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Psychophily in *Stachytarpheta jamaicensis* (L.) Vahl. (Verbenaceae)

P. Vara Lakshmi and A. J. Solomon Raju*

Department of Environmental Sciences, Andhra University, Visakhapatnam 530 003, India

***Stachytarpheta jamaicensis* is a seasonal shrub which produces flowers for a lengthy period during rainy and winter seasons. The floral characteristics such as bluish-violet flowers, no perceptible smell, narrow tubular corolla and concealed nectar accumulated at the corolla base conform to ‘psychophilous pollination syndrome’. The aggregated arrangement of flowers on the inflorescence is economical and energetically rewarding for the butterflies. The lower lip of the corolla is elaborate and provides comfortable landing place for the butterflies. The nectar is sucrose-rich with 28% sugar concentration and also carbohydrate-rich with little protein content. It is also an important source of five of the ten essential amino acids required by butterflies; they include isoleucine, valine, lysine, methionine and threonine. Further, it also contains the non-essential amino acids such as alanine, butyric acid, cystine, glutamic acid, glycine, hydroxyproline, proline, serine, aspartic acid and cysteine. With these floral morphological and functional characteristics, the plant is exclusively pollinated by butterflies. Among butterflies, nymphalids and pierids are relatively more diverse in species and consistent foragers than papilionids and hesperiids. Therefore, the interaction between *S. jamaicensis* and the butterflies is mutualistic; the former for pollination and the latter for nourishment. This floral source is available for a long period and hence is an important nectar source for the maintenance of local butterflies. Additionally, bees also visit the flowers for forage and their visits**

*For correspondence. (e-mail: ajsraju@yahoo.com)

could contribute to gene flow at population level to some extent.

S. jamaicensis produces fruits with minute seeds within a short span of time. Seed dispersal occurs through soil and water movement. They germinate immediately if the soil is sufficiently wet; if not, they remain dormant until the soil is charged with water during monsoon season. The plant with abundant seed production enjoys a 'minor weed' status only.

Keywords: Butterfly, minor weed, psychophily, *Stachytarpheta jamaicensis*.

THE genus *Stachytarpheta* (Verbenaceae) includes about 100 herbaceous species widely distributed in tropical and subtropical America, with a few members in tropical Asia, Africa and Oceania. The genus name comes from the Greek *stachy*, meaning 'spike' and *tarpheta*, meaning 'thick'. It is characterized by small, intense purple to pale rose flowers gathered in dense showy inflorescences¹. There are a few studies on *Stachytarpheta* reproductive biology and even studies that describe the reproductive aspects of the species are not comprehensive². The published information shows that lepidopterans are the main pollinators of *S. mutabilis*, *S. glabra*, *S. maximiliani*, *S. cayennensis* and *S. canescens*; other insects have also been shown to be potential pollinators of these species²⁻⁶. A recent study by Jacobi and Antonini⁷ documented that *S. glabra* is pollinated by a humming bird, *Colibri serrirostris*. This communication describes the mutualistic relationship between butterflies, and the floral biology and pollination of *S. jamaicensis*. Further, it also examines the value of *S. jamaicensis* for butterflies in the study area.

S. jamaicensis is characterized by patchy occurrence, with each patch consisting of a small population of plants (Figure 1a). Plants occurring at Adavivaram–Simhachalam hill range of the Eastern Ghats of Visakhapatnam, Andhra Pradesh, India, were used for the study. The study was carried out during 2008 and 2009. Twenty-five tagged, mature buds were followed for recording the time of anthesis and anther dehiscence; the mode of anther dehiscence was also noted using a 10× hand lens. Details of flower morphology such as flower sex, shape, size, colour, odour, sepals, petals, stamens and ovary were described. Ten mature but undehisced anthers were collected from five different plants and placed in a petri dish. Later, a single anther was taken out each time and placed on a clean microscope slide (75 × 25 mm) and dabbed with a needle in a drop of lactophenol–aniline blue. The anther tissue was then observed under the microscope for pollen, if any, and if pollen grains were not there, the tissue was removed from the slide. The pollen mass was drawn into a band, and the total number of pollen grains was counted under a compound microscope (40× objective, 10× eye piece). This procedure was followed for counting the number of pollen grains in each

