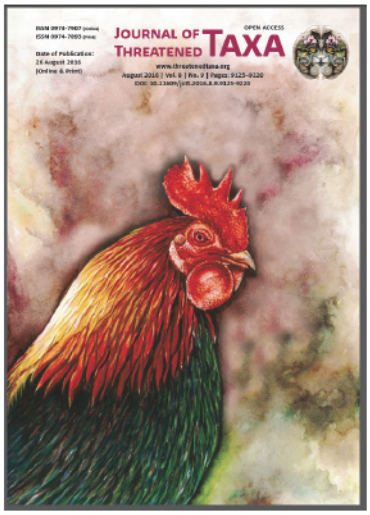

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COMMUNICATION

POLLINATION ECOLOGY AND FRUITING BEHAVIOR OF *PAVETTA INDICA* L. (RUBIACEAE), A KEYSTONE SHRUB SPECIES IN THE SOUTHERN EASTERN GHATS FOREST, ANDHRA PRADESH, INDIA

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Pollination ecology and fruiting behavior of *Pavetta indica* L. (Rubiaceae), a keystone shrub species in the southern Eastern Ghats forest, Andhra Pradesh, India

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OPEN ACCESS

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Abstract: *Pavetta indica* is a massive bloomer for a brief period in May. The flowers are hermaphroditic, strikingly protandrous, self and cross-compatible, nectariferous and psychophilous. They possess secondary pollen presentation mechanism as a device to avoid autonomous autogamy but it does not prevent geitonogamy. The fruit set largely occurs through geitonogamy and xenogamy. Butterflies, especially papilionids, pierids, nymphalids, and sphingid hawk moth pollinate the flowers while collecting nectar. Honey bees and blue-banded digger bees feed on pollen and effect only accidental pollination. The nectar is sucrose-rich and contains essential and non-essential amino acids. Birds are seed dispersal agents. Seeds are non-dormant and germinate readily during rainy season but their continued growth and establishment is subject to the availability of soil moisture and nutrients. The plant is not able to populate itself in its natural area. The local uses of different parts of the plant have been found to be affecting its reproductive success and natural regeneration rate. Therefore, regulation of the uses of this plant is recommended for its survival and restoration of its population size in the natural areas due to its role as a keystone species for bees and butterflies during dry season.

Keywords: Flowering phenology, keystone shrub species, mixed breeding system, ornithochory, *Pavetta indica*, psychophily.

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INTRODUCTION

Rubiaceae family is classified into three subfamilies, Ixoroideae, Cinchonoideae and Rubioideae. These subfamilies show three main reproductive mechanisms: heterostyly is more common in Rubioideae, secondary pollen presentation on the style in Ixoroideae whereas Cinchonoideae presents both mechanisms. The sexual systems include hermaphroditism, monoecy, polygamomonoecy, dioecy and heterostyly (Robbrecht 1988). In an elaborate study, Puff et al. (2005) stated that protandry in isostylous flowers of Rubiaceae is associated with secondary pollen presentation which occurs widely among all the three sub-families. This phenomenon was first noted in *Ixora* and hence is often referred to as "ixoroid pollination mechanism". This pollination mechanism is reported in *Pavetta, Duperrea, Catunaregam, Anthocephalus, Mitragyna, Uncaria* and many other species. Four types secondary pollen presentation have been recognized in this family, according to the presenting area and receptive surfaces.

1. Pollen deposition on the style only. Here, pollen deposition is strictly on non-receptive surfaces. The stigma and its receptive surfaces are higher up.
2. Pollen deposition on the style and outside of the stigma lobes. Pollen is solely deposited on non-receptive surfaces, but the abaxial surfaces of the stigma are also involved.
3. Pollen deposition on the outer side of the stigma.
4. Pollen deposition exclusively, largely or partly on the receptive surface of the stigma.

In types 2 and 3, the receptive areas are the inner sides of the stigma lobes or the furrows between two stigma lobes. At the time of pollen deposition the stigma lobes are fused so that contact between self-pollen and the receptive surfaces is improbable. Detailed information on the function of these types of secondary pollen presentation in individual species of all the three sub-families of Rubiaceae is almost totally lacking.

The genus *Pavetta* belongs to the sub-family Ixoroideae and tribe Pavetteae. It is widely distributed in the Old World tropics from Africa to Southeast Asia, New Guinea, Australia, New Caledonia and Vanuatu but does not occur in Madagascar, New Zealand and Oceania. It comprises of about 400 species of shrubs or small trees with the largest number of them distributed in Africa. Sri Lanka and the Philippines are also very rich in *Pavetta* species (Mabberley 1987; Reynolds 1993; de Block & Robbrecht 1998; Tao & Taylor 2011). In India, the genus is represented by about 30 species (Santapau & Henry 1972). Two explanations exist for the derivation of the genus name. It is either derived from *pawatta*, the Sinhalese (Sri Lankan) name for a plant in this genus (Schmidt et al. 2002) or from *pavetta*, the common name for *P. indica* in Malabar, India. It is also believed to have been derived from "pavimentum", a Latin word describing a pavement or mosaic of bricks or stones which possibly refer to the scattered bacterial nodules in the leaves; the bacteria take shelter, fix nitrogen from the air and release it in a form the plant can use (van Wyk 1974). *Pavetta* is characterized by its terminal or axillary corymbiform long-pedunculate inflorescences, white, tetramerous hermaphrodite flowers, long exserted stamens inserted in the mouth of the corolla tube, spheroidal tri-zonocolporate pollen with supratectal microgemmae, style with fusiform short bifid stigma, bilocular ovary with two ovules immersed in a fleshy placenta and drupes with one or two pyrenes (Reynolds 1993; de Block & Robbrecht 1998). *Pavetta* species produce sweet scented flowers which attract many pollinators such as birds, bees, wasps, beetles, ants and moths. These in turn attract birds and other predators. Birds and monkeys feed on fruits, which are obviously distributed by them (Schmidt et al. 2002; van Wyk 1974; Bridson 2003). *P. schumanniana*, *P. cooperi* and *P. lanceolata* produce white scented flowers; the first one is pollinated by moths which forage at twilight or at night while the other two by birds, bees, wasps, beetles, ants and moths. Their black, fleshy fruits appear to be dispersed by birds and monkeys (Bremekamp 1934; van Wyk 1974; Kok & Grobbelaar 1984; Johnson & Nichols 2002). In the monograph of the genus *Pavetta,* Bremekamp (1934) provided a brief account on *P. indica*. It is widely distributed from the Andaman Islands, India and the northwestern Himalaya to southern China and southwards throughout Malesia to northern Australia. But it is considered to be a controversial species because some authors claimed that it has a wide distribution area, and many varieties were then distinguished, mainly based on the hairiness of different plant parts, while other authors stated that this species is confined to India and Sri Lanka, and specimens resembling this species in other regions bear a multitude of different names such as *P. axillaris* Bremek., *P. montana* Reinw. ex Blume., *P. reinwardtii* Bremek., *P. subvelutina* Miq. and *P. sylvatica* Blume in Java. The plant is common in primary and secondary forests where it often forms a single stem but also occurs in open localities where branched types are more common, from sea level up to 1500m altitude. The plant is a medicinally important species

in Peninsular Malaysia, Philippines and India. Its leaves are used to treat nose ulcers while the root, root bark and stem bark are used to treat intestinal obstructions, haemorrhoids, rheumatism and urinary diseases. The flowers are also used as a cosmetic after bathing. The plant produces white, tubular, actinomorphic, hermaphroditic flowers which are foraged and pollinated by Papilionid butterflies (Momose et al. 1998; Kato et al. 2008). Since there is very little information on the pollination biology of *Pavetta* genus in general and the medicinally important species, *P. indica* in particular despite its medicinal importance, we initiated this study using field and laboratory approaches to investigate the details of its pollination ecology. In the study region, this species serves as a keystone species during May in the southern Eastern Ghats forest of Andhra Pradesh, India. The work presented in this paper on *P. indica* is useful to understand various aspects of pollination ecology and also enables to know how it acts as a keystone species in the month of May in the study area when almost all other plant species stay in deciduous state without flowering or fruiting.

