PSYCHOPHILY AND EVOLUTIONARY CONSIDERATIONS OF *CADABA FRUTICOSA* L. (CAPPARACEAE)[1]

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Cadaba fruticosa is a perennial shrub, which flowers almost round the year. Floral characters, such as the opening of the flower during early hours of the day, green colour of the flower, a nectarial tube with good amount of nectar, and this tube along with the androgynophore and petals serving as landing place for the probing flower visitors, conform to psychophily.

C. fruticosa breeds through geitonogamy and xenogamy only, and the pollination is effected exclusively by pierid butterflies, namely *Colotis eucharis*, *C. danae* and *Anaphaeis aurota*. This study concludes that *Cadaba* and *Colotis* have co-evolved and any disturbance in the habitat is bound to affect both.

INTRODUCTION

Certain plant species possess highly specialized floral forms and structures associated with particular species of insect pollinators. Specialization nearly always tends towards enabling the plant to adapt to a limited range of pollinating insects. The specialized forms of plants develop through morphological adaptations over a period of time.

The specialized floral forms adapted to butterfly-pollination have been scantily reported in literature (Cruden and Hermann-Parker 1979, Dronamraju 1960, Dronamraju and Spurway 1960, Hawkswood 1985, Ilse and Vaidya 1956, Jennerston 1984, Khare 1975, Levin 1972, Reddi and Meerabai 1984). These workers showed that the butterflies could serve as efficient pollinators, because the floral forms are specialized for foraging exclusively by them.

In the present study, it was found that an adaptive relationship existed between the flowers of *Cadaba fruticosa* and the pierid butterflies i.e. both partners exhibit interdependency. Structural and functional aspects of *C. fruticosa* flower and the foraging details of pierid butterflies are presented and discussed from the perspective of psychophily and co-evolution.

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MATERIAL AND METHODS

Cadaba fruticosa plants growing wild near the Indira Gandhi Zoological Park at Visakhapatnam (17° 42' N and 82° 18' E) were observed periodically. The phenology of their flowering was recorded. To study the flower production and life of an inflorescence, the opening of flowers of 20 marked inflorescences were recorded every day. Floral events, such as flower opening and anther dehiscence were recorded through continuous observation. The nectar, accumulated in flowers covered with butter paper bags, was quantified using graduated micropipettes. Its sugar concentration and composition were determined by a refractometer and paper chromatography respectively. Presence of proteins and amino acids was determined by spot tests as per Baker and Baker (1973) Method. Number of pollen grains per anther, pollen viability, stigma receptivity and mode of reproduction, natural fruit set, seed set and fecundity were determined as per Aluri and Reddi (1994) and Aluri *et al.* (1998). BUTTERFLIES OF THE INDIAN REGION (Wynter-Blyth 1957) was used

to identify butterflies captured at flowers of *C. fruticosa*. The number of foraging visits made in a single foraging bout was recorded for each butterfly species, and number of visits per minute were counted using a stopwatch. The relative frequency of visits of different butterfly species was determined through censuses on different days at different plants. The behaviour of butterflies at the flowers was also noted carefully. The floral characters and foraging behaviour of butterflies were thoroughly examined for their adaptive relationship.

RESULTS

Flowering Phenology: It is a perennial shrub which flowers almost round the year. Flowering of different conspecific individuals is largely synchronous during the rainy season from June to September, and asynchronous during the rest of the year. Intense flowering occurs during the rainy season. The inflorescence is a fascicle with solitary and axillary flowers, and bears an average of 9 flowers that mature over 14-30 ($\bar{x}$ = 22) days. The mature flower buds that arise from the axial point do not all mature on the same day.

Flower Morphology: Flowers pedicellate, oriented horizontally. Thalamus elongated into a slender structure on which floral parts occur at different levels. Androphore is a part of the thalamus between the perianth and the stamens, whereas gynophore is present between the stamens and the gynaecium. The entire structure is known as an androgynophore. Additionally, there is a nectar-secreting tubular structure separated from the base of the androgynophore. Four free sepals arranged in two whorls of two each (two median sepals in the outer whorl and two inner sepals transverse). Four free, clawed petals arranged in one whorl alternate with the four stamens. Gynaecium raised up on a prominent gynophore, bicarpellary, syncarpous, unilocular, with an average of 11 ovules arranged on the parietal placentation.

