SEXUAL SYSTEM AND POLLINATION ECOLOGY OF *CARDIOSPERMUM HALICACABUM* L. (SAPINDACEAE)[1]

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Cardiospermum halicacabum is a weed perennating through rootstock, and also reproducing through seed. it produces inflorescences on long peduncles in leaf axils in acropetal succession. The inflorescence is a trichasial compound cyme, each cyme consisting of three flowers. Only one flower of a cyme antheses at a time, not necessarily in sequence, reflecting a 'steady state' pattern of flowering. Flowers are either staminate or pistillate, and at any given time both types occur on a plant, facilitating geitonogamy. *C. halicacabum* is also cross-compatible, and the small number of flowers opening daily and limited nectar production compel the floral visitors, both bees and wasps, to fly from patch to patch, thereby accomplishing xenogamy. The wasps *Rhynchium* sp. and *Vespa* sp. are particularly more mobile and assume greater importance as cross-pollinators. The small, white flowers with a yellow nectar guide exhibit wasp flower syndrome. The sexual system with options for both geitonogamy and xenogamy enables this twining weed to survive in changing environments.

INTRODUCTION

The information available on the reproductive ecology of Sapindaceae is limited. The studied species include both Neotropical and Paleotropical members. *Cupania guatemalensis* bears first staminate, then usually pistillate and finally staminate flowers; the temporal separation of sexual phases largely facilitates outcrossing. It is primarily pollinated by species of *Trigona* in Costa Rica (Bawa 1977). *Urvillea ulmacea* is self-compatible and temporally dioecious and pollinated by bees in secondary tropical forests in Venezuela (Zapata and Arroyo 1978). *Sapindus emarginatus* exhibits temporal dioecism with the same sequence of sexual phases as that of *Cupania guatemalensis*. It is geitonogamously pollinated by bees and flies and xenogamously by wasps and butterflies in India (Subba Reddi *et al.* 1983). *Litchi chinensis* also exhibits temporal dioecism and is pollinated by insects in India (Khan 1929). Cruden (1988) reports that temporal dioecism may be a common sexual system in Sapindaceae.

Cardiospermum is another genus in Sapindaceae consisting of 23 species. The species are herbaceous tendrilar climbers and distributed chiefly in tropical America and Africa. Two species have been reported to occur in India, *C. halicacabum* and *C. canescens* (Cooke 1902; Anonymous 1950). There appears to be no published reports on the reproductive ecology of the members of this genus. The present study describes the sexual system and pollination ecology of *Cardiospermum halicacabum* which is a major component of the ground vegetation which thrives during the rainy season in the study area. Besides, it has some medicinal value. The root is used as a diuretic, laxative, and for treating rheumatism and nervous diseases. The leaf juice is used as ear drops to cure ear ache and foul smell in the ear. The leaves are rubbed with castor-oil and applied externally as a paste to reduce swellings and tumours (Thammanna and Narayana Rao 1990).

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Material and Methods

The dense patches of *Cardiospermum halicacabum* L. found along roadsides, fallows and at the peripheries of the degraded scrubland in Visakhapatnam (17° 42' N Long and 82° 18' E Lat.), Andhra Pradesh, India were studied. After witnessing the flowering season, observations on the phenology of flowering at population, individual and inflorescence levels were made. To determine inflorescence flowering phenology, 25 mature inflorescences were tagged to record the daily anthesis rate and the duration of flowering life. As this species bears staminate and pistillate flowers within the same inflorescence, their numbers were separately counted each day. From these numbers, the sex ratios for the inflorescence and for an individual plant were arrived at. Whether the anthesis of the staminate and pistillate flowers overlapped or not have also been observed at different phases of flowering. The daily anthesis schedule, anther dehiscence time, mode of dehiscence, determination of pollen production, pollen-ovule ratio, duration of pollen viability and stigma receptivity, flower life-time, nectar secretion, breeding systems, natural fruit set rates, etc., were examined using the methodology given by Aluri and Subba Reddi (1994). The flower visitors were captured and identified by tallying them with specimens already identified by Commonwealth Institute of Entomology, London. Foraging activity, foraging behaviour, forage resources sought, and foraging efficiency of the visitor species were thoroughly observed.