MATERIALS AND METHODS

Study area

Twenty-five scattered plants of *Pavetta indica* located in the deciduous forest near Alampur in Kadiri area (14^{0}06'N & 78^{0}09'E; 360m) of Anantapur District in the southern Eastern Ghats of Andhra Pradesh, was used for the study during 2014–2015. The forest is characterized by steep slopes, rocky terrain, dry and poor stony soils with deciduous vegetation. The vegetation is a unique mix of the dry deciduous and moist deciduous types. The area is totally dry and experiences very high temperature during summer season. In this area, *Hildegardia populifolia* (Sterculiaceae), *Pavetta indica* and *P. tomentosa* are the only species that bloom during dry season; the first species is an endemic and endangered tree, while the other two are shrub or small tree. These three species represent a small population with scattered distribution in this area. Of these, *H. populifolia* blooms during February–April, *P. indica* during May and *P. tomentosa* during May–June. *Pavetta* species with flowering during May/June assume importance as keystone species to support certain local flower-foragers.

Flowering and floral biology

Flowering season was defined based on regular field trips made. Observations regarding the organization of inflorescences, the spatial positioning of flowers, and their position (terminal, axillary, etc.) on the plants were made since these features are regarded as important for foraging and effecting pollination by flower-visitors. The flower life was recorded by marking twenty five just anthesed flowers and following them until fall off. Anthesis was initially recorded by observing 25 marked mature buds in the field. Later, the observations were repeated five times on different days in order to provide accurate anthesis schedule for each species. Similarly, the mature buds were followed for recording the time of anther dehiscence. The presentation pattern of pollen was also investigated by recording how anthers dehisced and confirmed by observing the anthers under a 10x hand lens. The details of flower morphology such as flower sex, shape, size, colour, odour, sepals, petals, stamens and ovary were described based on 25 flowers randomly collected from a population of plants for each species. The order of wilting or dropping off of floral parts was recorded. Observations regarding the position and spatial relationships of stamens and stigma in mature bud, at anthesis and after, during the flower-life with reference to self and/or cross-pollination were made very carefully.

Pollen output

Thirty mature, but un-dehisced anthers from five different plants were collected and placed in a Petri dish. Later, each time a single anther was taken out and placed on a clean microscope slide (75x25 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 (40x objective, 10x 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 produced per anther was determined. The mean pollen output per anther was multiplied by the number of anthers in the flower for obtaining the mean number of pollen grains per flower. The characteristics of pollen grains were also recorded.

Pollen-ovule ratio

The pollen-ovule ratio was determined by dividing the average number of pollen grains per flower by the number of ovules per flower. The value thus obtained was taken as pollen-ovule ratio (Cruden 1977).

Nectar characters

The presence of nectar was determined by observing the mature buds and open flowers. The volume of nectar from 10 flowers of each plant species was determined. Then, the average volume of nectar per flower was estimated and expressed in µl. The flowers used for this purpose were bagged at mature bud stage, opened after cessation of nectar secretion and squeezed nectar into micropipette for measuring the volume of nectar. Nectar sugar concentration was determined using a Hand Sugar Refractometer (Erma, Japan). Ten samples were used for examining the range of sugar concentration in the nectar. For the analysis of sugar types, paper chromatography method described by Harborne (1973) was followed. Nectar was placed on Whatman No. 1 of filter paper along with standard samples of glucose, fructose and sucrose. The paper was run ascendingly for 24 hours with a solvent system of n-butanol-acetone-water (4:5:1), sprayed with aniline oxalate spray reagent and dried at 120^{0}C in an electric oven for 20 minutes for the development of spots from the nectar and the standard sugars. Then, the sugar types present and also the most dominant sugar type were recorded based on the area and colour intensity of the spot. The sugar content/flower is expressed as the product of nectar volume and sugar concentration per unit volume, mg/µl. This is done by first noting the conversion value for the recorded sugar concentration on the refractometer scale and then by multiplying it with the volume of nectar/flower. Table 5.6 given in Dafni et al. (2005) was followed for recording the conversion value to mg of sugars present in one µl of nectar. Nectar amino acid types were recorded as per the paper chromatography method of Baker & Baker (1973). Nectar was spotted on Whatman No. 1 filter paper along with the standard samples of nineteen amino acids, namely, alanine, arginine, aspartic acid, cysteine, cystine, glutamic acid, glycine, histidine, isolecuine, leucine, lysine, methionine, phenylalanine, proline, serine, threonine, tryptophan, tyrosine and valine. The paper was run ascendingly in chromatography chamber for 24 hours with a solvent system of n-butanol-glacial acetic acid-water (4:1:5). The chromatogram was detected with 0.2% ninhydrin reagent and dried at 85^{o}C in an electric oven for 15 minutes for the development of spots from the nectar and the standard amino acids. The developed nectar spots were compared with the spots of the standard amino acids. Then, the amino acid types were recorded.

Stigma receptivity

The stigma receptivity was observed visually and by H_2O_2 test. In visual method, the stigma physical state (wet or dry) and the unfolding of its lobes were considered to record the commencement of receptivity; withering of the lobes was taken as loss of receptivity. H_2O_2 test as given in Dafni et al. (2005) was followed for noting stigma receptivity period. This test is widely followed although it does not indicate the exact location of the receptive area. In the present study, the period of slow release of bubbles from the surface of stigma following the application of hydrogen peroxide was taken as stigma receptivity.

Breeding Systems

Mature flower buds of some inflorescences on different individuals were tagged and enclosed in paper bags. They were tested in the following way and the number of flower buds used for each mode of pollination was given in Table 1.

1. The flowers were fine-mesh bagged without hand pollination for autonomous autogamy.
2. The stigmas of flowers were pollinated with the pollen of the same flower manually by using a brush; they were bagged and followed to observe fruit set in manipulated autogamy.
3. The emasculated flowers were hand-pollinated with the pollen of a different flower on the same plant; they were bagged and followed for fruit set in geitonogamy.
4. The emasculated flowers were pollinated with the pollen of a different individual plant; they were bagged and followed for fruit set in xenogamy.

All these categories of flower pollinations were followed for fruit set. If fruit set is there, the percentage of fruit set was calculated for each mode.

Natural fruit set, seed dispersal and seedling ecology

A sample of flowers on ten plants were tagged on different plants prior to anthesis and followed for fruit set rate in open-pollinations. Fruit maturation period, fruit dehiscence and seed dispersal aspects were observed to

Table 1. Results of breeding systems in *Pavetta indica*

Pollination mode	No. of flowers pollinated	No. of fruits formed	Fruit set (%)
Autogamy (un-manipulated and bagged)	60	0	0
Autogamy (hand-pollinated and bagged)	60	9	15
Geitonogamy	60	31	52
Xenogamy	60	45	75
Open-pollination	422	131	31

the extent possible. Field observations were also made on the emergence of new growth from old shoots, seed germination and seedling establishment aspects.

Flower-visitors and seed dispersal agents

After making preliminary observations on flower visitors, a thorough knowledge of the local insect species was obtained by observing the representative species of insects available with the Pollination Ecology Laboratory in the Department of Environmental Sciences, Andhra University, Visakhapatnam. With the knowledge of local insect species, attempts were made to observe flower visitors. The hourly foraging visits of each insect species were recorded on 3 or 4 occasions depending on the possibility and the data was tabulated to use the same for further analysis. Fully blooming plants were selected to record the foraging visits of insects. The data obtained was used to calculate the percentage of foraging visits made by each insect species per day and also to calculate the percentage of foraging visits of each category of insects per day in order to understand the relative importance of each insect species or category of insects. The foraging behaviour of insects was observed on a number of occasions for the mode of approach, landing, probing behavior with reference to floral sex organs, the type of forage collected, contact with essential organs to result in pollination, inter-plant foraging activity for their role in self- and cross-pollination.