anther collected. Based on these counts, the mean number of pollen grains produced per anther was determined. The mean pollen output per anther was multiplied by the number of anthers of a flower for obtaining the mean number of pollen grains per flower. The characteristics of pollen grains were also recorded. To record the pollen–ovule ratio, the mean pollen output of a flower was divided by the number of ovules of a flower, and the value thus obtained was taken as the *p/o* ratio. Ten fresh flowers were used to measure the total volume of nectar/flower. The nectar sugar concentration was measured using a Hand Sugar Refractometer (Erma, Japan) according to Dafni *et al.*⁸. Nectar analysis for sugar types was done according to the paper chromatography method of Harborne⁹. Total carbohydrate content was also estimated following the anthrone method of Sadasivam and Manickam¹⁰. Individual sugar concentrations were also estimated for sucrose, glucose and fructose. For the first two types of sugars, dinitrosalicylic acid method and for the last sugar, resorcinol method of Sadasivam and Manickam¹⁰ were followed. Nectar analysis for amino acid types was done according to the paper chromatography method of Baker and Baker¹¹. Nectar protein content was estimated according to Lowry *et al.*¹². The stigma receptivity was tested with hydrogen peroxide from mature bud stage to flower drop according to Dafni *et al.*⁸. Regular observations were made on the insect species visiting the flowers for forage. The insects were observed for their foraging behaviour such as mode of approach, landing, probing behaviour, type of forage that they collect, contact with essential organs to result in pollination, inter-plant foraging activity in terms of cross-pollination, etc. Casual observations were made on fruit and seed characteristics.

The plant is a small perennial shrub which usually occurs as patches of small populations during the rainy and winter seasons. Flowering occurs during July–February, with profuse flowering during September–December. It produces terminal spikes bearing an average number of 166 (range 160–170) flowers, which anthese over an average period of 34 (range 29–39) days. An average number of five flowers are produced by each spike daily (Figure 1b). The flowers are borne terminally on long, stringy spikes at the end of the stems. They are small, sessile, no perceptible smell, tubular, bisexual and zygomorphic. The sepals are four, tubular and free at the distal end. The petals are five, blue to violet, fused at the base forming an 8 mm long tube and bi-lipped at the distal end. The upper lip consists of two lobes and the lower one has three lobes; the central one being small and the other two relatively large. A rim of glandular hairs is present at the corolla throat. The corolla tube is white on its inner side and covered with white hairs. The stamens are two, epipetalous and inserted at the corolla throat (Figure 1c). The staminal filaments are short and bear linear and divaricated, 2 mm long anthers. The anthers are two-celled,

