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FLOWERING PHENOLOGY, BREEDING SYSTEM, POLLINATORS AND FRUITING BEHAVIOUR OF *PAVETTA TOMENTOSA* (RUBIACEAE) ROXB. EX SM., A KEYSTONE SHRUB SPECIES IN THE SOUTHERN EASTERN GHATS FOREST, ANDHRA PRADESH, INDIA

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ABSTRACT – *Pavetta tomentosa* is a massive bloomer for a brief period during May-June. 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. The papilionid and pierid butterflies, 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 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. Further, the local uses of flowers and leaves of this plant appear to be negatively affecting its reproductive success. *P. tomentosa* serves as a keystone species for bees and butterflies because this is the only prominent and profuse flowering species during dry season in the study region.

KEYWORDS: *PAVETTA TOMENTOSA,* FLOWERING PHENOLOGY, MIXED BREEDING SYSTEM, PSYCHOPHILY, ORNITHOCHORY, KEYSTONE SHRUB SPECIES

INTRODUCTION

Rubiaceae presents a wide range of flower forms, sizes and colours adapted for different types of pollinators. Insects are the major pollinators while birds and bats play a minor role in pollination. Among insects, bees are important pollinators especially for small-flowered species while butterflies and hawk-moths for the large-flowered species. The butterflies are pollinators for scentless flowers while hawkmoths for long-tubed fragrant flowers (Sobrevilla et al., 1983; Hamilton, 1990; Nilsson et al., 1990; Ree, 1997; Consolaro et al., 2005; Puff et al., 2005). *Ixora coccinea* with its fiery red tubular flowers is pollinated by papilionid butterflies (Duara, 2014). *Pagamea duckei* with melittophilous pollination syndrome is pollinated by meliponini bees (Terra-Araujo et al., 2012). In *Psychotria,* many species of bees including those of *Trigona* and *Euglossa,* and some wasps are reported to be efficient pollen vectors (Teixera & Machado, 2004). In *Amaioua guianensis*, large bees such as *Bombus atratus, Centris* sp., *Epicharis flava* and *Eulema nigrita* are the most efficient pollen vectors (Amorim & Oliveira, 2006). Pollination by lepidopterans have been documented in *Psychotria* and *Palicourea* (Castro & Oliveira, 2002; Coelho & Barbosa, 2003). In *Randia itatiaiae*, the flowers are gender-heteromorphic, hypocrateriform and exhale strong sweet smell and their floral morphology precludes pollination by animals other than lepidopterans. The flowers are pollinated by hesperiid butterflies during the day and by sphingid hawk moths at night (Rubem & Freitas, 2011). *Mussaendra frondosa* flowers attract pollinators at short distances while conspicuous, non-rewarding accessory bracts are detectable at long distance by long-ranging

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pollinators. Butterflies, carpenter bees and sunbirds visit the flowers, but only butterflies are legitimate pollinators while the others are nectar robbers. The bracts are white and ultra-violet absorbing, and attract butterflies even in the absence of flowers (Borges et al., 2003). *Ferdinandusa speciosa* is pollinated by hummingbirds (Castro & Oliviera, 2001). *Hamelia patens* with ornithophilous pollination syndrome is pollinated by hummingbirds in Costa Rica (Thomas et al., 1986). But the same species in India is pollinated by honeybees, butterflies, wasps, houseflies, ants and sunbirds. Of these, ants and houseflies are nectar robbers while all other insect groups are pollinators (Chauhan & Galetto, 2009). *Wenlandia glabrata* with psychophilous pollination syndrome is principally pollinated by honey bees in the Eastern Ghats of India (Solomon Raju & Venkata Ramana, 2014). Similarly, *Wendlandia tinctoria* displays psychophilous syndrome; it is principally psychophilous although bees, wasps and flies visit the flowers for forage (Solomon Raju et al., 2012). *Scyphiphora hydrophyllacea* with tubular flowers is pollinated by bees and wind (Solomon Raju & Rajesh, 2014).