Determination of pollen carryover efficiency of insects

The hawk moths captured during morning and afternoon hours and bees and butterflies captured during 10:00–12:00 hr were brought to the laboratory. For each insect species, 10 specimens were captured and each specimen was washed first in ethyl alcohol and the contents stained with aniline-blue on a glass slide and observed under microscope to count the number of pollen grains present. From this, the average number of pollen grains carried by each insect species was calculated to know the pollen carryover efficiency of different insect species. In case of bees, pollen loads were removed prior to pollen count and only those pollen grains that were present on the forehead, dorsal and ventral parts of the bee body were counted. In case of butterflies and hawk moths, the proboscis, forehead and wings were used to record the pollen carried by them.

Photography

Plant habitat, flowering inflorescences, flower and fruit details, bees, butterflies and hawk moths were photographed with Nikon D40X Digital SLR (10.1 pixel) and TZ240 Stereo Zoom Microscope with SP-350 Olympus Digital Camera (8.1 pixel). Olympus Binoculars (PX35 DPSR Model) was also used to make field observations on the foraging behavior of foragers. Magnus Compound Microscope - 5x, 10x, 40x and 100x magnification was used for studying the pollen grain characteristics, pollen output and floral internal details.

RESULTS

Phenology

P. indica is a shrub or small tree with tomentose branches. It occurs as isolated individuals or a few individuals grouped together. It is evergreen with leaf fall and leaf flushing taking place throughout the year in the locations where soil is either optimally or partially saturated with water or moisture while it is semi-deciduous with complete leaf fall during February–March and leaf flushing during April-May in the locations where soil is semi-dry or totally dry (Image 1a). But, leaf flushing is bit delayed in the plants occurring in totally dry locations. The flowering occurs during May in all plants irrespective of their occurrence in dry or wet soils. But, the duration of flowering at plant level is two weeks in dry locations while it is nearly three weeks in moist locations. Inflorescence is an axillary, long pedunculate, densely tomentose, dichotomously branched corymbose cyme, consisting of 35.16±9.50 pedicellate flowers which open over a period of 3–4 days (Image 1b,c). Individual flowering inflorescences stand out prominently against the new foliage and are quite attractive from a long distance.

Flower morphology

The flowers are white, fragrant, medium-sized (28.6±2.4 mm long and 1.16±0.13 mm wide), tubular with funneliform corolla throat, actinomorphic and bisexual. The calyx has a short tube with four ovate lobes terminally; it is green and densely tomentose. The corolla is white, 17.5±0.5 mm long, tubular (11.5±1.1 mm) with four petals (6.4±1.0 mm long and 3.4±0.04 mm wide). The corolla tube is cylindrical, slender, glabrous outside and sparsely pilose inside at throat. The stamens are four and have short-filaments inserted alternate to the petals at the mouth of the corolla tube and the anthers are greenish-yellow (6.2±0.4 mm), dorsifixed, dithecous, linear, with a prolonged connective at apex, sagittate at base and conspicuously twisted at anthesis. The ovary is bicarpellary, bilocular syncarpous with a total

Image 1. *Pavetta indica*: a - Leaf flushing phase; b & c - Flowering inflorescences; d–h - Different stages of anthesis; i–l - Bee foragers: i - *Apis dorsata*, j. *Apis cerana indica*, k. *Apis florea*, l. *Amegilla* sp. © Prof. A.J. Solomon Raju.

of two ovules slightly immersed in fleshy placenta. The total length of the pistil is 30.1±1.3 mm of which ovary is 2.6±0.5 mm long and style and stigma are 24.9±1.5 mm long. The ovary is green, while style and stigma are white. The style is slender, filiform, thickened in the upper part, exserted; the exserted portion is longer than corolla lobes. The stigma is linear, sparsely pubescent all over and shortly bifid. The style and stigma extend far beyond the anthers.

Floral biology

Mature buds bulge slowly and open during 06:00–09:00 hr and the anthers dehisce synchronously during anthesis by longitudinal slits while the stigma

is unreceptive at this time as the its lobes remained appressed (Image 1d–h). The sub-terminal and terminal portions of the style are continuous, not clearly distinguishable and the stigmatic lobes in appressed state terminate the style. The outer surface of the stigmatic lobes is unreceptive while the inner surface of the stigmatic lobes is receptive. During anthesis, pollen is presented along the terminal portion of the style and the non-receptive outer surface of the appressed stigmatic lobes, which are passively loaded via the action of introrsely shedding pollen. The dehisced anthers reflex backwards soon after anthesis. The pollen output per anther is 9,352±435 and per flower is 37,408. The pollen-ovule ratio is 18,704: 1. The pollen grains are creamy white, powdery, spheroidal, trizonocolporate with supratectal microgemmae and 22.68±3.79 µm in size, ornamented and have thick exine. The style and stigma extend 12–14 mm beyond the height of anthers after anthesis and the stigma attains receptivity around 16:00 hr of the same day by the slight separation of stigmatic lobes during which their inner surfaces are semi-wet. The stigma receptivity lasts until noon time of the 3rd day. The annular disc crowning the ovary begins nectar secretion from the time of anthesis and ceases its secretion by 1600 h on the day of anthesis. Individual flowers produce 5.5±2.0 µl of nectar with 17±3.4 % (13–26 %) sugar concentration. The sugar types present in the nectar include sucrose, fructose and glucose with the first as dominant. The total sugar present in the nectar of individual flowers is 1.05 mg. The nectar also contains five essential amino acids (arginine, histidine, lysine, methionine and threonine) and eight non-essential amino acids (alanine, aspartic acid, butyric acid, cysteine, cystine, glutamic acid, glycine and hydroxyproline). In pollinated flowers, the floral parts - petals, stamens, style and stigma fall off on the evening of the 3rd day while the calyx remains intact and forms the strong base for the growing fruit. The entire flower falls off on the 3rd day in case of un-pollinated flowers.

Breeding Systems

The results of breeding systems indicated that the plant is self-compatible and self-pollinating. The fruit set does not occur through autonomous autogamy but occurs in all other modes of pollination. It is 15% in facilitated autogamy, 52% in geitonogamy, 75% in xenogamy and 31% in open pollinations (Table 1).