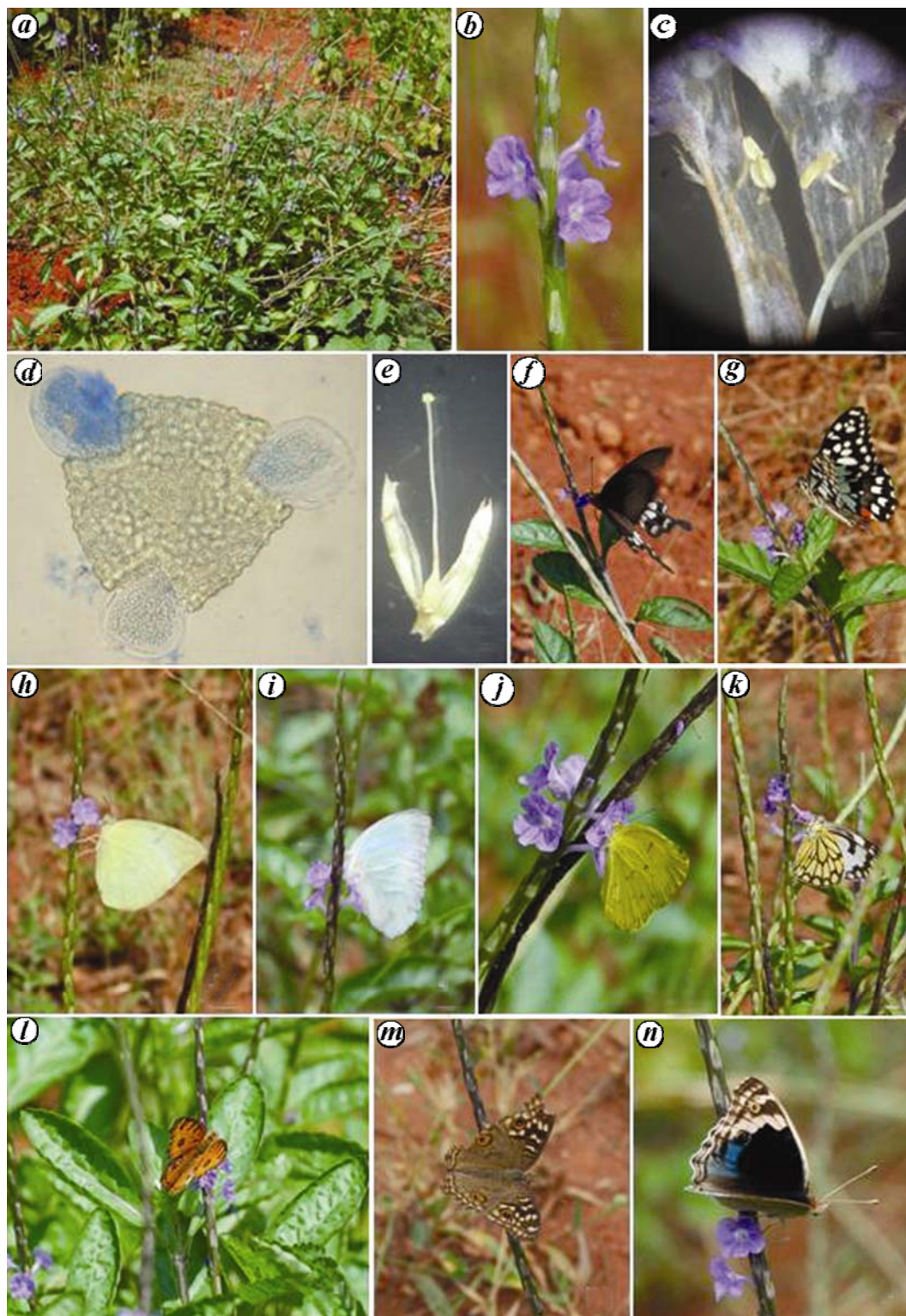


Figure 1. *Stachytarpheta jamaicensis*: *a*, Habit; *b*, Flowers; *c*, Epipetalous stamens; *d*, Pollen grain; *e*, Ovary with style and capitata stigma; *f*, *Pachliopta aristolochiae*; *g*, *Papilio demoleus*; *h*, *Catopsilia pomona*; *i*, *Catopsilia pyranthe*; *j*, *Eurema hecabe*; *k*, *Anaphaeis aurota*, *l*, *Junonia almana*; *m*, *Junonia lemonias* and *Junonia orithya*.

introrse, pendulous and dorsifixed. The ovary consists of two unilocular carpels with one ovule in each carpel on axile placentation. The style is 7 mm long and springs up from the centre of the flower passing through the anthers.

It has a dilated capitata stigma extending beyond the length of the anthers (Figure 1 *e*).

The flowers open daily during 0400–0500 h. The nectary disc present at the base of the ovary produces nectar,

which is collected in the corolla tube. A flower produces $1.59 \pm 0.48 \mu\text{l}$ of nectar with $28.60 \pm 2.22\%$ sugar concentration consisting of sucrose, glucose and fructose in that order of dominance. Sucrose content is $0.795 \mu\text{g}$, glucose $0.302 \mu\text{g}$ and fructose $0.24 \mu\text{g}$. Total carbohydrate content is $1.337 \mu\text{g}$, whereas protein content is $0.0829 \mu\text{g}$ per flower. The essential amino acids are isoleucine, valine, lysine, methionine and threonine; they are dominant in the same order. The non-essential amino acids are alanine, butyric acid, cystine, glutamic acid, glycine, hydroxyproline, proline, serine, aspartic acid and cysteine; these acids occur in the same order of dominance. Anther dehiscence occurs at anthesis; it takes place by longitudinal slits. An anther produces an average number of 41 (range 36–46) three-lobed pollen grains (Figure 1 d); the average pollen output per flower is 82. The pollen-ovule ratio is 41 : 1. The stigma appears viscid and shiny; it shows receptivity immediately after anther dehiscence and remains receptive for a period of 6 h. The corolla together with the stamens fall off from late afternoon to early evening.