The genus *Pavetta* is widely distributed in the Old World tropics from Africa to South East 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). *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. indica* produces white, tubular, actinomorphic hermaphroditic flowers which are foraged and pollinated by Papilionid butterflies (Momose et al., 1998; Kato et al., 2008). *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). *P. tomentosa* is a shrub or small tree with tomentose branches. 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. In the study area, local tribal 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 where available. The white and fragrant nature of the flowers is an added attraction for the women to use them. In areas where the flowers are used in this way, the fruit or seed set rate stands very much reduced due to non-availability of flowers soon after anthesis. Further, the locals apply the leaf sap of this plant externally for relief from rheumatic pains. They collect leaves soon after leaf flushing due to which photosynthetic activity gets affected which in turn would show impact on flowering and fruiting rate. The intent of the present study is to evaluate the floral traits of *P. tomentosa* to characterize the pollination syndrome and its suitability to the local pollinator fauna to effect pollination. The study is also intended to assess the functional breeding systems through which fruit and seed set occurs and finally to examine seed dispersal and seedling aspects. Finally, the study also focuses on the importance of *P. tomentosa* for pollinator fauna.

MATERIALS AND METHODS

Study area

The study area comprises of Seshachalam Hills of southern Eastern Ghats of Andhra Pradesh, India (13°42' N & 79°20' E, elevation 751 m) (Fig. 1). The vegetation is a unique mix of the dry deciduous and moist deciduous types. The terrain undulating with deep forest-covered valleys and characterized by steep slopes, rocky terrain, dry and poor stony soils. The area receives most of the rainfall from northeast monsoon and little from southwest monsoon (Guptha et al., 2012).

Flowering and floral biology

Twenty individuals of *Pavetta tomentosa* were randomly selected for the study during 2014-2015. Flowering season was defined based on regular field trips made. Observations regarding the organization of inflorescences, the spatial

Fig. 1. Map showing the study area.

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. Twenty five mature buds were marked and followed until flower fall to record the timing of anther dehiscence, anthesis schedule and define flower life. 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 another set of twenty five flowers collected randomly from five individuals. 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 individuals were collected and placed in a Petri dish. A single anther was taken out each time and placed on a clean microscope slide (75 x 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 grains. 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. 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 to record 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. Ten flowers were used to determine the average volume of nectar per flower. 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°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°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

Twenty mature buds selected randomly on four individuals were marked and followed until flower drop to define the stigma receptivity duration. 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 to calculate the percentage of fruit set.

Natural fruit set, seed dispersal and seedling ecology

Four hundred and twenty two flowers on ten individuals were tagged prior to anthesis and followed for fruit set rate in open-pollinations. Fruit maturation period, fruit dehiscence, fruit characters and seed characters, seed dispersal aspects were observed in the field. Frugivorous birds feeding on the fruits were recorded and their role in fruit and seed dispersal were observed. Twenty old shoots were marked and followed for the new growth. One hundred and twenty seeds were used to record seed germination and seedling establishment rate during rainy season.

Flower-visitors

Ten fully blooming individuals were randomly selected to record the foraging visits of insects. Flower-visitors were observed and identified by comparing the representative species already identified by the Zoological Society of India and Commonwealth Institute of Entomology, and deposited in the Pollination Ecology Laboratory in the Department of Environmental Sciences, Andhra University, Visakhapatnam. The hourly foraging visits of each insect species were recorded on 4 different days, each day from 06:00 to 18:00 h and the data was tabulated to use the same for further analysis. 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 was observed for ten days, each day from 07:00 to 16:00 h for the mode of approach, landing, probing behaviour, the type of forage collected, contact with essential organs to result in pollination, inter-plant foraging activity in terms of cross-pollination, etc.

Determination of pollen carryover efficiency of insects

The hawk moths captured during morning and afternoon hours and all other flower visitors captured during 10:00-12:00 h 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 proboscides, forehead and wings were used to record the pollen carried by them.