Pollinator guilds and pollination

Thrips were found using the flower buds for breeding. They were abundantly present in bud stage and emerged out following anthesis and fed on both pollen and nectar. The thrips collected the forage continuously from the flowers of the same plant; they were considered to be largely contributing to geitonogamy due to non-receptive stigma on the day of anthesis until late evening. The first foragers at the flowers were the diurnal hawk moths (*Macroglossum gyrans* and *Cephonodes hylas* (Sphingidae). They foraged during 0500-0700 and 1600-1800; the flowers foraged by them before 06:00hr were 1 or 2 day old ones since the anthesis occurs after 06:00hr. The bees and butterflies commenced their foraging activity from 07:00hr onwards; the former ceased foraging at 16:00 hr while the latter ceased foraging at 14:00hr. Both bees showed a gradual increase in foraging visits until 11:00hr while butterflies showed a gradually increase in foraging visits until 10:00hr but both categories of insects showed a gradual decrease thereafter until they ceased foraging for the day (Figs. 1–7). The bees contributed 10%, hawk moths 11% and butterflies 79% of total average foraging visits recorded for the day (Fig. 8). The bees included honey bees, *Apis dorsata* (Image 1i), *A. cerana indica* (Image 1j), *A. florea* (Image 1k) and the digger bee *Amegilla* sp. (Image 1l). The butterflies were *Pachliopta aristolochiae* (Image 2a,f), *P. hector* (Image 2b,e), *Papilio polytes* (Image 2c), *P. demoleus* (Image 2d) (Family - Papilionidae), *Catopsilia pomona* (Image 2g,h), *C. pyranthe* (Image 2i), *Eurema hecabe* (Image 2j), *Delias eucharis* (Image 2k), *Belenois aurota* (Image 3a,b), *Ixias marianne* (Image 3c), *Colotis fausta* (Image 3d), *C. etrida* (Image 3e), *C. danae* (Image 3f) (Family Pieridae), *Acraea terpsicore* (Image 3g), *Junonia hierta* (Image 3h), *Euploea core* (Image 3i) (Family - Nymphalidae), *Castalius rosimon* (Image 3j), *Freyeria trochylus* (Image 3k), *Spindasis vulcanus* (Image 3l), *Tajuria cippus* (Image 3m) (Family Lycaenidae) and *Hasora chromus* (Image 3n) (Family Hesperiidae). The hawk moths were *Macroglossum gyrans* (Image 3o) and *Cephonodes hylas* (Image 3p)(Family Sphingidae) (Table 2). All the three categories of insects were regular and consistent foragers during the flowering period. The bees were exclusive pollen foragers as pollen is easily available due to its location at the corolla throat while the nectar is not accessible due to its concealed position at the base of the corolla tube. They approached the flowers in upright position, landed on the petals and gathered pollen from the dehisced anthers. During pollen collection, they never had any contact with the stigma to result in pollination. However, in their consecutive foraging visits in the same bout to the flowers of the same or other inflorescences of the same or different nearby conspecific plants had accidental

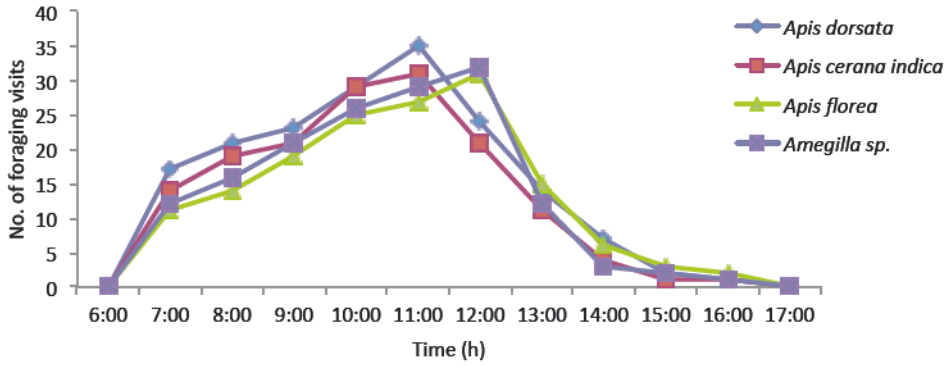

Figure 1. Hourly foraging activity of bees on *Pavetta indica*

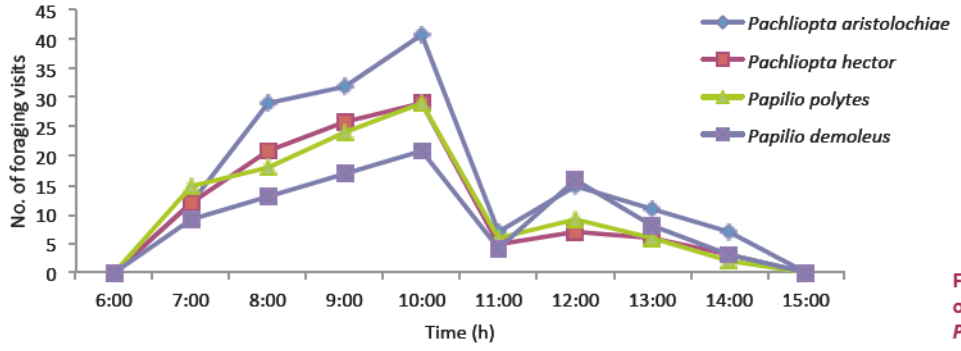

Figure 2. Hourly foraging activity of Papilionid butterflies on *Pavetta indica*

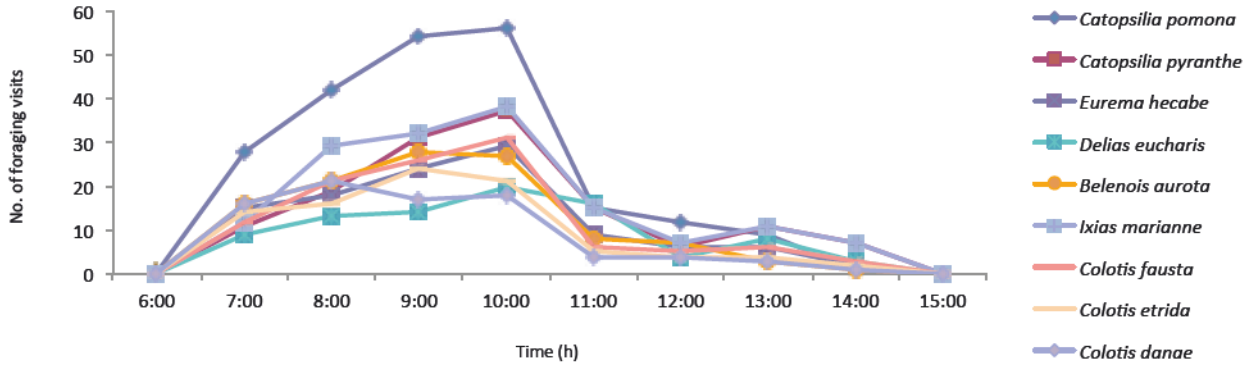

Figure 3. Hourly foraging activity of Pierid butterflies on *Pavetta indica*

contact with the stigmas due to which pollination occurred. The hawk moths and butterflies were exclusive nectar foragers; all these except lycaenids collected nectar easily with their proboscis which exceeded the length of the corolla tube. Lycaenids with proboscis length smaller than corolla tube length had difficulty to collect nectar from the base of the corolla tube; in effect they tended to visit the flowers that oriented downwards in which the nectar flows to the mid-part of the corolla tube by gravity. The corymbose cymes with closely spaced flowers provide flat-topped platform for the foraging butterflies. The butterflies landed on the top of the inflorescence, probed the flowers one by one in succession in the same bout and effected pollination by touching their forehead and ventral side against the stigmas. The hawk moths hovered at the flowers, swiftly collected nectar from several flowers in a short span of time (2–5 seconds). The body washings of foraging insects showed variation in the pollen carrying capacity; the average pollen recorded ranged between 98.1–162.1 in case of bees, between 18.1–45.3 in case of butterflies and between 33.6–40.2 in case of hawk moths (Table 3). Although bees carried more pollen on their bodies, they were not effecting pollination while probing the flowers but effecting accidental pollination only when flying between flowers of the same or different inflorescences

Table 2. List of insect foragers on *Pavetta indica*

Order/Family	Scientific name	Common name
HYMENOPTERA		
Apidae	*Apis dorsata* F.	Rock Bee
	Apis cerana indica F.	Indian Bee
	Apis florea F.	Dwarf Bee
	Amegilla sp.	Blue Banded Bee
LEPIDOPTERA		
Papilionidae	*Pachliopta aristolochiae* F.	Common Rose
	Pachliopta hector L.	Crimson Rose
	Papilio polytes L.	Common Mormon
	Papilio demoleus L.	Lime Butterfly
Pieridae	*Catopsilia pomona* F.	Common Emigrant
	Catopsilia pyranthe L.	Mottled Emigrant
	Eurema hecabe L.	Common Grass Yellow
	Delias eucharis Drury	Common Jezebel
	Belenois aurota F.	Pioneer
	Ixias marianne Cramer	White Orange Tip
	Colotis fausta Wallace	Large Salmon Arab
	Colotis etrida Boisduval	Little Orange Tip
	Colotis danae F.	Crimson Tip
Nymphalidae	*Acraea terpsicore* F.	Tawny Coster
	Junonia hierta F.	Yellow Pansy
	Euploea core Cramer	Common Crow
Lycaenidae	*Castalius rosimon* F.	Common Pierrot
	Freyeria trochylus Freyer	Grass Jewel
	Spindasis vulcanus F.	Common Silverline
	Tajuria cippus F.	Peacock Royal
Hesperiidae	*Hasora chromus* Cramer	Common Banded Awl
Sphingidae	*Macroglossum gyrans* Walker	Diurnal hawk moth
	Cephonodes hylas L.	Diurnal hawk moth

