knudsen *et al.* 1993, Pellmyr & Thien 1986), resulting in pollen deposition onto receptive stigmas. Additionally, a significant increase in temperature measured in male flowers during the early morning of staminate anthesis suggests an effective way of warming up the beetles so that they can fly at lower metabolic cost to a female-phased inflorescence (Burquez *et al.* 1987, Heinrich & Bartholomew 1979).

Baker & Hurd (1968) suggested three criteria for assessing the effectiveness of floral visitors as pollinators: (1) the presence of the visitor in both sexual stages of the flower; (2) transport of pollen on the visitor's body in a manner that effects contact of that pollen with a receptive stigma; and (3) determining whether excluding the visitor from the flower results in reduced fruit set. Despite the visitation to *A. vulgare* by several other insect taxa (Table 2), Coleoptera were the exclusive pollinators of this palm. An effective pollinator must, in the course of its activities, transport pollen to receptive stigmas. This requirement eliminated all of the visiting Hymenoptera and Diptera species that were observed only on male flowers and behaved as pollen predators, while the reproductive and foraging behaviour of beetle visitors led to a transfer of pollen to the stigmas during female anthesis. Coleoptera species were present at both female and male phases during periods of receptivity and behaved in

a manner that effected pollen transfer from their bodies to stigmas. Pollen liberation in a male-phase inflorescence preceded female flower maturation on a different inflorescence by about 1–2 h.

Visitor numbers and diversity for *A. vulgare* were much lower than those reported for *A. mexicanum* (Burquez *et al.* 1987), but similar to those for *Bactris* spp. (Beach 1984). Habitat structure may be a factor in the low diversity of insect visitors we observed for *A. vulgare* compared to those reported for *A. mexicanum*. Isolation from primary forest may limit the diversity of insect fauna (Armstrong & Irvine 1989). However, the most common beetle pollinators of palms belong to two families, Nitidulidae and Curculionidae (Henderson 1986). We found Nitidulidae in high numbers (20 000 to 30 000) at the beginning of pollen liberation, and at the beginning of female anthesis, Nitidulidae were also present in high numbers carrying pollen on their bodies. Pollen-carrying Curculionidae were observed in low numbers (50–100) during both sexual phases of an inflorescence. The relative abundance of pollen-carrying Nitidulidae observed during both sexual phases of an inflorescence made these beetles the most likely insect pollinators of *A. vulgare*; second in importance were the Curculionidae.

Floral biology of the wind pollination syndrome

Wind pollination has long been attributed to many palm species because they fit the wind pollination syndrome – numerous, small flowers, and production of copious amounts of light pollen (Schmid 1970a, b). Other morphological characters interpreted as adaptations to wind pollination include a high pollen/ovule ratio, rapid discharge of pollen, hermaphroditic flowers and protandry (Faegri & van der Pijl 1979, Uhl & Moore 1977). Many palm pollination studies rule out anemophily based on floral characteristics and the presence of insect pollinators, but few experimental studies have been done (Henderson 1986, Silberbauer-Gottsberger 1990). Although the slope coefficient for the wind pollination treatment was not significantly different from zero in this study, 47% of the wind-pollinated flowers set fruit. Additionally, pollen dispersed into the air whenever inflorescences were touched, there was a rapid discharge of pollen upon initial opening of the male flowers, and the inflorescences had a high pollen/ovule ratio of 50 000:1. These morphological characteristics and the results of the pollination treatments suggested *A. vulgare* also employed wind pollination. However, the percentage of fruit set that resulted from wind pollination treatments may have been increased indirectly by beetles carrying pollen on their bodies as they moved across the mesh exclusion bags. Note that mesh size in bags used to allow wind-borne pollen penetration was initially tested by shaking pollen from one rachilla over the opening of a glass vial covered by cloth that was used to construct bags. This test indicated that pollen freely penetrated the cloth mesh as evidenced by pollen deposited in the vial. Insect visitors were unable to penetrate the wind pollination bags. However,

this did not exclude the strong possibility that our beetle pollination treatments inherently included wind blown pollen (J. Ollerton *pers. comm.*), thus producing an additive effect for wind and beetle pollination (Table 3).