The flowers were foraged daily by butterflies and occasionally by bees during daylight hours. The butterflies included 18 species representing Papilionidae (4), Pieridae (6), Nymphalidae (7) and Hesperidae (1; Figure 2). The papilionids were *Pachliopta aristolochiae* (Figure 1 f), *P. hector*, *Papilio demoleus* (Figure 1 g) and *P. polytes*. The pierids were *Catopsilia pomona* (Figure 1 h), *C. pyranthe* (Figure 1 i), *Eurema hecabe* (Figure 1 j), *Anaphaeis aurota* (Figure 1 k), *Colotis danae* and *C. fausta*. The nymphalids were *Acraea violae*, *Junonia lemonias* (Figure 1 m), *J. alamana* (Figure 1 l), *J. orithya* (Figure 1 n), *J. atlites* (Figure 3 a), *Hypolimnas misippus* and *Danaus chrysippus* (Figure 3 b). The hesperiid was *Borbo cinnara* (Figure 3 c). Among these, the individuals of nymphalid and pierid butterflies frequented more at the flowers, than butterflies of all other families. The foraging activity of these butterflies showed a general trend characterized by a gradual increase from morning to noon, and a sudden decrease in the afternoon due to gradual flower drop and gradual decrease in the quantity of standing nectar crop (Figures 4–7). The data collected on the foraging visits of butterflies of each family showed that

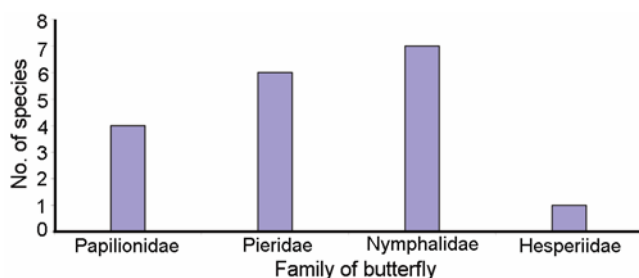


Figure 2. Family-wise number of butterfly species foraging on *S. jamaicensis*.

nymphalids made 40%, pierids 33%, papilionids 22% and hesperids 5% of total visits (Figure 8). Individual flowers provided convenient landing place for butterflies and the close arrangement of flowers in spike inflorescences enabled them to probe several flowers in succession for nectar before their departure. They insert the proboscis through the centre of the narrow corolla tube during which it establishes contact with the stigma and dehisced anthers lying below. This probing behaviour was considered to be effecting pollination. A sample of six specimens of each butterfly species was used to examine the pollen-carrying capacity of their proboscides. The results indicated that the proboscides invariably contained pollen grains ranging from 11 to 23 in papilionids, 9 to 18 in pierids, 11 to 29 in nymphalids and 6 to 11 in the hesperiid. They frequently visited the flowers of different individual plants of *S. jamaicensis*; this inter-plant foraging activity within and between plants was considered to be important in promoting cross-pollination.

The bees were *Xylocopa latipes* (Figure 3 d) (Apidae), *Anthophora bicincta* (Figure 3 e; Anthophoridae) and an unidentified bee species (Figure 3 f). *X. latipes* bees were juveniles and occasionally visited the flowers to collect nectar; but there was a mismatch between the length of the tongue of the bee (<5 mm) and the length of the corolla tube (8 mm). Similar mismatch was evidenced with the other two bees also; their tongue lengths also measured <5 mm. These bees were also occasional foragers. The deep-seated nectar and the dehisced anthers placed half way along the length of the corolla tube mostly prevented forage collection by bee foragers. Therefore, their attempts to collect either nectar or pollen were found to be mostly abortive and hence were considered to be of little importance in pollination.

Fruits develop as soon as the ovules are fertilized. They are 4 mm long, 1.5 mm wide and contain seeds within. Details of fruit and seed aspects were not examined due to their inconspicuous nature. However, field studies indicated that seeds mature within a month, fall to the ground and germinate immediately to produce the next batch of new plants if the soil is sufficiently wet; if not, they remain dormant and germinate in the next rainy season. Seed dispersal occurs by movement of soil and water.