Table 3. Pollen recorded in the body washings of insect foragers on *Pavetta indica*

Insect species	Sample size (N)	Number of pollen grains		
		Range	Mean	S.D
Bees				
Apis dorsata F.	10	93–157	99.2	19.44
Apis cerana indica F.	10	54–209	115.5	50.08
Apis florea F.	10	67–302	162.1	75.49
Amegilla sp.	10	95–129	98.1	12.23
Butterflies				
Pachliopta aristolochiae F.	10	23–64	37.4	11.48
Pachliopta hector L.	10	12–31	20.6	4.92
Papilio polytes L.	10	17–42	28.4	8.11
Papilio demoleus L.	10	10–38	23.9	8.06
Catopsilia pomona F.	10	22–47	31.8	7.38
Catopsilia pyranthe L.	10	34–69	45.3	10.00
Eurema hecabe L.	10	27–64	43.8	11.76
Delias eucharis Drury	10	12–31	19.8	5.38
Anaphaeis aurota F.	10	9–28	18.1	5.37
Ixias marianne Cramer	10	16–39	25.5	6.40
Colotis fausta Wallace	10	20–45	29.1	7.81
Colotis etrida Boisduval	10	24–78	48.5	15.71
Colotis danae F.	10	18–66	40.7	14.77
Acraea violae F.	10	15–59	36.6	12.81
Junonia hierta F.	10	12–48	29.6	10.68
Euploea core Cramer	10	23–64	42.1	12.62
Castalius rosimon F.	10	14–53	30.9	11.31
Chilades trochylus Freyer	10	25–66	42.9	13.03
Spindasis vulcanus F.	10	16–49	30.4	9.99
Tajuria cippus F.	10	21–54	38.9	10.23
Hasora chromus Cramer	10	11–61	35.6	15.48
Hawk moths				
Macroglossum gyrans Walker	10	45–78	40.2	9.05
Cephonodes hylas L.	10	52–69	33.6	7.31

of the same or different plants. Therefore, butterflies and hawk moths were considered to be the principal pollinators while bees were supplementary pollinators. Further, bees by collecting huge pollen from the plant could considerably reduce the availability of pollen for pollination.

Fruiting behaviour and seed dispersal

The fertilized flowers produce fruits within three weeks. The peduncle of the inflorescence and pedicel of fertilized flowers elongate rapidly markedly as fruits develop. The fruit is a globose drupe, 5.5±0.4 mm diameter, crowned by persistent calyx lobes, initially green and finally black and shiny. It produces two or one seed by abortion and the seed(s) are attached to the center of septum, hemispherical, 2–3 mm diameter, thin-walled, and plano-convex with a wide circular excavation. Fruits fall to the ground when mature and ripe. The seeds are non-dormant, germinated in July and in subsequent months depending on the soil moisture status. Field study during July–October months showed that only 10% of seedlings continued growth while all other seedlings perished subsequently. The seedlings that showed growth were almost confined to areas where soil is optimally wet despite dry spell during rainy season. The soil in such areas is moderately rich in litter content.

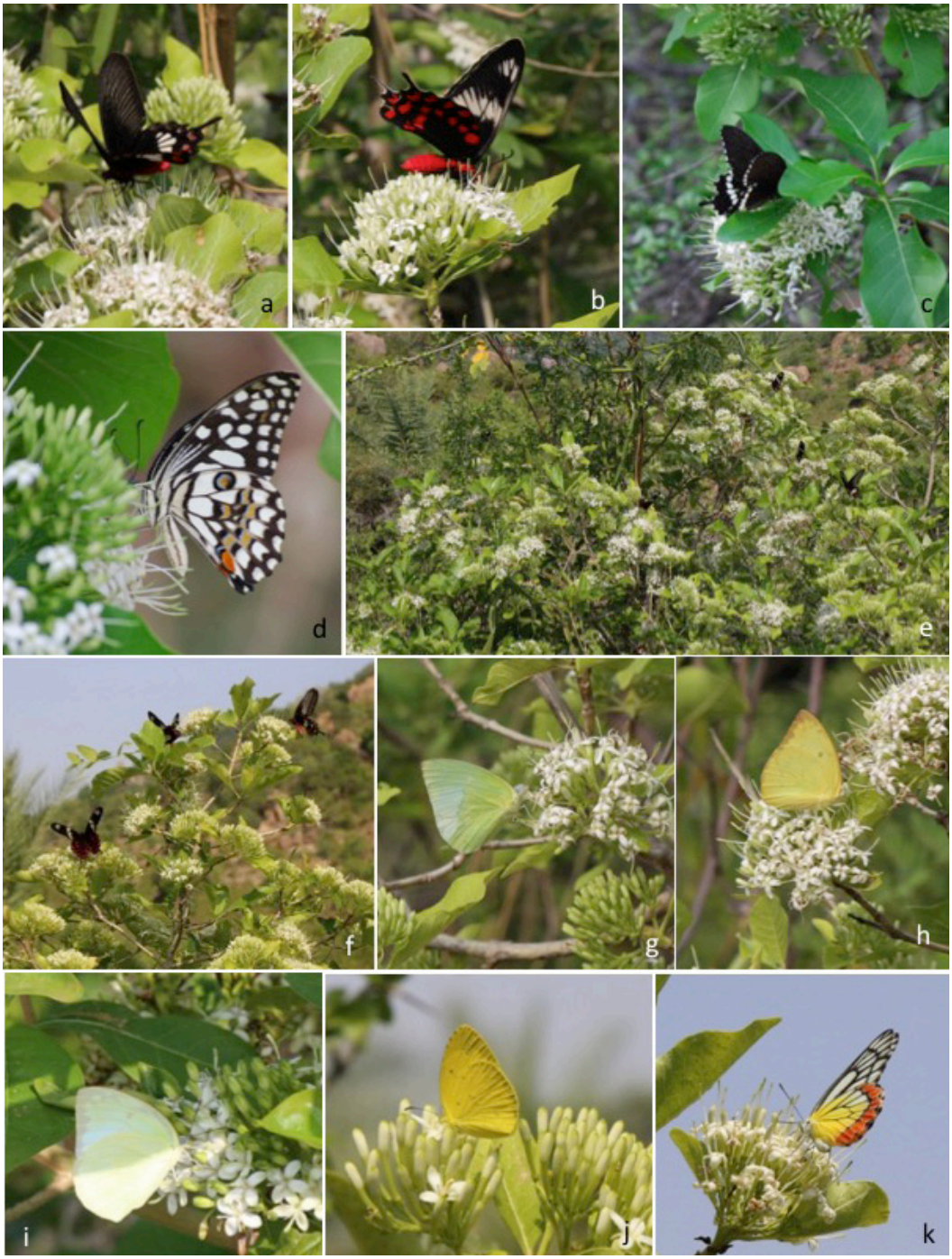

Image 2. *Pavetta indica*: a-f. Papilionids - a. *Pachliopta aristolochiae*, b. *Pachliopta hector*, c. *Papilio polytes*, d. *Papilio demoleus*, e. *Pachliopta hector* congregations, f. *Papilio aristolochiae* congregations, g-k. Pierids – g. & h. *Catopsilia pomona*, i. *Catopsilia pyranthe*, j. *Eurema hecabe*, k. *Delias eucharis*. © Prof. A.J. Solomon Raju.