Our study plants live in an open-canopied, windy habitat of an abandoned slash-and-burn farm. *Astrocaryum vulgare* is frequently found in white-sand-savanna communities and disturbed forests (Boer 1965, Henderson 1995). Anderson *et al.* (1988) reported that the babassu palm, *Orbignya phalerata*, exhibits a similar dual pollination system in which wind-pollinated flowers set more fruit in open savanna than those in closed forest. Similarly, Scariot *et al.* (1991) reported wind pollination in *Acrocomia aculeata* as most likely favoured in open environments. Burquez *et al.* (1987) did not test for wind pollination in *Astrocaryum mexicanum*. However, given its occurrence in the understorey of closed canopy rain forest where wind is less prevalent and more obstructions are present, wind pollination may have been unimportant.

Breeding system

The results of pollination treatments, P/O ratio and OCI classification for *A. vulgare* indicated that it was an outcrossing species that employed some degree of self pollination. Fruit set occurred in 53% of the flowers that were artificially self pollinated. However, three lines of evidence suggested that cross pollination was favoured in *A. vulgare*: (1) the flowers were protogynous with the female and male phases well-separated temporally; (2) only one inflorescence matures on a palm at the same time; and (3) artificial self-pollination treatments produced reduced fruit set compared to cross-pollinated flowers. The relatively high percentage of fruit set in the artificially self-pollinated flowers may also be influenced by applying larger quantities of pollen to stigmas than would naturally have occurred (Bawa 1979, Burd 1994). In fact, supplemental hand pollination increased female fertility in 62% of 258 studies reviewed by Burd (1994). This led to the conclusion that, contrary to expectation from marginal values (*sensu* Haig & Westoby 1988), pollen usually appears to limit female fertility (Burd 1994). Nevertheless, natural self pollination was possible in *A. vulgare*, because the female and male phases overlapped for 6–8 h within an inflorescence. Burquez *et al.* (1987) reported self-fertilization in *A. mexicanum* but noted that fruit set is significantly lower for self-pollinated compared to cross-pollinated flowers. Moreover, the high P/O ratio of 50 000:1 and OCI designated *A. vulgare* as facultatively xenogamous.

Predictive value of pollination syndromes in Astrocaryum vulgare

The floral biology of *A. mexicanum* apparently fits the classic beetle pollination syndrome, but Burquez *et al.* (1987) showed that both beetles and flies pollinate this species. Classifying this species as strictly cantharophilous based on its 'specialized' floral characteristics highlights the danger of inferring putative pollinators without empirical evidence (Johnson & Steiner 2000, Ollerton

1998). Furthermore, a palm species does not have to exhibit floral characteristics of a cantharophilous pollination syndrome to be pollinated by beetles. For example, the palm, *Butia leiospatha*, exhibits the typical bee pollination syndrome features of protandry, yellow flowers, nectar production, and fragrance; yet, it is pollinated by species of Nitidulidae and Curculionidae beetles as well as bees (Silberbauer-Gottsberger 1990).

A combination of insect and wind pollination has been known for some time in several palm cultigens (Beach 1984, Sholdt & Mitchell 1967, Syed 1979). The floral biology of *A. vulgare* has aspects that exemplify the beetle pollination syndrome. However, observations and pollination experiments indicated a dual mode of beetle and wind pollination for this palm species. According to J. Ollerton (*pers. comm.*) this was not surprising since an unpublished multidimensional scaling analysis of classical pollination syndromes, similar to Figure 1 in Ollerton & Watts (2000), indicated close proximity between wind and beetle syndromes. Thus, beetle and wind pollination could evolve from each other more readily than bee and wind pollination syndromes (J. Ollerton, *pers. comm.*). In any case, this dual pollination strategy by *A. vulgare* probably enhanced its reproductive success under a broad range of ecological conditions. The combination of wind and beetle pollination may be important for palm species in open, low density habitats where strong wind currents are prevalent (Anderson *et al.* 1988, Silberbauer-Gottsberger 1990, Whitehead 1983). The mixture of traits in *A. vulgare* and other angiosperm species illustrates the imprecise nature of the syndrome concept (Johnson & Steiner 2000, Wyatt 1983). Thus, the predictive value of potential pollinator agents for *A. vulgare* was inadequate because its inflorescences exhibited floral traits found in both cantharophilous and anemophilous pollination syndromes.

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