Results

Plant flowering phenology: This is a herbaceous vine reproducing sexually by seed and asexually by vegetative growth. The seeds germinate soon after the southwest monsoon showers in June; they germinate and grow vegetatively at a rapid pace. Perennating rootstock remains underground and becomes active, producing vegetative growth and/or flowering vigorously, as soon as moisture is available in the soil. After 2-3 weeks of vegetative growth, they gradually produce inflorescences and initiate flowering in the 1st week of June. Once flowering begins in the mature inflorescences, it continues until all flowers are anthesed. With the periodic rainfall during the monsoon, new branches originate from the stem and produce new leaves and inflorescences. With the addition of new inflorescences, vigorous blooming in an individual plant extends to November/December. Plants in wet soil flowered even to the end of January. In such soils, the seeds produced in July germinated in the same season, produced a few leaves and immediately started flowering. Within 2-3 weeks, they terminated flowering and withered. Flowering is not observed on days preceded by heavy rains. The inflorescences which completed flowering quickly produced fruit in about 15 days. Soon after fruit production, the fruit-bearing parts become dry. Thus the plant bears some withered branches and some branches in either vegetative phase or flowering phase at the same time. The total duration of the flowering of an individual plant lasts for 8-9 months. The plants in an area and in different areas come to bloom nearly at the same time.

It is observed that summer rains in April/May also trigger seed germination and subsequent vegetative growth and flowering. Once the plants begin vegetative growth as a response to summer showers, they continue to grow due to subsequent monsoon showers or rain in June.

Inflorescence flowering phenology: The plants produce trichasial compound cymes in the axils of leaves. Each trichasial cyme is subtended above by a pair of tendrils. In a trichasial compound cyme, each cyme bears 3 flowers, and altogether 9 flowers are produced. Once flowering in a trichasial cyme starts it produces 1 or 2 flowers a day until all 9 flowers are anthesed. Within a 3-flowered cyme, only one

flower matures at a time. The flowering life of a trichasial cyme is 5-6 days.

Flower morphology and sexuality: The staminate and bisexual flowers are morphologically identical except for the essential organs. The flowers are small (5 mm), pedicellate, white and odourless. The calyx is light green and has four sepals arranged in two rows. The outer two are small while the inner ones are twice as large as the outer ones; all sepals are regulose and concave. The calyx is persistent, even after fruit maturation in bisexual flowers. The corolla is white and contains four obovate petals. They are free and arranged alternately with the sepals; each petal is 2.0-2.5 mm long. Additionally, there are four scales originating inside the petals and covering the vertically held staminal complex/ovary from the base to the top. The two anterior scales are fused to 1/4 of their length from the base and are villous to glabrous. The scales are white except for the apex, which is yellow and quite prominent at a distance to attract flower-visitors. Further, the apices have an appendage which is white, deltoid, villous and deflected towards the anthers situated on the posterior side. The two posterior scales are completely white, free from the base to the top and sparsely villous to almost glabrous giving the appearance of a hood sheltering the staminal complex. These scales do not possess the appendage. Androecium constitutes 8 stamens in both flower types. They are free, aggregated and hooded by the posterior scales. The stamens are of three different lengths. In staminate flowers, the longer three stamens are 2.5 mm long, the two medium stamens 2.0 mm and the three shorter ones 1.5 mm long. All three lengths of stamens are 0.5 mm less and not aggregated in bisexual flowers. In bisexual flowers, the gynoecium consists of a 3-carpelled syncarpous ovary with a short style having 3 stigmas. Each carpel has one locule containing one ovule. The ovary is 3-lobed, obcordate and densely villous. The stigmas are white in colour like the anthers. At a glance, the stigmas give the impression that they are stamens. The stigmas become persistent crowning the fruit apex. There is a disc with 2 broad glands on the side of the posterior scales and two small glands on the side of anterior scales situated at the base of the flower in both staminate and bisexual flowers. This glandular disc secretes nectar and is fully protected by the closed vertical column formed by both anterior and posterior scales.