Local uses

Local women decorate their hair with a crown made of flowers of this plant. Since the flowering occurs almost during dry season and the conventionally used flowers are scarce or not available, the flowers of this plant are readily used. The white and fragrant nature of the flowers is an added attraction for the women to use them. Different parts of the plant are locally used for treating certain human ailments. Further, the seeds are collected and sold locally; they are used to adulterate black pepper seeds (*Piper nigrum* - Piperaceae) which have commercial importance. These various uses of the

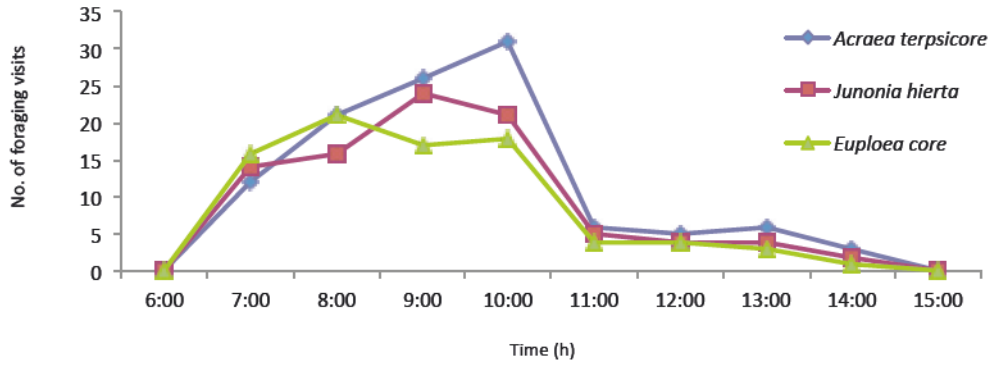

Figure 4. Hourly foraging activity of Nymphalid butterflies on *Pavetta indica*

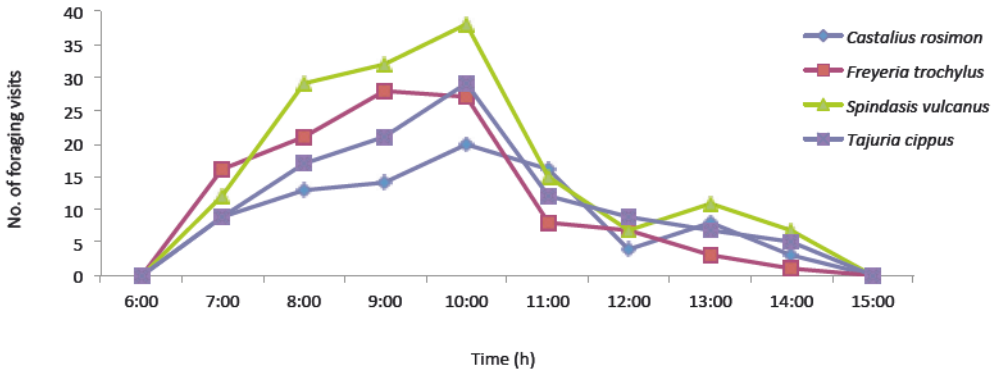

Figure 5. Hourly foraging activity of Lycaenid butterflies on *Pavetta indica*

plant were found to be greatly affecting the reproductive success as well as natural regeneration rate.

DISCUSSION

The study site of *Pavetta indica* representing tropical monsoon forest is a constituent of southern Eastern Ghats forest of Andhra Pradesh, India. Field observations indicate that the flowering of many tree species of this forest peaks during early to mid part of dry season and is in conformity with the report by Murali & Sukumar (1994) that in tropical monsoon forest in southern Asia, the mean temperature drastically increases from January to April and many trees bloom during this dry, hot season. But, the shrub, *P. indica* blooms during May when there is almost no flowering from other co-occurring plant species at this forest site. Individual plants of this species flower massively for a brief period and the white flowers standout prominently against the foliage, the situation of which attracts certain appropriate insect foragers which use this floral source as a potential pollen/nectar source by displaying fidelity, and hence *P. indica* is a keystone species for such foragers during this period.

In Rubiaceae, the sub-family Ixoroideae displays isostylous flowers with protandry associated with Secondary Pollen Presentation (SPP). This pollination mechanism is reported in *Ixora, Pavetta, Duperrea, Catunaregam, Anthocephalus, Mitragyna, Uncaria* and many other species. Four types secondary pollen presentation have been recognized based on the presenting area of pollen and receptive surfaces, as described in the introduction. The present study has revealed that *P. indica* is characteristically isostylous, protandrous, self-compatible and displays SPP characterized by the presentation of pollen on the style, outside the non-receptive stigma surfaces. This type of SPP is similar to the terminal stylar presentation in the flowers of Asteraceae but it is distinguished by the passive pollen loading mechanism and occurs during anthesis (Howell et al. 1993). This form of SPP has been termed the "ixoroid" type by Nilsson et al. (1990). The occurrence of SPP in *P. indica* appears to have arisen to cope with the introrse anther dehiscence in funnel-like flower. The production of stamens with short filaments is definitely due to lack of space to accommodate long filaments within the flower. Further, the anthers situated in the throat of the corolla would ensure the pollen to carry upwards and place it on the style

when the latter extends beyond the corolla through the introrsely dehisced anthers during anthesis (Yeo 2012). In this species, the SPP with strong protandry ensures the non-occurrence of autonomous selfing but facilitates vector-mediated geitonogamy and is functional due to self-compatible stigma. The flowers are also cross-compatible and produce fruit through xenogamy. The results of breeding systems indicate that the hermaphroditic sexual system with strong protandry is evolved to promote out-crossing while keeping the option open for fruit set through geitonogamic mode of self-pollination. Therefore, the breeding system functional in *P. indica* is one step evolved in the path of avoiding selfing through autonomous autogamy and the recorded fruit set rate in open-pollinations is a function of vector-mediated self- and cross-pollination.