Results

Phenology

The flowering occurs during May-June in all plants irrespective of their occurrence in dry or wet soils. But, the duration of flowering at plant level is three weeks in dry locations while it is nearly two months in moist locations. The flowering phenology recorded for fifteen individuals showed that the flowering is confined to May-June months (Fig. 2).

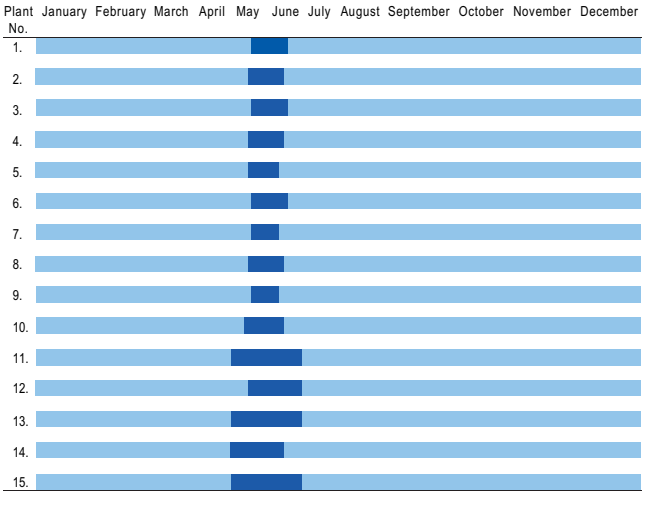

Fig. 2. Flowering phenology of *Pavetta tomentosa*. Dark blue bars indicate peak flowering; Light blue bars indicate no flowering.

Flower morphology

Inflorescence is an axillary long pedunculate densely tomentose, dichotomously branched corymbose cyme consisting of 39.15 ± 4.99 pedicellate flowers which open over a period of 3-4 days (Fig. 3b). Individual flowering inflorescences stand out prominently against the new foliage and are quite attractive from a long distance (Figure 3a). The flowers are white, fragrant, medium-sized (29.8 ± 1.3 mm long and 13.1 ± 0.7 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 (11.1 ± 0.7mm) with four petals (6.4 ± 0.6mm long and 2.8 ± 0.4mm 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 of two ovules slightly immersed in fleshy placenta (Fig. 3g). The total length of the pistil is 30.6 ± 0.8 mm of which ovary is 2.6 ± 0.5 mm long and style and stigma are 28.2 ± 0.7 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 stand far above the anthers.

Floral biology

Mature buds bulge slowly and open during 0600-0800 h and the anthers dehisce synchronously during anthesis by longitudinal slits while the stigma is unreceptive at this time as the its lobes remained appressed. The sub-terminal and terminal portions of the style are continuous, not clearly distinguishable and the stigmatic lobes in appressed state terminate the style (Fig. 3d). 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 (Fig. 3c). The dehisced anthers reflex backwards soon after anthesis. The pollen output per anther is 9964.2 ± 672.02 and per flower is 39,856. The pollen-ovule ratio is 19,928: 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 sexine (Fig. 3f). The style and stigma extend 12-14 mm beyond the height of anthers after anthesis and the stigma attains receptivity around 1600 h 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 (Fig. 3e). The annual 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 5.2 ± 1.26 µl of nectar with 19 ± 3.1% (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 1.06 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.