The stamens in bisexual flowers are not prominent because of their small size and attachment to the sides of the ovary lobes below. They possess pollen-bearing but non-dehiscing anthers. In staminate flowers, the stamens are prominent and possess pollen-bearing dehiscing anthers. Therefore, the apparently bisexual flowers are functionally pistillate, and hereafter mentioned like that. The plants are thus functionally monoecious.

Sex ratios: Each trichasial cyme produces both staminate and pistillate flowers; both flower sexes are produced within a simple cyme. In the simple cyme if the first flower is pistillate, the other two are staminate flowers; if the first one is a staminate flower, the other two are one staminate and the other pistillate. Both flower sexes were produced on the same day but on different cymes and within the same trichasial cyme. There is no staggering of sexual phases. The ratio of staminate versus pistillate flowers in a trichasial cyme is either 1.25:1 or 1:1.25 or 2:1. The first ratio is found in 50% of trichasial cymes, the second in 30% and the third in 20% of the cymes. At plant level, the ratio of staminate and pistillate flowers is 1.2:1 (Table 1). Overall, the observed ratio is biased in favour of staminate flowers. The ratios remained constant throughout the flowering period.

Anthesis and anther dehiscence: Both the flowers open, irrespective of their gender, during 0500-0900 hrs; with a higher frequency (65%) during 0500-0600 hrs at 29-32°C and relative humidity of 70-80% (Table 2). The anthesis is delayed on cool and/or cloudy days; the length of delay from the scheduled time is subject to

TABLE 1
NUMBER OF STAMINATE AND PISTILLATE FLOWERS ON DIFFERENT INFLORESCENCES IN *CARDIOSPERMUM HALICACABUM*

Inflorescence number	No. of flowers per inflorescence	Staminate flowers	Pistillate flowers
1	9	5	4
2	9	4	5
3	9	4	5
4	9	5	4
5	9	5	4
6	9	6	3
7	9	5	4
8	9	4	5
9	9	4	5
10	9	6	3

the degree of coolness, it ranged from 1 to 2 hours. In both flower sexes, anthesis starts with gradual unfolding of petals, which take about 35-40 minutes for complete unfolding. The vertical column comprising anterior and posterior scales and covering the stamen/ovary remains in the same position and the scales do not unfold during the entire period of flower life. In staminate flowers, the anthers dehisce by longitudinal slits an hour after anthesis.

TABLE 2
RATE OF ANTHESIS IN *CARDIOSPERMUM HALICACABUM*

Time (hrs)	No. of flowers anthesed	Anthesis (%)	Temperature (°C)	Relative humidity (%)
2200	—	—	30.5	82
2300	—	—	30.5	82
2400	—	—	30.5	78
0100	—	—	30.5	78
0200	—	—	30.5	76
0300	—	—	29.5	76
0400	—	—	29.0	80
0500	52	34	29.0	80
0600	48	31	30.0	78
0700	26	17	30.5	78
0800	19	12	30.5	76
0900	09	6	31.5	72
1000	—	—	32.0	70
1100	—	—	33.0	70

Nectar characters: The glandular disc present at the base of both staminate and pistillate flowers produces nectar in traces soon after anthesis and is protected by the vertical column formed by the scales.

Pollen characters: Pollen grains of staminate and pistillate flowers are the same except for the size and germinability/viability. Both grains are smooth on exine, without ornamentation, triangular and tricolpate, light and powdery. The size of the pollen grain in staminate flowers is 40-63 µm and that in pistillate flowers is about half of the size of the former. The pollen grains in the pistillate flowers are normally deformed.