S. jamaicensis is a seasonal shrub which produces flowers for a lengthy period during the rainy and winter seasons. The floral characteristics of this plant such as bluish-violet flowers, no perceptible smell, narrow tubular corolla and concealed nectar accumulated at the corolla base strongly select the foragers, which require a more elaborate flower handling and probing behaviour to access the forage. Such selected foragers contact the anthers and stigma using their proboscis and forehead, while accessing the nectar located at the corolla base and the pollen concealed in the corolla tube. The elaborate intra-floral behaviour exhibited by such foragers surely contributes to

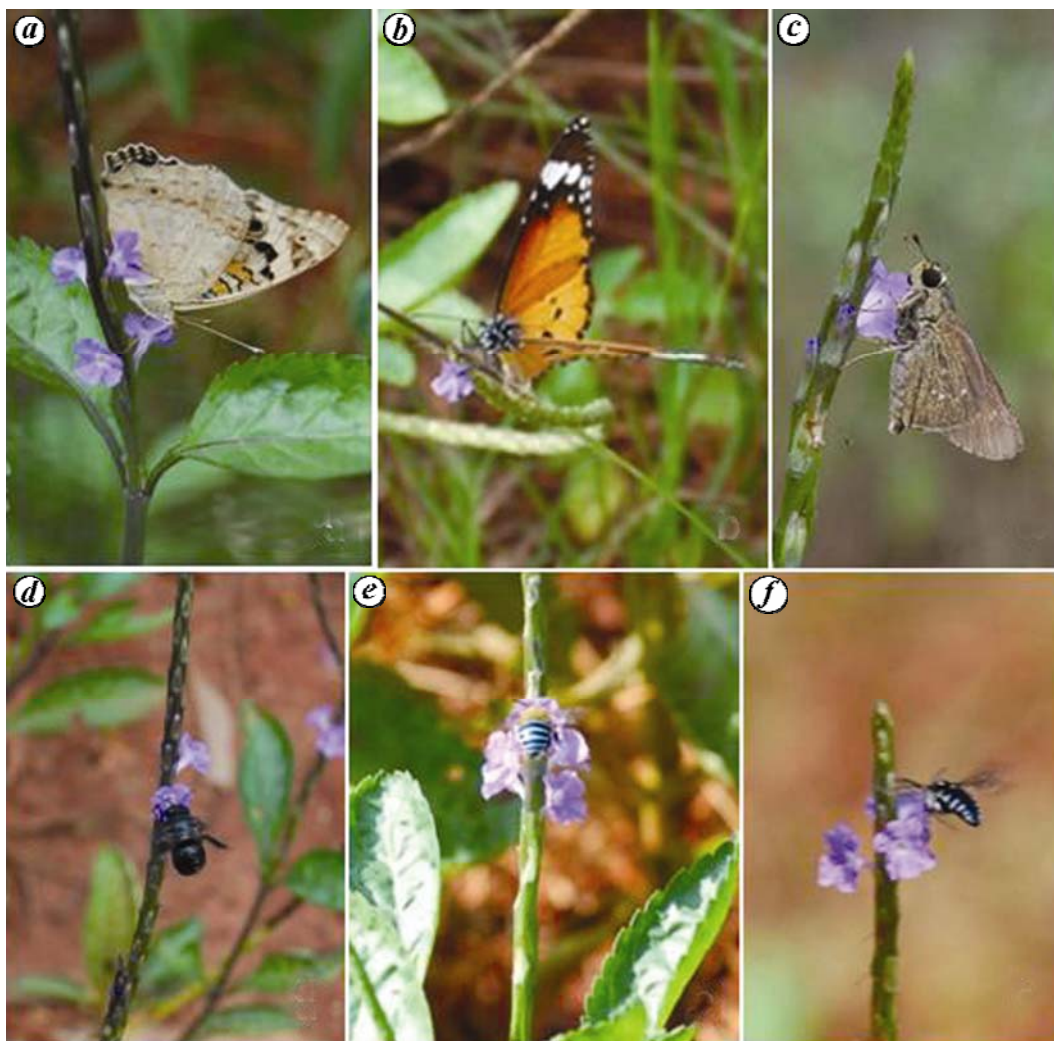


Figure 3. *S. jamaicensis*: a, *Junonia atlites*; b, *Danaus chrysippus*; c, *Borbo cinnara*; d, Juvenile *Xylocopa latipes*, e, *Anthophora bicincta* and f, Unidentified bee.