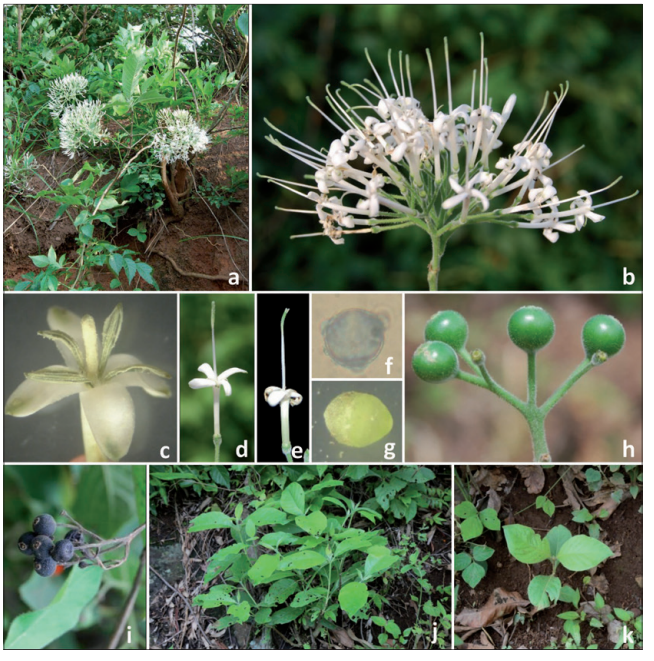

Fig. 3. *Pavetta tomentosa:* **a**) Individual plant in flowering phase, **b**) Flowering inflorescence, **c**) Anthesed flower showing coating of style with self-pollen, **d**) Flower with elongated style with appressed stigmatic lobes, **e** Flower with receptive stigma, **f**) Pollen grain, **g**) Ovule, **h**) Immature fruit, **i**) Mature, pulpy fruits, **j**) Emergence of new branches from old shoot, **k**) Seedling.

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 12% in facilitated autogamy, 57% in geitonogamy, 82% in xenogamy and 35% in open pollinations (Table 1).

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

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	7	12
Geitonogamy	60	34	57
Xenogamy	60	49	82
Open-pollination	422	147	35

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. The first foragers at the flowers were the diurnal hawk moths (*Macroglossum gyrans* and *Cephonodes hylas* (Sphingidae). They foraged during 05:00-07:00 and 16:00-18:00; the flowers foraged by them before 0600 h were 1 or 2 day old ones since the anthesis occurs after 06:00 h (Fig. 4). The bees and butterflies commenced their foraging activity from 07:00 h onwards; the former ceased foraging at 16:00 h while the latter ceased foraging at 14:00 h. Both bees and butterflies showed a gradually increase in foraging visits until 11:00 h and a gradually decrease thereafter until they ceased foraging for the day (Figs. 5-7). The bees and hawk moths contributed 15% each while butterflies contributed 70% of total foraging visits recorded for the day (Fig. 8). The bees were honey bees (*Apis dorsata, A. cerana, A. florea*) and digger bees (*Amegilla* sp.). The butterflies were *Pachliopta aristolochiae, P. hector, Papilio polytes, P. demoleus* (Family - Papilionidae), *Catopsilia pomona, C. pyranthe, Eurema hecabe, Delias eucharis, Anaphaeis aurota, Ixias marianne, Colotis fausta* and *C. danae* (Family - Pieridae). The hawk moths were *Macroglossum gyrans* and *Cephonodes hylas* (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 contact with the stigmas. The butterflies were exclusive nectar foragers and collected nectar with great ease with their proboscides which exceeded the length of the corolla tube. 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 body washings of foraging insects showed variation in the pollen carrying capacity; the average pollen recorded ranged between 65.3-99.2 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).