Floral Events: Flowers begin to open slowly from 0130 hrs and proceed to unfold the sexual organs in about 2½ hours. The flowers with exposed sex organs are available from 0345 hrs onwards on sunny days and an hour later on cloudy and rainy days. Anther dehiscence occurs after sunrise at 0730 hrs in flowers under sunshine, and an hour later in flowers which are in shade. The pollen grains are spheroidal with psilate exine, separable into two size classes, 28 µm and 19.4 µm. Their number per anther ranged from 7,870-8,240 ($\bar{x}$ = 8,080). *In vivo* tests showed that the pollen grains remain viable for 27 hours after anther dehiscence; the grains stored for 15 hours have 80% fruit set. Pollen-ovule ratio is 3000:1. In the early flower-life, the style and stigma are curving while the dehisced anthers stand erect. Gradually, the stigma uncurves, stands erect and attains equal height with the stamens at 1100 hrs and remains so till the flower withers. *In vivo* tests showed that the stigma receptivity lasts for 89 hours. The nectar secreting tubular structure secretes 5 µl of nectar during the life of the flower. The sugar concentration of the nectar varied from 18 to 26%. It contained three common sugars — sucrose, glucose and fructose, in that order of dominance. The nectar also contained amino acids with a histidine score of 5.5 and proteins. The stamens dropped off after 36 hours, sepals and petals after another 36 hours. Then the stigma gradually withered and dropped off 20 hours later. The nectar harbouring tubular structure remained throughout fruit formation and fell off subsequently.

Breeding behaviour: Hand-pollination tests for the modes of breeding showed that the plant does not breed through autogamy but through geitonogamy and xenogamy; geitonogamy is less successful than xenogamy (Table 1). The fruiting success rate in open-pollinated flowers is limited, compared to the success rate of hand-pollinated flowers (Table 2).

TABLE 1
RESULTS OF BREEDING EXPERIMENTS FOR *CADABA FRUTICOSA*

Treatment	No. of flowers pollinated	No. of flowers set fruit	No. of ovules set seed	Fruit set (%)	Seed set (%)	Fecundity (%)
Autogamy	25	0	0	0	0	0
Geitonogamy	25	21	126	84	54	46
Xenogamy	25	23	207	92	82	75

TABLE 2
NATURAL FRUIT, SEED AND FECUNDITY RATES IN *CADABA FRUTICOSA*

Study area	No. of flowers observed	Fruit set (%)	Seed set (%)	Fecundity (%)
Outside Zoo Park	145	14	76	16
Inside Zoo Park	189	5	58	3
Interiors of Zoo Park	98	15	93	8

TABLE 3
PERCENTAGE OF BUTTERFLY SPECIES VISITS TO *CDABA FRUTICOSA* FLOWERS

Date of observation	Mean temp.	Mean relative humidity	*Colotis eucharis*	*Colotis danae*	*Anaphaeis aurota*
Oct. 1, 1999	28.3	67	70	20	10
Nov. 18, 1999	25.6	74	73	13	14
Nov. 30, 1999	25.2	83	91	7	2
Dec. 11, 1999	24.3	68	90	8	2
Apr. 9, 2000	25.6	83	49	19	32

TABLE 4
PROBOSCIS LENGTH OF DIFFERENT BUTTERFLY SPECIES VERSUS NECTARIAL TUBE LENGTH OF *CADABA FRUTICOSA*

Butterfly species	No. of samples	Mean (mm)	Nectarial tube length (mm)
Colotis eucharis	5	17	
C. danae	5	17	10
Anaphaeis aurota	5	20	

Flower-visitors and pollination: The pierid butterflies *Colotis eucharis*, *C. danae* and *Anaphaeis aurota* are the exclusive foragers on *Cadaba fruticosa*. They foraged for nectar from 0630-1500 hrs, with intense activity between 0900 and 1200 hrs. Of these, *Colotis eucharis* is the most frequent and regular forager and made an outstanding percentage of visits during the study period. *C. danae* came second, and made more visits than *A. aurota* (Table 3).

Colotis eucharis and *C. danae,* with an average proboscis length of 17 mm each and *A. aurota* with an average proboscis length of 20 mm probed and succeeded in obtaining the nectar from the nectarial tube (Table 4). To obtain the nectar, butterflies land on the nectarial tube itself or the androgynophore or petals. In this case, they landed mostly on the androgynophore. Contact between anthers and stigma, and the wings of foraging butterflies takes place if they use the androgynophore or nectarial tube; even this contact is achieved only when the gynaecium is erect and stands parallel to the level of the anthers. No such contact is made if the butterflies land on the petals. Examination of the 119 foraging visits of butterflies to the 20 open flowers indicated that wing contact with the anthers and stigma was made in only 66 and 47 visits respectively, while in 6 visits no contact was made with either. The butterflies visited an average of 2-4 flowers per foraging bout. *C. eucharis* foraged more flowers per minute compared to *C. danae* and *A. aurota* (Table 5). All three butterfly species foraged flowers of different conspecific plants very frequently. Only those visits where there was contact between the stigma and anthers resulted in pollination. Since the plant lacks autogamy, such visits are required to bring about either geitonogamy or xenogamy.