Kato et al. (2008) compiled the flowering season, floral features and pollinators of certain Ixoroideae members such as *Ixora flexilis, I. kerii, I. coccinea, I. cephanolophora, Mitragyna rotundifolia, Pavetta indica, Rothmannia sootepensis* and *R. wittii* which flower for a brief period between March and July. Of these, *M. rotundifolia, P. indica* and *R. wittii* are trees while all others are shrubs. *I. coccinea* produces orange flowers, *M. rotundifolia* cream flowers while all others produce white flowers. All these species are functionally hermaphroditic with actinomorphic floral symmetry. The flowers of *R. wittii* are gullet-shaped and pollinated by *Xylocopa* bees while those of *M. rotundifolia* are brush-like and pollinated by bees, wasps and butterflies. In all others, the flowers are tubular and pollinated by butterflies—*I. flexilis*, *I. coccinea* and *P. indica* are exclusively pollinated by Papilionidae, *I. kerii* by Pieridae and *R. sootepensis* by Hesperiidae. Different studies showed that *P. schumanniana*, *P. cooperi* and *P. lanceolata* produce white scented flowers; the first one is pollinated by moths which forage at twilight or at night while the other two by birds, bees, wasps, beetles, ants and moths (Bremekamp 1934; van Wyk 1974; Kok & Grobbelaar 1984; Johnson & Nichols 2002). In this study, *P. indica* with white, fragrant, tubular flowers with actinomorphic symmetry and functional hermaphroditism is principally pollinated by butterflies (especially papilionids, pierids and nymphalids) and sphingid hawk moths, and accidentally pollinated by bees. Bremekamp (1934) noted that this species is mainly pollinated by moths and butterflies. Further, Balasubramanian (1950) also mentioned that *P. indica* is pollinated by butterflies which are treated as pests of crops and also by sphingid moth which plays a secondary role in the pollination of this shrub. Burkhardt (1964) and Faegri & van der Pijl (1979) described that butterfly-flowers usually possess large, white, pink, red, yellow or blue, narrow, tubular flowers with deep nectaries and often yellow rings or other markings on the petals which function as nectar guides. Further, Kato et al. (2008) stated that the secondary pollen presentation system is often found in butterfly-pollinated species with a long slender corolla-tube and far exserted style. In the present study also, *P. indica* principally pollinated by butterflies and hawk moths display the characteristics stated by these authors but in this species, nectar guides are totally absent. Baker & Baker (1983) distinguished butterfly-visited flowers into two subgroups: flowers primarily visited by butterflies and flowers visited almost equally by butterflies and short-tongued bees. The first subgroup includes the flowers with deep, narrow corolla-tube producing copious nectar while second subgroup includes the flowers which are smaller and often grouped in conspicuous inflorescences with a small amount of nectar. *P. indica* belongs to the first group with flowers possessing deep, narrow corolla-tube producing copious nectar. Kevan & Baker (1983) stated that the butterflies can imbibe only the less viscous nectars but some secrete saliva to dilute heavy syrupy nectars and they enable imbibition. Baker & Baker (1983) showed that butterfly and hawk moth flowers are strongly sucrose-rich or dominant. Butterfly-flowers with long corolla tubes are diurnal in flowering and they usually produce sucrose-rich nectar. Cruden et al. (1983) documented that the nectars of most butterfly-pollinated flowers fall within the range of 15–25 % sugar concentration. Kingsolver & Daniel (1979) suggested that the nectar sugar concentrations of 20–25 % optimize the net energy gain by the butterflies. These generalizations are true with *P. indica* in which the nectar is sucrose-rich with 13–26 % sugar concentration. Further, the net sugar content in the nectar energy is profitable for butterflies and hawk moths. Nectar is a potential source of amino acids for the nutrition of insects. They require ten essential amino acids (threonine, valine, methionine, leucine, iso-leucine, phenylalanine, lysine, histidine, arginine and tryptophan) 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 (DeGroot 1953; Baker & Baker 1982, 1983). The nectar of *P. indica* is a source for five essential amino acids (arginine, histidine, lysine, methionine and threonine) and ten non-essential amino acids (alanine, aspartic acid, butyric acid, cysteine, cystine, glutamic acid, glycine and hydroxyproline). The foragers using this floral nectar derive the benefit of sugars and amino acids. The plant

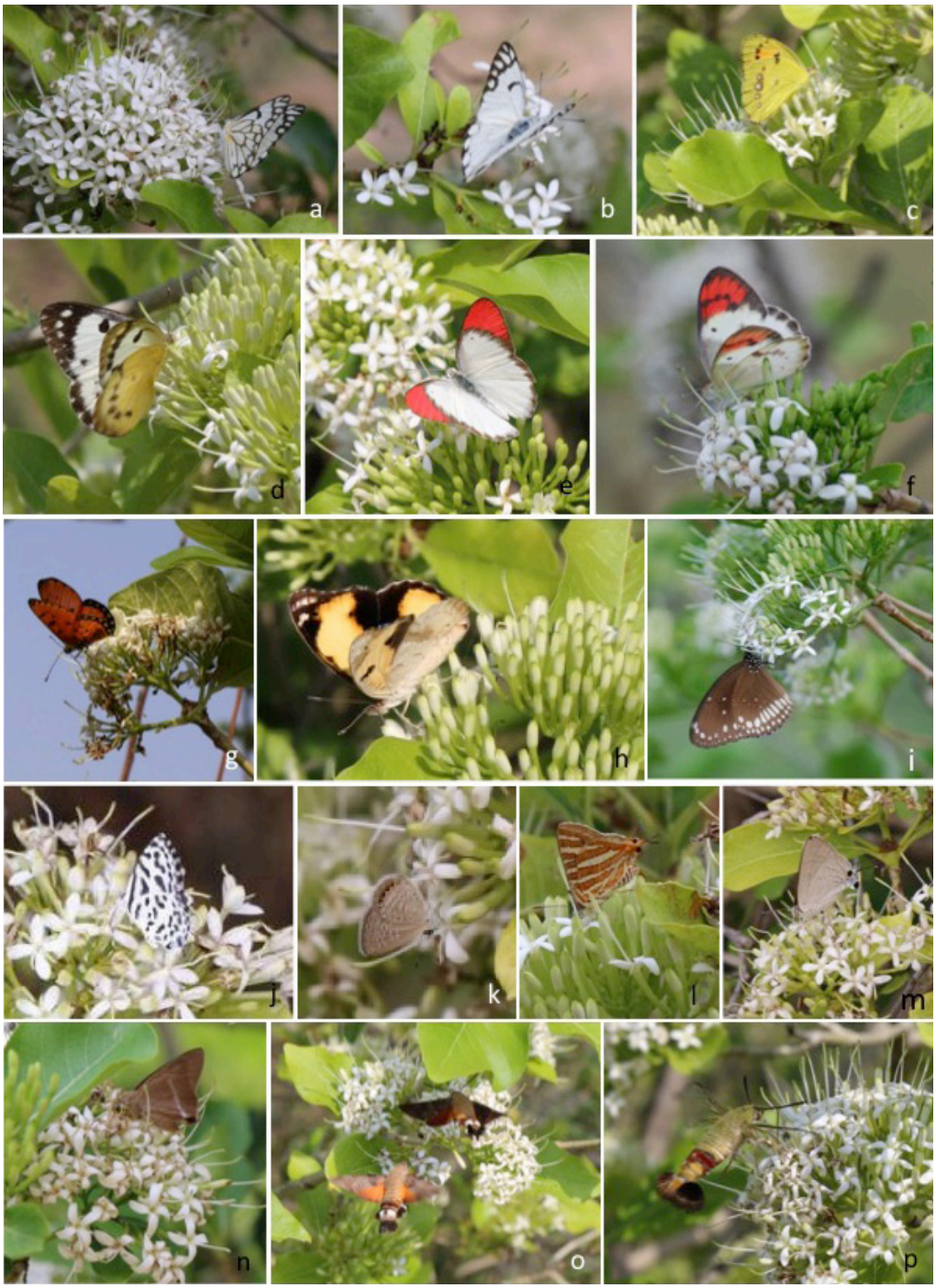

Image 3. ***Pavetta indica*****: a–f - Pierids: a & b -** ***Belenois aurota*****; c -** ***Ixias marianne*****; d -** ***Colotis fausta*****; e -** ***Colotis etrida;*** **f -** ***Colotis danae*****; g–i - Nymphalids: g -** ***Acraea terpsicore*****; h -** ***Junonia hierta*****, i -** ***Euploea core*****; j–n - Lycaenids: j -** ***Castalius rosimon*****; k -** ***Freyeria trochylus*****; l -** ***Spindasis vulcanus*****; m -** ***Tajuria cippus*****; n - Hesperid,** ***Hasora chromus*****; o–p - Sphingids: o -** ***Macroglossum gyrans*****; p -** ***Cephonodes hylas*****. © Prof. A.J. Solomon Raju.**

being a partly dry and partly wet season bloomer is an important nectar source for all the visiting butterflies and hawk moths. Baker & Baker (1983) reported that butterfly nectars are normally rich in amino acids and the total amino acid concentration is a potential source in their nutrition. Jervis & Boggs (2005) reported that the butterflies are agents of selection for higher nectar amino acid production. The larval food plant has a key role in the evolution of the flower-butterfly mutualism, and demonstrates that the importance to butterfly