The number of pollen grains per anther of staminate flowers averaged 360 (R 340-395), and that per flower came to 2880. In pistillate flowers, an anther produced an average of 175 pollen grains (R 160-188).

Pollen-ovule ratio: The anthers of pistillate flowers are indehiscent. Therefore, their pollen is not considered for calculating the pollen-ovule ratio. At the inflorescence level, the ratio of viable pollen grains (from staminate flowers) per single ovule is either 1200:1 or 768:1 or 1920:1. At the plant level, the P/O ratio is 6136:1.

Pollen viability: The pollen grains of staminate flowers are viable with anther dehiscence. They germinated well in 20-25% sucrose solution with 5 ppm detergent. Viability lasted for 24 hrs. The stored grains after 6 hrs showed 100% germination, after 18 hrs and 24 hrs showed 30% and 10% germination respectively. Thus, the grains appear to remain viable throughout the flower life (Table 3).

Although anthers of pistillate flowers do not dehisce, they were also tested for viability. The grains did not germinate in any of the sugar concentrations from 0 to 60% with or without detergent. Thus, the pollen grains in pistillate flowers are completely sterile.

TABLE 3
RESULTS OF *IN VITRO* OF POLLEN IN *CARDIOSPERMUM HALICACABUM*

Time (hrs)	No. of pollen grains observed	No. of germinated pollen grains	Germination (%)
6	50	50	100
12	40	28	60
18	35	10	30
24	30	03	10
48	25	0	0

Stigma receptivity: The stigmas of pistillate flowers attained receptivity by the time the anthers of staminate flowers release their pollen. The stigmas were viscid and shiny at this time and remained in that state for about 12 hrs. The stigma receptivity was also tested by fruit set. The fresh stigmas and also the 7 hrs old ones yielded 100% fruit set. The 10 hrs old stigmas produced 40% fruit set and 12 hrs old ones gave 10%. The stigmas which were 13 hrs old did not fruit. Therefore, the stigma receptivity in a flower lasted for 12 hours (Table 4).

TABLE 4
RESULTS OF *IN VIVO* STIGMA RECEPTIVITY IN *CARDIOSPERMUM HALICACABUM*

Time (hrs)	No. of stigmas pollinated	No. of flowers set fruit	Fruit set (%)
3	20	20	100
5	20	20	100
7	20	20	100
10	20	8	40
11	20	4	20
12	20	2	10
13	20	0	0

Breeding behaviour: The results of breeding experiments indicated that pistillate flowers do not produce fruit through apomixis. Geitonogamy and xenogamy operate, the former with 100% success and the latter with 66% (Table 5). As the staminate and pistillate flowers anthese at about the same time at the inflorescence level and plant level, geitonogamy is likely to occur. Xenogamy is also operative because the plants occurring in an area and in different areas come to flower nearly at the same time.

TABLE 5
RESULTS OF BREEDING EXPERIMENTS IN *CARDIOSPERMUM HALICACABUM*

Treatment	No. of flowers pollinated	No. of flowers set fruit	Fruit set (%)
Apomixis	30	0	0
Geitonogamy	30	30	100
Xenogamy	30	20	66

Natural fruit set: The intensity of fruiting varied in different phases of flowering. The rate of fruiting corresponds to the degree of foraging activity of the visitors. The fruiting in the initial phase was 80%, followed by 100% during the peak phase of flowering. The fruiting rate gradually declined from 75 to 45% towards the end of the flowering period (Table 6).