self- or cross-pollination. The flowers with these characteristics have been shown to be pollinated by butterflies or in short referred to as ‘psychophilous’^{13,14}. The present study showed that the flowers of *S. jamaicensis* are exclusively pollinated by butterflies. The flowers are also aggregated into a spike and such an arrangement is economical and energetically rewarding for the butterflies¹⁵. The elaborate lower lip of the corolla provides comfortable landing place for the butterflies. The newly open flowers offer fresh nectar and also pollen due to anther dehiscence at anthesis. The nectar is sucrose-rich, but it is not in agreement with the generalization that Verbenaceae nectars are characteristically hexose-rich¹⁶. The nectar sugar concentration stands at 28%. A wide range exists in the sugar concentration of nectars utilized by butterflies: 15–25% (ref. 17), 13–44% (ref. 18), 16–40% (ref. 19) and 20–25% (ref. 20). Kevan and Baker²¹ stated that butterflies can also utilize viscous nectars, diluting them by secreting a type of saliva. The nectar

sugar concentration recorded in *S. jamaicensis* is expected to optimize the net energy gain by the visiting butterflies²⁰. The nectar is carbohydrate-rich with little protein content; but both provide important nutrition to the butterflies.

Nectar is a potential source of amino acids for the nutrition of butterflies. Naturally, butterfly nectars are rich in amino acids²². Butterflies require ten essential amino acids, but all of them are not normally found in all nectars. Usually, three to four essential amino acids and several non-essential amino acids are found in floral nectars^{22,23}. Baker and Baker²⁴ reported that the amino acids add taste to the floral nectar and this depends on their concentration. Their presence serves as an important cue for butterflies to make flower visits and in the process effect pollination. In *S. jamaicensis*, the nectar contains some essential and non-essential amino acids. Its nectar is an important source for five of the ten essential amino acids required by butterflies during their adult life for

growth and development²⁵. They include isoleucine, valine, lysine, methionine and threonine. Non-essential amino acids are metabolized by butterflies from the food they take; however, floral nectar provides some of these amino acids instantaneously. The nectar of *S. jamaicensis* provides alanine, butyric acid, cystine, glutamic acid, glycine, hydroxyproline, proline, serine, aspartic acid and cysteine. Gardener and Gillman²⁶ mentioned that if local soil conditions favour higher concentration of amino acids in the nectar, then local populations of butterflies may derive certain benefits. Adult feeding on amino acid-

rich food has been shown to increase longevity and reproductive ability in certain heliconine butterflies^{27,28}. A later study on a temperate species, *Euphydryas editha* showed that amino acids in the adult diet led to heavier eggs²⁹. Jervis and Boggs³⁰ reported that the butterflies are agents of selection for higher nectar amino-acid production. The requirement of amino acids during adult stage of the butterfly is also related to the larval nutritional condition. The larval food plant has a key role in the evolution of the flower–butterfly mutualism, and demonstrates that the importance to butterfly reproduction, and of different nutrient sources varies with butterfly nutritional state. Gardener and Gillman³¹ reported that soil conditions can affect the amino acid complement of nectar. This may have implications for plant–butterfly interactions, as local populations of butterflies may benefit from the increased amino acid content of the nectar and preferentially visit plants growing in high nutrient conditions. The fidelity of butterflies to *S. jamaicensis* during flowering phase attests the fact that they are in need of amino acids present in this nectar and in the process contributing to pollination.

Butterflies begin their nectar collection activity as soon as the flowers of *S. jamaicensis* are open and continue nectar collection until flower-drop. With their proboscis, they reach the bottom of the corolla tube to take the nectar. The presence of pollen grains on the proboscis of butterflies indicates that they are pollen carriers and effect pollination while collecting nectar. *S. jamaicensis* flowers attract papilionid, pierid, nymphalid and hesperiid butterflies. Nymphalid and pierid butterflies are relatively more diverse in species and collect nectar consistently during the entire period of the flowering season. All families of butterflies collect nectar throughout the period of flower life, suggesting that this floral nectar is an important source for them. The consistent interaction of butterflies with *S. jamaicensis* constitutes mutualism in which the former obtains nourishment, while the latter pollination service. Additionally, bees also visit the flowers for forage, but they are mostly unable to collect either pollen or nectar due to mismatch between their tongue length and corolla tube length. Their foraging visits, however, can be effective for pollination; further, bees being long-distance fliers may contribute to gene flow at population level. Therefore, *S. jamaicensis* is primarily psychophilous. The low pollen–ovule ratio evidenced in this plant suggests that it is primarily self-pollinating³² and hence psychophily is effective for both self- and cross-pollination. Haber *et al.*³³ reported that *S. jamaicensis* is also pollinated by hummingbirds in the New World. Ormond *et al.*² suggested the occurrence of psychophily in the allied species, *S. canescens* and *S. cayennensis* due to the presence of a set of morphological characteristics adapted for probing by butterflies. Fonseca *et al.*⁵ reported that *S. cayennensis* attracts papilionids, pierids, lycaenids, nymphalids and hesperiids, but the butterflies of the last family