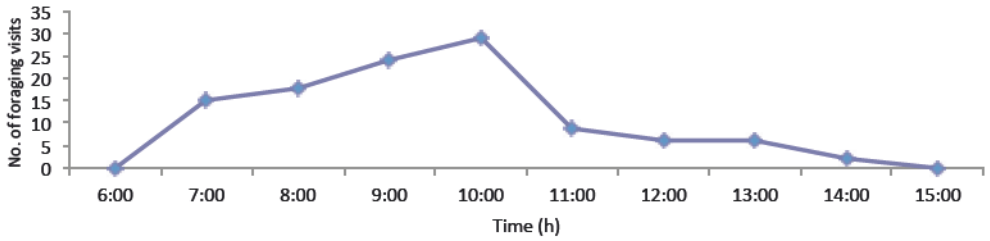

Figure 6. Hourly foraging activity of Hesperiid, *Hasora chromus* on *Pavetta indica*

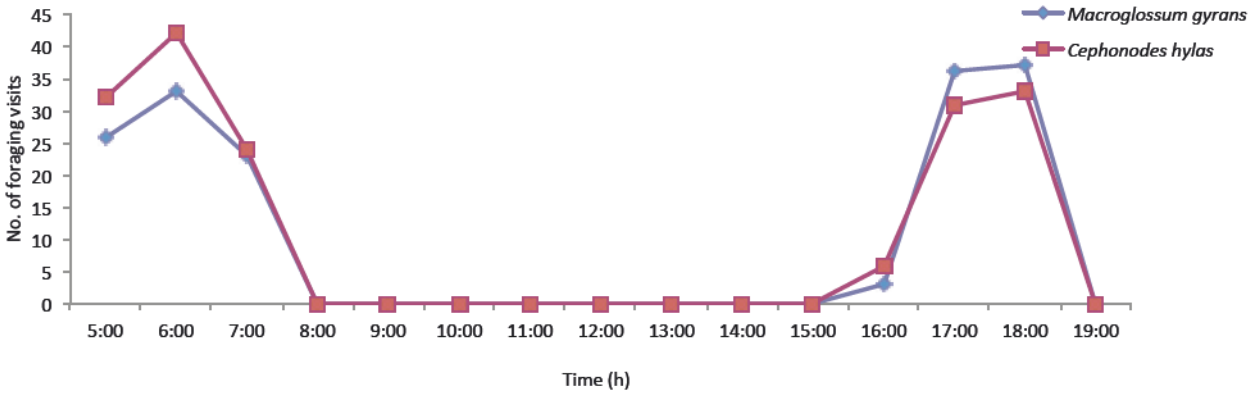

Figure 7. Foraging activity of diurnal hawk moths on *Pavetta indica*

reproduction, of different nutrient source varies with butterfly nutritional state. The requirement of amino acids during adult stage of the butterfly is also related to the larval nutritional condition. Gardener & Gillman (2001) reported that soil conditions can affect the amino acid complement of nectar. This may have implications for plant-insect interactions, as local populations of pollinators may benefit from the increased amino acid content of the nectar and preferentially visit plants growing in high nutrient conditions. In the light of these reports, it is not unreasonable to state that *P. indica* is a promising source of certain amino acids for butterflies and hawk moths during the transitional period between dry and wet season in this tropical monsoon forest, the floor of which is characterized by rocky, dry and nutrient-deficient soils. The lepidopterans involved in pollination carry considerable pollen and transfer to other flowers on the same or other conspecific plants promoting both geitonogamy and xenogamy. The bees also carry pollen in their corbiculae and also on other parts of their body but they are not important in pollination due to accidental contact between them and the stigma.

Momose et al. (1998) noted that butterfly-pollination referred to as "psychophily" is the widespread pollination system in the tropical monsoon forest of Vientiane plain in Laos. Sub-canopy trees, shrubs, and lianas belonging to Apocynaceae, Capparaceae, Fabaceae, Oleaceae, Rubiaceae (*Catunaregum, Isora, Mitragyna, Pavetta, Rothmannia* and *Vangueria*), Sterculiaceae and Verbenaceae are pollinated by danaid, pierid, and papilionid butterflies. In this study, *P. indica* is also a constituent of tropical monsoon forest and pollinated by butterflies and hawk moths. The abundance of these butterflies in this forest during the flowering season of *P. indica* reflects the availability of their larval host plants such as Apocynaceae, Fabaceae and Rutaceae. Honey bees and blue-banded *Amegilla* bees also consistently utilize *P. indica* flowers as a source of pollen but not of nectar; these bees do not contact the stigma while collecting pollen but contact the stigma with their ventral side and effect accidental pollination during hopping from flower to flower on the same or different inflorescences. This finding is not in agreement with the report by Kato (1996) that *Amegilla* bees are important pollinators of perennial plants with deep flowers in the tropical monsoon forest. Kato et al. (2008) reported that *Amegilla* bees are of two different types, brown-banded (subgenus *Glossamegilla*) and blue-banded (subgenus *Zonamegilla*); the former type is shade-loving and never leaves the dark forest floor while the latter type prefers flying in sunny habitats and in sunbeams streaming through leaves. This behavioural difference corresponds to the light environment at the forest floor, always dark in tropical rain forests but rather bright in

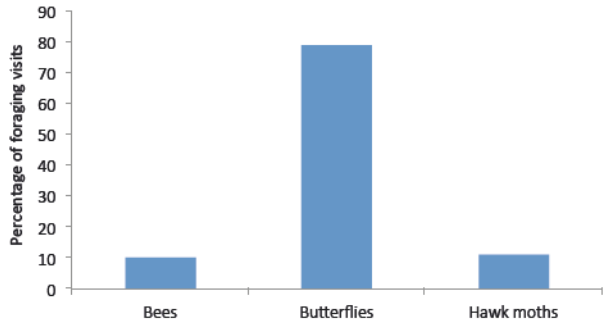

Figure 8. Percentage of foraging visits of different categories of insects on *Pavetta indica*

tropical monsoon deciduous forests, especially in the dry season. In the present study site of tropical monsoon deciduous forest, only blue-banded *Amegilla* bees are present and they fly in sunlight in areas where there is no canopy and fly in areas where sunbeams stream through canopy which consists of new foliage emerged during late dry season. The study suggests that *P. indica* is characteristically psychophilous. Bees foraging on this floral source are opportunists and using it as a potential pollen source.

The fruits of *Pavetta* species attract birds and monkeys which upon consumption of the fleshy part distribute them to different places (Schmidt et al. 2002; Bridson 2003). The black, fleshy fruits of *P. schumanniana*, *P. cooperi* and *P. lanceolata* appear to be dispersed by birds and monkeys (Bremekamp 1934; van Wyk 1974; Kok & Grobbelaar 1984; Johnson & Nichols 2002). In this study, *P. indica* produces fruits within a short time span and displays them on the long pedicels and peduncles. The black, fleshy ripe globose drupaceous fruits stand out prominently against the foliage but they were never used by birds. The fruits fall to the ground when mature and ripe; they remain in the same area and not used by local birds for their dispersal, but the rain water could disperse them to other places through runoff. Since seeds are non-dormant and their dispersal occurs almost in the wet season, they germinate readily but their continued growth and subsequent establishment is subject to the availability of soil moisture and nutrients. Old shoots also produce new branches and leaf flushing during rainy season, and form a part of under-canopy of the forest. Field observations indicated that *P. indica* despite setting significant percentage of fruit set is not able to populate itself in its natural area. Its regeneration failure could be attributed to non-availability of seeds due to their collection by locals to adulterate the commercially important seeds of black pepper, rocky terrain with severe water and nutrient stress, insufficient rainfall and intermittent long dry spells within the rainy season. Further, the use of flowers for the decoration of hair by local women and of different plant parts for treating rheumatic pains by external application are important factors affecting the reproductive success through sexual mode of reproduction, which subsequently affects natural regeneration rate. Therefore, regulation of uses of this plant to enhance fruit set rate, so as to improve regeneration during wet season is essential to ensure the survival and restoration of population of *P. indica* in the natural forests. This will also facilitate the plant to play its role as a keystone species in the ecosystem.

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