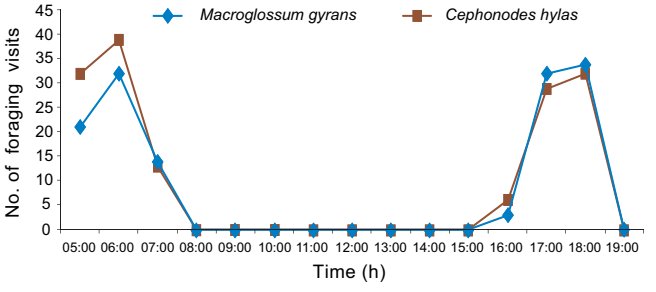

Fig. 4. Foraging activity of diurnal hawk moths on *Pavetta tomentosa.*

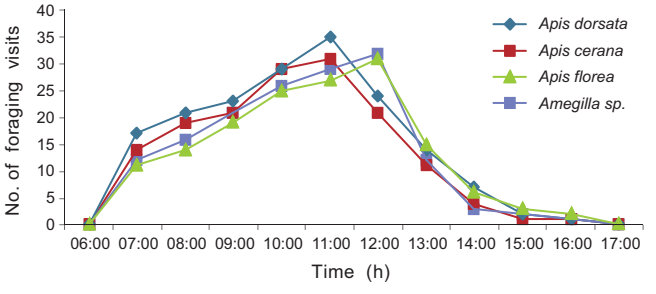

Fig. 5. Hourly foraging activity of bees on *Pavetta tomentosa.*

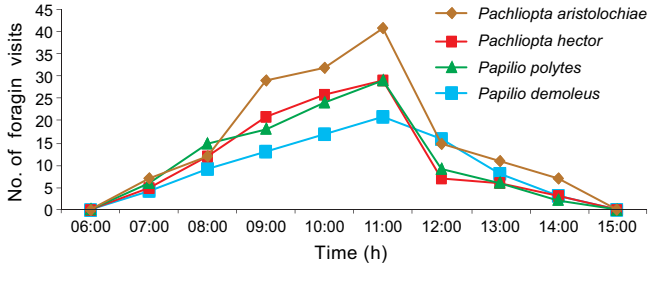

Fig. 6. Hourly foraging activity of Papilionid butterflies on *Pavetta tomentosa.*

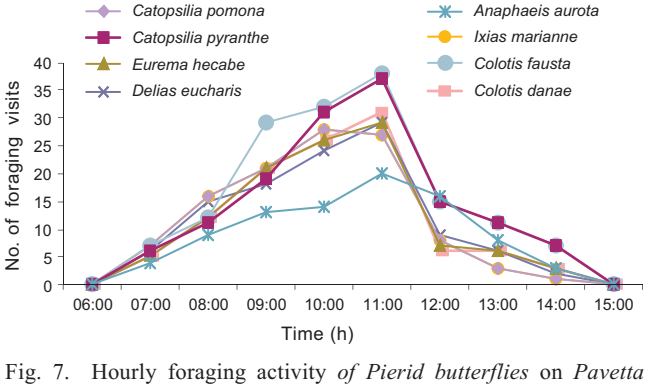

Fig. 7. Hourly foraging activity *of Pierid butterflies* on *Pavetta tomentosa.*

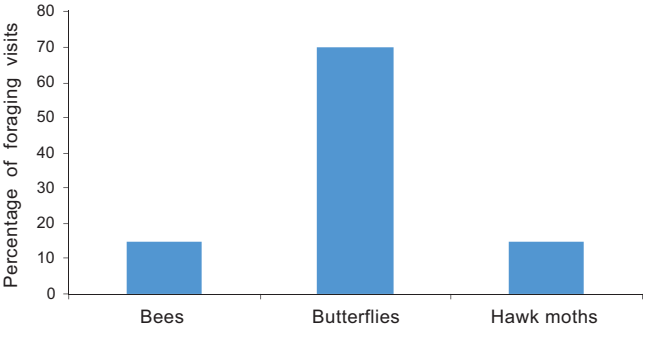

Fig. 8. Percentage of foraging visits of different categories of insects on *Pavetta tomentosa*.

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

Scientific name		Common name
HYMENOPTERA		
Apidae	*Apis dorsata* F.	Rock Bee
	Apis cerana 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
	Anaphaeis aurota F.	Pioneer
	Ixias marianne Cramer	White Orange Tip
	Colotis fausta Wallace	Large Salmon Arab
	Colotis danae F.	Crimson Tip
Sphingidae	*Macroglossum gyrans*	Diurnal hawk moth
	Cephonodes hylas	Diurnal hawk moth

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 (Fig. 3h) and finally black and shiny (Fig. 3i). 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 being pulpy outside the seed attracts birds such as *Acridotheres tristis* (Indian Myna), *Corvus splendens* (House Crow), *Corvus macrorhynchos* (Jungle Crow) and *Turdoides caudatus* (Common Babbler). These birds fed on the pulpy

