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POLLINATION ECOLOGY OF *TARENNA ASIATICA* (L.) KUNTZ EX. K. SCHUM. (RUBIACEAE), A KEYSTONE EVERGREEN SPECIES IN THE EASTERN GHATS FOREST- ANDHRA PRADESH, INDIA

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Abstract – *Tarenna asiatica* flowers throughout the year with profuse flowering during December-April. The flowers are hermaphroditic, self- and cross-compatible, protandrous, nectariferous and entomophilous. The mating system is facultatively xenogamous with highest fruit set in xenogamy. The protandry facilitates autonomous selfing. Bees and butterflies effect both self- and cross-pollinations. Fruits mature within a short period and the fallen seeds germinate following monsoon rains in June-July. A dearth of floral resources exists during December-April period; *T. asiatica* with profuse flowering during this period plays a key role to provide pollen and nectar for the probing flower foragers and hence is considered to be a keystone species in the Eastern Ghats Forest.

Keywords: Jungle forest ecosystem, *Tarenna asiatica*, hermaphroditism, entomophily, keystone shrub species

Introduction

The family Rubiaceae is cosmopolitan in distribution with approximately 13,200 species in 615 genera (Ruhsam et al., 2008). The species are concentrated in warmer and tropical climates around the world. In this family, three sub-families Rubioideae, Cinchonoideae and Ixoroideae have been recognized (Robbrecht & Jean-Francois, 2006). *Tarenna* genus has been assigned to Ixoroideae sub-family (Rova et al., 2002). *Tarenna* consists of approximately 370 species of shrubs and small trees distributed in the old world tropics. The species occur in lowlands as well as at higher altitudes (Mabberley, 1987). They are very common in tropical forests but less in the scrub jungles at an altitude of 1400 m in Sri Lanka, Peninsular India and Malaysia. The species are hermaphroditic, homostylous or heterostylous. The pollination mechanism is conspicuously specialized or unspecialized (Reynolds & Forster, 2005). But, there are almost no studies on the pollination ecology of individual species in this genus. As an initiative, the present study is contemplated to provide the details of pollination ecology of *Tarenna asiatica*. *T. asiatica* is a large compact evergreen shrub which grows up to 6 m tall. The bark is grayish brown, scaly, blaze with orange speckles. Leaves are dark glossy green, oblong to oblanceolate and coriaceous. Complete leaf shedding occurs during summer season from late April to late May in areas where soil is dry and deficient in nutrients. Chetty et al. (2008) reported that this shrub is used in herbal medicine by tribals; the fruits are used for treating boils and indigestion. In the Eastern Ghats Forest representing deciduous forest ecosystem in Andhra Pradesh, India, this shrub has sporadic distribution but serves as a keystone evergreen shrub species with profuse flowering during December-April when certain bees, especially honey bees and butterflies almost confine to this shrub for collecting floral reward(s).

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Materials and methods

Study site

The study region is the southernmost region of Andhra Pradesh and is an integral part of Southern Eastern Ghats of Peninsular India. The area is located at 13°40'N latitude and 79°19'E longitude, and at an elevation of 745 m a.s.l. The exact study area is the forest cover of Tirumala Hills a constituent of Seshachalam Hill Range in Chittoor District, Andhra Pradesh. The deciduous forest ecosystem is distributed in the entire region. The site is characterized by a combination of rocky, undulating and steep terrain with some litter content formed from grass and other herbaceous plants. This forest is known as hot-spot for some rare, endangered, vulnerable, threatened and endemic plants (Chetty et al., 2008). In this area, *Tarenna asiatica* was selected for studying during 2014-2015.

Floral biology

Regular fields visits were made to define the flowering season. Twenty inflorescences were tagged and followed to record the length of flowering and the number of flowers produced. Twenty five fresh flowers were used to record the floral details such as flower shape, colour, odour, sex, symmetry, floral mechanism, calyx, corolla, stamens and style and stigma. Seventy five mature buds were marked to record anthesis and anther dehiscence schedule. The pollen presentation pattern was examined by recording how anthers dehisced, whether all anthers in a flower dehisce simultaneously or not and the same was confirmed by observing the anthers under a 10x hand lens. The just dehisced anthers collected from twenty five bagged flowers were placed in a Petri dish. A single anther was taken 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 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). Then, the number of pollen grains present in each anther was counted. 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. Another set of dehisced anthers was collected in a Petri dish and the pollen removed from these anthers was examined under microscope to record the pollen grain features. The pollen-ovule ratio was determined by dividing the average of the number of pollen grains per flower by the exact number or average number of ovules per flower. The value thus obtained was taken as pollen-ovule ratio (Cruden, 1977). Ten flowers each from five individuals were used to test stigma receptivity. It was tested with hydrogen peroxide from mature bud stage to flower closure/drop as per Dafni et al. (2005). Further, the receptivity was also observed visually whether the stigma is shiny, wet or changing colors or withering. The presence of nectar was determined by observing the mature buds and open flowers. The nectar secreted at flower level was found to be in traces or minute quantity and hence it was not measured. Nectar sugar concentration was determined with great difficulty using a Hand Sugar Refractometer (Erma, Japan).