TABLE 6
NATURAL FRUIT SET RATES AT DIFFERENT PHASES OF FLOWERING IN *CARDIOSPERMUM HALICACABUM*

Flowering month	Flowers tagged	Flowers set fruit	Fruit set (%)
INITIAL			
July	20	16	80
PEAK			
September	20	20	100
November	20	15	75
FINAL			
January	20	9	45

Flower visitors: There were eight different species of insects foraging at both staminate and pistillate flowers (Table 7). These included bees, wasps, a fly and a butterfly. The species of foragers at two different sites were common between the two sites. But, species appearance at different phases of flowering at each site varied slightly. *Apis* and *Trigona* (bees), *Vespa* (wasp) and *Eristalinus* (fly) were evident throughout the flowering period at the two sites. *Ceratina* (bee)

TABLE 7
FLOWER VISITORS AND THEIR FORAGE TYPE IN *CARDIOSPERMUM HALICACABUM*

Visitor species	Forage type Nectar	Forage type Pollen	Region of contact with pollen/stigmas
HYMENOPTERA			
Apidae			
Apis cerana indica	+	+	Head and ventral side
A. florea	+	+	Head and ventral side
Trigona sp.	+	+	Head and ventral side
Ceratina sp.	+	+	Head and ventral side
Eumenidae			
Rhynchium metallicum	+	—	Head and ventral side
Vespidae			
Vespa sp.	+	—	Head and ventral side
DIPTERA			
Syrphidae			
Eristalinus quinquestratus	+	+	Head and ventral side
LEPIDOPTERA			
Lycaenidae			
Euchrysops cnejus	+	—	Proboscis, head and anterior body

TABLE 8
CENSUS OF FORAGERS ON *CARDIOSPERMUM HALICACABUM* DURING THE INITIAL, PEAK AND FINAL PHASES OF FLOWERING
(Flowers under observation 100 at each site)

Forager species	Site I			Site II		
	Initial	Peak	Final	Initial	Peak	Final
Apis cerana indica	250	440	283	300	480	100
A. florea	240	400	198	280	420	160
Trigona sp.	110	220	92	90	104	90
Ceratina sp.	45	80	31	40	56	0
Rhynchium metallicum	98	120	82	100	164	0
Vespa sp.	30	42	18	20	52	10
Eristalinus quinquestratus	10	12	12	28	48	16
Euchrysops cnejus	0	20	6	12	24	0

Site I: Wild habitat behind A.U.R.S. Hostel (WAURSH)
Site II: Wild habitat behind A.U. Healthcare Centre (WAUHC)

and *Rhynchium* (wasp) appeared during the initial and peak phases of flowering only. The unidentified butterfly species foraged at the peak and final phase of flowering at WAURSH site and at the initial and peak phase at the WAUHC site. Overall, the foraging visits of bee species were more than those of wasps, fly and butterfly species taken separately or collectively (Table 8).

The *Apis* species were the first to forage on either flower sexes. They commenced their foraging even before sunrise at 0530 hrs and continued upto 1100 hrs. They resumed from 1430 hrs and ceased by 1600 hrs. Their activity was very brisk during morning hours. *Trigona* and *Ceratina* nearly commenced their foraging activity at the same time from 0830 hrs onwards and ceased foraging by 1500 hrs with occasional visits during 1200-1330 hrs. The wasp species first appeared to forage at the flowers at 0830 hrs and continued until 1500 hrs. They were relatively more active during 0830-1100 hrs and made occasional visits at other times. *Eristalinus* foraged during 0800-1100 hrs and again during 1500-1600 hrs. The butterfly species was active from 0730 hrs foraging now and then until 1500 hrs; thereafter it ceased foraging.