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

Insect species	Sample size (N)	Number of pollen grains		
		Range	Mean	S.D
Bees				
Apis dorsata	10	93 – 159	127.4	22.43
Apis cerana	10	68 – 102	81.8	13.96
Apis florea	10	51 – 92	73.8	15.99
Amegilla sp.	10	95 – 110	102.1	4.79
Butterflies				
Pachliopta aristolochiae	10	23 – 64	43.5	14.66
Pachliopta hector	10	12 – 31	22.1	6.24
Papilio polytes	10	17 – 42	30.7	8.83
Papilio demoleus	10	10 – 38	24.6	8.50
Catopsilia pomona	10	22 – 47	34.1	7.97
Catopsilia pyranthe	10	34 – 69	49.9	11.61
Eurema hecabe	10	15 – 53	31.9	12.86
Delias eucharis	10	27 – 64	41.9	13.51
Anaphaeis aurota	10	12 – 31	22.0	6.28
Ixias marianne	10	9 – 28	19.0	6.34
Colotis fausta	10	16 – 39	29.7	8.06
Colotis danae	10	20 – 45	33.2	8.9
Hawk moths				
Macroglossum gyrans	10	45 – 78	61.3	11.65
Cephonodes hylas	10	52 – 69	61.1	6.17

part either at the plant site or carried it with their beak to other places where they leisurely consumed the fruit pulp and dropped the seeds. 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 8% of seedlings continued growth while all other seedlings perished subsequently (Fig. 3k). 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. Further, the new leaf growth and subsequent branching formation occurs from old shoots (Fig. 3j). Leaf flushing is quick from old shoots while it is slow from newly emerging plants.

DISCUSSION

The study site of *Pavetta tomentosa* 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 South Asia, the mean temperature drastically increases from January to April and many trees bloom during this dry, hot season. But, the shrub, *P. tomentosa* blooms during May-June when there is sparse 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. tomentosa* 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 - (i) pollen deposition on the style only, (ii) pollen deposition on the style and outside of the non-receptive stigma surface, (iii) pollen deposition on the outside of the stigma, and (iv) pollen deposition exclusively, largely or partly on the receptive surface of the stigma (Puff et al., 2005). In the present study, *P. tomentosa* is characteristically isostylous, protandrous, self-compatible and displays SPP characterized by the presentation of pollen on the style outside of 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. tomentosa* 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. tomentosa* 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. tomentosa* with white, fragrant, tubular flowers with actinomorphic symmetry and functional hermaphroditism is principally pollinated by Papilionid and Pierid butterflies, Sphingid hawk moths, and accidentally pollinated by bees. 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. tomentosa* principally pollinated by butterflies and hawk moths display the characteristics stated by these authors but in this species, nectar guides are totally absent. Beetles never made any visits to the flowers of this species. 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. tomentosa* 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 to 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. tomentosa* in which the nectar is sucrose 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. tomentosa* 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 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 and 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 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. tomentosa* 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. tomentosa* is also a constituent of tropical monsoon forest and pollinated by papilionid and pierid butterflies, and hawk moths. The abundance of these butterflies in this forest during the flowering season of *P. tomentosa* 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. tomentosa* 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 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. tomentosa* is characteristically psychophilous.

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. tomentosa* 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 and attract certain common local birds which disperse seeds after feeding on the fruit pulp. Such a mode of dispersal typifies ornithochory. 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. tomentosa* despite setting significant percentage of fruit set is not able to populate itself in its natural area. The present state of population of *P. tomentosa* could be attributable to several factors such as rocky terrain with severe water and nutrient stress, insufficient rainfall and intermittent long dry spells within the rainy season, and local uses of flowers and leaves by tribal people. Nevertheless, *P. tomentosa* serves as a keystone species for bees and butterflies because this is the only prominent and profuse flowering species during dry season in the study region.

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