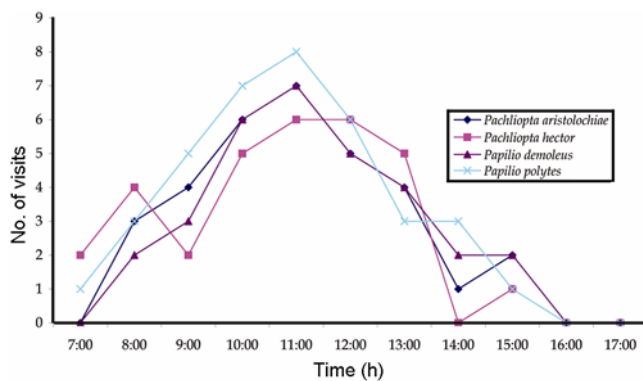


Figure 4. Hourly nectar foraging activity of papilionid butterflies on *S. jamaicensis*.

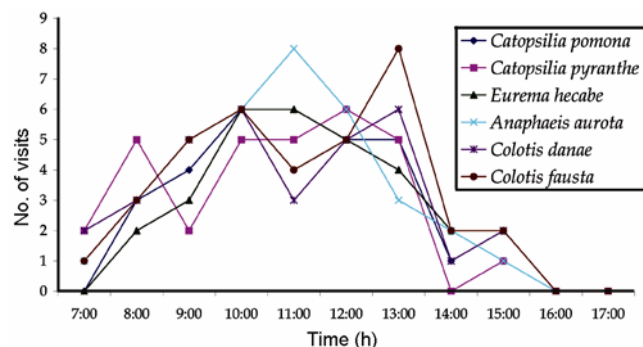


Figure 5. Hourly nectar foraging activity of pierid butterflies on *S. jamaicensis*.

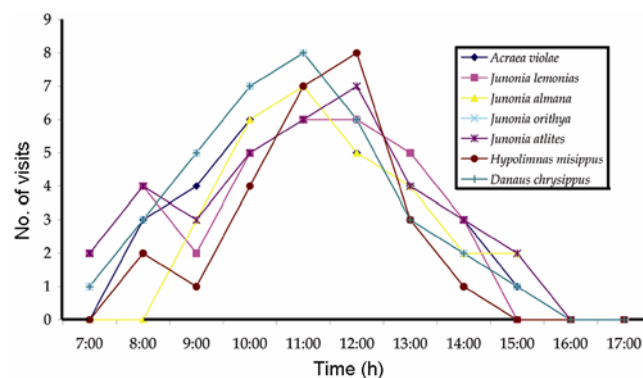


Figure 6. Hourly nectar foraging activity of nymphalid butterflies on *S. jamaicensis*.

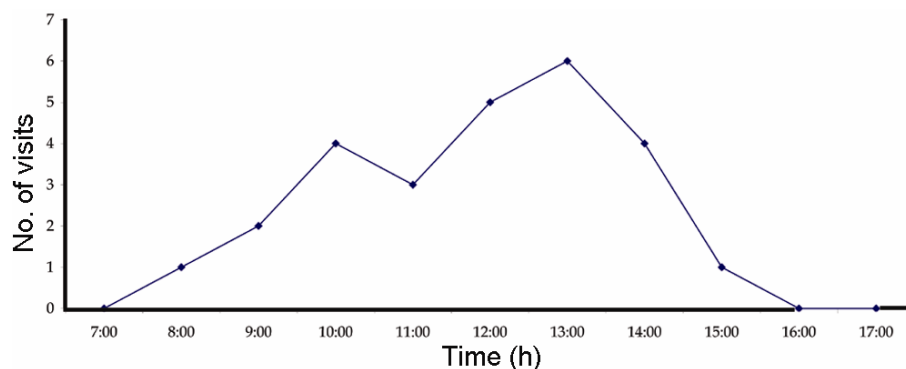


Figure 7. Hourly nectar foraging activity of hesperiid butterfly, *Borbo cinnara* on *S. jamaicensis*.