Foraging behaviour: In both flower sexes, the yellow spots on the anterior scales appeared to serve as nectar guides for the flower visitors. Accordingly, the insect visitors approached the flower frontally by landing or hovering on the vertically held posterior scales sheltering the stamen/ovary. The bee species foraged for both nectar and pollen. For collecting nectar, they inserted their proboscids into the floral base from above on the side of anterior scales with yellow spots. After collecting nectar, they withdrew their proboscids from the flower. For collecting pollen, they first held the posterior scales with their legs and collected pollen from the dehisced anthers. In either case, the pollen got deposited on the lower part of the head and the entire ventral side of the bee body. When the medium sized *Apis* species landed and foraged, the flower swung and the insects probing activity resulted in the separation of vertically held scales to some extent. This facilitated collection of floral rewards very

easily by these bees. After the departure of these bees, the separated scales did not get back to their original position. Subsequent visits, 2 or 3, by these bees to such flowers led to the near complete removal of pollen in the staminate flowers and the deposition of pollen grains on stigmata in pistillate flowers. *Trigona* and *Ceratina* bees are small in size and their landing or probing behaviour did not result in the separation of scales in fresh flowers. They easily probed the flowers which were visited earlier by *Apis* species. The two wasp species approached the flower on the side of posterior scales and hovered while inserting their proboscides from above through the staminal complex touching the appendages of the anterior scales for collecting nectar. During collection, the ventral side of their body and the lower part of their head were dusted with pollen grains in staminate flowers and if they made subsequent visits to pistillate flowers, the pollen grains were transferred from their ventral surface to the stigmas, effecting pollination. While the wasps foraged at the flower, the scales were not separated to the extent in the case of foraging by *Apis* bees. The fly and butterfly species were ineffective in separating the scales, but both collected floral rewards without disturbing the flower and pollen grains were carried away on the head/ventral surface of the body in the former and on the proboscis, head, anterior/ventral side of the body in the latter. All visitor species moved between staminate and pistillate flowers within and between plants, the inter-plant movement rate varying with each group of insects. All these visitors foraged on both staminate and pistillate flowers without any discrimination.

Foraging efficiency: In a single visit, the bees and the flies collected nectar and pollen in staminate flowers; sometimes, only one reward, nectar or pollen per visit was collected. As the staminate flowers offered two floral rewards and the pistillate flowers only one, the flower visitors spent more time per flower in the former and less time for exploiting nectar in the latter. However, determination of length of time spent in each case became difficult because of morphological similarity of both flower sexes. In general, the time spent per flower by all species was 7-9 seconds except for *Trigona* which spent more time (11.5 seconds) than other visitors. In terms of mobility, the *Apis* species and the wasps were mobile and foraged 7-9 flowers in a unit time while the others foraged 1-2 flowers (Table 9). It indicated that honeybees and wasps are efficient in foraging and in their flight from one flower to another.

TABLE 9
FLOWERS VISITED PER MINUTE AND LENGTH OF A FORAGING BOUT IN SECONDS

Visitor species	Average no. of flowers foraged per minute	Average time spent per flower in seconds
Apis cerana indica	9.0	9.0
A. florea	7.0	8.0
Trigona sp.	1.5	11.5
Ceratina sp.	1.0	9.0
Rhynchium metallicum	7.0	8.0
Vespa sp.	8.0	7.0
Eristalinus quinquestratus	1.5	7.0
Euchrysops cnejus	1.0	8.5

Pollination: The complete overlapping of sex stages of a plant is clearly an adaptation favouring geitonogamy. The almost synchronous flowering in the plants of an area and in different areas provides possibilities for xenogamous pollination. The bees and the fly tended to stay on the same patch and infrequently moved between patches, while the wasps and the butterfly tended to move frequently between patches. This indicated that the bees and the fly are important for geitonogamy, while the wasps and the butterfly are more important for xenogamy.

DISCUSSION

Cardiospermum halicacabum is functionally monoecious. The plants appear annually

with the monsoon rains both from the perennial rootstock and from the seed produced after sexual reproduction. The rootstock gives rise to bushy growth while the seed gives rise to a plant which subsequently ramifies. Both forms produce trichasial compound cymes. A mature branch produces inflorescences in the leaf axils; it continues to produce inflorescences in the tender leaf axils. Thus, inflorescence production is in acropetal succession. After maturation and dispersal of fruits in these branches, secondary branches arise from below and they in turn produce inflorescences in acropetal succession. Such branching depends on the availability of moisture. During the dry periods, the mature active flowering branches are at a pause. Thus, depending on the moisture availability, flowering is seen at intervals. This is comparable to the 'episodic' flowering of certain plant species, *sensu* Bullock *et al.* (1983).