TABLE 5
TIME SPENT BY THE BUTTERFLIES AT THE FLOWERS OF *CADABA FRUTICOSA*

Butterfly species	No. of flowers visited in a single bout ($\bar{x}$)	No. of visits per minute ($\bar{x}$)	Average time spent per flower (sec)
Colotis eucharis	4.0	6.5	1.2
C. danae	2.0	4.6	2.0
Anaphaeis aurota	2.3	3.3	3.1

DISCUSSION

Butterfly pollination has been reported in *Rhianthus hirsutus* (McLean and Cook 1956), *Asclepias syriaca* (Percival 1965), *Phlox* species (Grant and Grant 1965, Levin and Berube 1972), *Dianthus* and *Gymnadenia* (Proctor and Yeo 1972), *Anguria* (Gilbert 1975), *Platanthera ciliaris* (Smith and Snow 1976), *Caesalpinia pulcherrima* (Cruden and Hermann-Parker 1979), *Cnidoscolus urens* (Bawa *et al.* 1983) and *Tridax procumbens* (Balasubramanian 1989). In *Cadaba fruticosa* also, floral characters such as opening of the flower during daytime, production of a good amount of nectar, a separate nectar-hosting tubular structure, and a nectarial tube, androgynophore and petals providing a platform for landing, all conform to psychophilous pollination syndrome *sensu* Meeuse and Morris (1984).

C. fruticosa exhibits weak protandry and the anthers are viable for a short period when compared to the lengthy duration of stigma receptivity. This floral sexual behaviour facilitates autogamy for a brief period; but hand pollination tests showed the absence of autogamy. Further, the hand pollination tests performed for geitonogamy and xenogamy showed that the plant is capable of breeding through these two modes of reproduction, xenogamy being more successful. The study of breeding behaviour reveals that pollen flow between flowers of the same or conspecific plants is imperative for geitono- or xenogamous pollination.

The flowers of *C. fruticosa* with psychophilous characters have been observed to be foraged and pollinated exclusively by three pierid butterfly species, namely *Colotis eucharis*, *C. danae* and *Anaphaeis aurota*. The foraging behaviour, mobility rate and foraging frequency of these three butterflies were seen to effect geitono- and xenogamous pollination, and on this basis, these butterflies may be treated as exclusive pollinators. However, *C. eucharis* with its greater foraging frequency is a dominant pollinator. The nectarial tube of the flower is perfectly tailored to the length of the butterfly's proboscis, enabling *C. eucharis* to withdraw the nectar easily while excluding other flower-visitors. Although the flower is exclusively suited for butterfly pollination, butterflies do not effect pollination in each visit. Of the total visits, only 40% effect pollination, 55% carry pollen and 5% simply deplete nectar. The butterflies contact the stigma and anthers with their wings only, and this contact is directly related to the place of landing on the nectarial tube, androgynophore and petals, and also to the relative position between them. The butterflies effect pollination or carry pollen only if they use either the nectarial tube or the androgynophore. Even this pollination is effected only when the gynaecium is erect and stands parallel to the level of the anthers. These limitations, and the observed foraging frequency of butterflies, are bound to influence natural reproductive success. The natural fruit set, seed set and fecundity rates recorded in the study are in tune with the above observations. Nevertheless, and whatever be the limitations, *C. fruticosa* is an excellent example of psychophilous pollination syndrome.

C. fruticosa flowers almost throughout the year and the butterflies forage on this plant all through the year for their nectar requirement, while occasionally foraging on associated plant species such as *Tridax procumbens*, *Justicia*

procumbens, *Borreria hispida* and *Lantana camara,* which flower largely in the rainy season. The study clearly indicates that *Cadaba fruticosa* is the adult's principal nectar host plant. Further, it is found that the two *Colotis* butterflies oviposit on the leaves and flower buds of *C. fruticosa* and their larvae feed on the same leaves. On the other hand, *Anaphaeis aurota* does the same on *Capparis spinosa*, which occurs in the same study area. Therefore, the study considers the plant *Cadaba* and the pierid butterflies belonging to *Colotis* as a co-evolved system. The *A. aurota* - *C. fruticosa* system appears to be a one sided adaptation, as the plant allows only butterflies of *A. aurota* to feed on its nectar and pollinate it, and not the larvae.

The *C. fruticosa-Colotis* relationship appears to be a specialized system and any disturbance in the habitat is bound to affect the existence of both. It is imperative to protect the habitats where these two partners occur, in order to ensure their perpetuation.

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