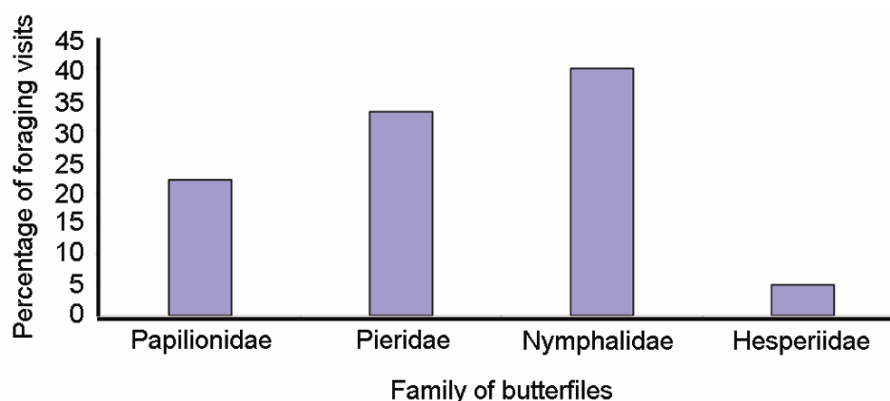


Figure 8. Family-wise percentage of foraging visits of butterflies on *S. jamaicensis*.

are the most diverse and common foragers. Barbola *et al.*⁶ reported that different insect groups visit the flowers of *S. maximiliani*, but bees and butterflies are the main pollinators. The pollinating butterflies include papilionids, nymphalids, pierids and hesperiids, but the butterflies of the last family are more frequent and diverse. Stone *et al.*³ documented that *S. mutabilis* is primarily pollinated by papilionid butterflies and the digger bee, *Amegilla sapiens*. In the Neotropics, *S. glabra* attracts a wide array of insect groups, but butterflies and bees are the potential pollinators⁴. On the contrary, Jacobi and Antonini⁷ reported that the hummingbird *C. serrirostris* is the main pollinator, although butterflies and bees effect pollination in *S. glabra* in Brazil. The hummingbird also defends this floral resource from other hummingbirds and large insects. These studies suggest that *Stachytarpheta* appears to be primarily psychophilous and sometimes it is also mellitophilous throughout its distribution range in tropical latitudes. Further, it is also hummingbird-pollinated in the Neotropics. The present study suggests that *S. jamaicensis*, with a long period of flowering, is an important nectar source for the maintenance of local butterfly species. However, it does not invade new areas quickly like major exotic weeds such as *Lantana camara* and *Hyptis suaveolens* do in India or in other tropical countries; such a restricted establishment could be attributable to soil conditions, seed predation and seed degradation.

Therefore, *S. jamaicensis* being a minor weed with spreading and establishment difficulties, does not occur everywhere and hence is not a common nectar source for the butterflies.

S. jamaicensis produces fruits with minute seeds within a short span of time. The seeds disperse through soil and water movement during rainy season. The dispersal distance through these modes depends on the local factors such as topography, vegetation status and local land-use practices. They germinate immediately if the soil is sufficiently wet; if not, they remain dormant to germinate during the monsoon season. Despite the abundant production and effective migration of the seeds, the plant has not been successful as a weed. Therefore, it enjoys a 'minor weed' status only.

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Regional geological studies over parts of Deccan Syncline using remote sensing and geophysical data for understanding hydrocarbon prospects

P. Chandrasekhar^{1,*}, Tapas R. Martha¹, N. Venkateswarlu², S. K. Subramanian¹ and M. V. V. Kamaraju¹

¹National Remote Sensing Centre, Indian Space Research Organisation, Hyderabad 500 625, India

²National Geophysical Research Institute (Council of Scientific and Industrial Research), Hyderabad 500 606, India

An integrated study using remote sensing and multi-geophysical data was carried out over parts of Deccan Syncline, for eliminating the inherent ambiguities associated with each of the individual methods, and to understand the hydrocarbon prospects. The subsurface sections constructed using geophysical data such as gravity, electrical resistivity, deep resistivity sounding, magnetotellurics and seismics along various profiles were interpreted for identification of subsurface faults along with their stratigraphic association. The locations of these faults were projected vertically upwards onto the ground surface and marked as point locations on the map in order to facilitate conjunctive study with satellite data interpretation by superimposing one over the other. Additionally, some more regional faults were interpreted from gravity data and superimposed over the above. A prominent geomorphic anomaly was also interpreted from satellite data and correlated with geophysical signatures. Based on

*For correspondence. (e-mail: chandrasekhar_p@nrs.gov.in)