Inflorescence is a trichasial compound cyme and produces nine flowers, at the rate of three flowers per cyme, over a period of 5-6 days, and within a three-flowered cyme, only one flower antheses at a time, not necessarily in sequence. This pattern of producing a limited number or few flowers on a daily basis reflects the pattern of 'steady state' flowering, *sensu* Gentry (1974). At any time, both staminate and pistillate flowers are available on the plant, and the staggering of sexual phases which is supposed to be characteristic of Sapindaceae (Bawa 1977, Subba Reddi *et al.* 1983) was not seen. The co-occurrence of the two sexual phases on this functionally monoecious plant might be a strategy for geitonogamous reproduction. Experimental manipulation of selfing through geitonogamy has resulted in 100% fruit, showing that the taxon has adapted to selfing through geitonogamy.

C. halicacabum is a herbaceous twiner weed and a species by its occurrence in situations disturbed by man (Baker 1965). Certain characters are associated with weeds, among which those related to reproduction are: (1) low pollen/ovule ratio with self-pollination, and thus an economy of pollen production; (2) when cross-pollinated this is achieved by a non-specialised flower visitor or wind; and (3) very high seed output (Baker 1955, Mulligan 1965, Allard 1965, Cruden 1973). Mulligan and Findley (1970) found that all the annual weeds they studied were capable of selfing and concluded that selfing is of special adaptive value to annual weeds. Stebbins (1965) while studying the colonising species of the native Californian flora stated that the material he analysed suggested that for an annual weed species, the most adaptive condition is self-fertilisation and for a perennial obligate outcrossing is most often favoured by selection. Bentley (1979) based on her study of the role of heterostyly in the pollination and seed set of *Turnera trioniflora,* a roadside weed of the Amazon basin suggested that a high level of genetic heterogeneity is advantageous for tropical weed plants. The reproductive traits of *C. halicacabum* comply with the above cited weed characters.

C. halicacabum is also compatible to xenogamous pollination, if not of the same level as of geitonogamy, and such pollination in experiments yielded 66% fruit set. In plant species with a provision for outcrossing, the amount of legitimate pollen transfer decreases with each flower visited and 6-10 flowers is the maximum number that can be visited before all pollinations become geitonogamous (Levin *et al.* 1971). Therefore, a flowering strategy with a small number of flowers opening at a given time would maximise cross-pollination and hence fruit set (Cruden 1976). This strategy is adopted by *C. halicacabum* and enables it to achieve cross-pollination and cross-fertilisation with the attendant genetic variability. The small number of anthesed flowers and limited nectar production compel the flower visitors to move from patch to patch, thereby moving xenogamous pollen (Heinrich and Raven 1972, Cruden 1976). The two wasp species (*Rynchium* sp. and *Vespa* sp.) are particularly mobile, and assume importance as cross-pollinators. The small size of the flower

with white corolla, and a yellow nectar guide appear to correspond with the wasp pollination syndrome described by Heithaus (1979) and Faegri and van der Pijl (1979).

The hetergeneity of both physical and biotic factors over a local scale in both space and time is being increasingly recognised in tropical environments (Ashton 1969, Bentley 1979). Where environmental heterogeneity is high, it seems that selection would favour a sexual system which produces both the parental genotypes as well as genotypes "pre-adapted" to conditions different from those under which the parent germinated and established (Bentley 1979). The sexual system of the functionally monoecious *C. halicacabum* and its flowering strategy ensuring geitonogamy with possibilities for xenogamy attest to the above prediction.

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