Pollinator guilds and pollination

The insect species were observed visually and by using binoculars; the insect species that could not be identified on spot were captured and later identified with the help of the identified specimens available in the Department of Environmental Sciences, Andhra University. The hourly foraging visits of each insect species on each plant species were recorded on four different days and the data was tabulated for further analysis. Approximately a patch of seven hundred flowers were selected to record the foraging visits of insects. The data obtained was used to calculate the percentage of foraging visits of each category of insects per day to evaluate the relative importance of each category of insects. The insects were observed on different days for their foraging behavior such as mode of approach, landing, probing behavior, the type of forage collected, contact with essential organs and inter-plant foraging activity. The hourly forage collection activity of each forager species was also recorded to understand whether any relationship exists between standing crop of nectar or pollen and flower visiting activity.

Breeding systems

Mature flower buds of some inflorescences on different individuals were tagged and enclosed in finemesh 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. The percentage of fruit set in each mode was calculated based on the number of flowers set fruit against the number of flowers tagged/bagged.

1. The flowers were fine-mesh bagged without hand pollination to record fruit set in autonomous autogamy.
2. The flowers were manually self-pollinated and bagged to record fruit set in autogamy.

3. The emasculated flowers were pollinated with the pollen of other flowers of the same plant and bagged to record fruit set in geitonogamy.
4. The emasculated flowers were pollinated with the pollen of flowers of other plants and bagged to record fruit set in xenogamy.
5. The inflorescences were tagged and followed to record fruit set in open-pollination mode.

Fruiting behavior

Two hundred flowers on twenty individual plants were tagged prior to anthesis and followed for fruit and seed set for two months. The resulting fruit and seed output were pooled for calculating fruit and seed set rates. Fruit maturation period, the fruit and seed characteristics were recorded. A sample of 162 seeds collected randomly was used to calculate the percentage of viable and in-viable seeds. Seed germination and establishment of new plants were observed briefly by making regular field visits during wet season.

Photography and equipment used

Plant habit, flowers, fruits, seeds and flower foragers 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 while making field observations especially for making flower probing behavior of the insects to note the physical contact between them and the floral sex organs. Magnus Compound Microscope - 5x, 10x, 40x and 100x magnification was used for studying the pollen characteristics. Leica M165C Stereo Computer-assisted Digital Microscope was used for observing finer details of certain studied aspects. Magellan Explorist 210 Model Digital Global Positioning System was used to record the coordinates - latitude and longitude for the study area.

Results

Phenology

During the period from late April to late May, *T. asiatica* does not exhibit either flowering or fruiting. The flowering occurs throughout the year depending on the soil moisture and nutrient status but intense flowering and fruiting is confined to December-April (Fig. 1). Leaf flushing occurs during June-August (Fig. 2a). Inflorescences are trichotomous corymbose cymes and borne terminally at the end of the branches. Individual inflorescence flower for about 10 days depending on the number of flowers produced (Fig. 2b). The average number of flowers in an inflorescence is 24.32± 7.93 (Fig. 2c, d).

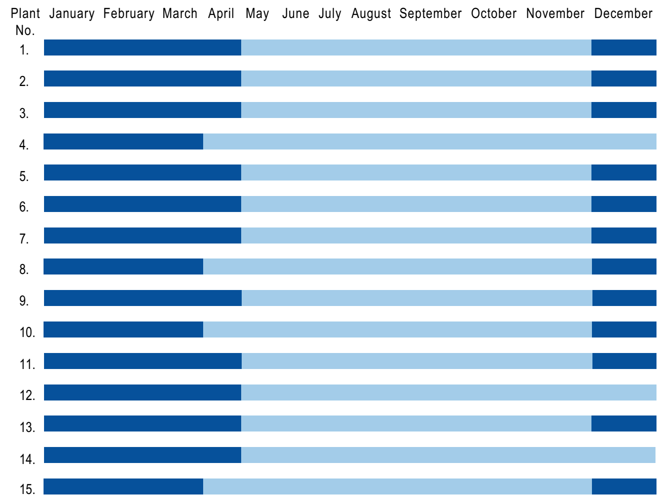

Fig. 1. Flowering phenology of *Tarenna asiatica.* Dark coloured bars indicate Peak flowering and fruiting phase; Light-coloured bars indicate sparse and intermittent flowering and fruiting phase.

Flower morphology

The flowers are short stalked, 13.7 ± 0.6 mm long, 15.9 ± 0.6 mm wide, creamy white, fragrant, actinomorphic and bisexual. The calyx is green, 3.4 ± 0.4 mm and ovoid with 5 lobes. It is persistent and turns into fruiting calyx. The corolla is creamy white, 11.6 ± 0.4 mm, funnel-shaped with 3.4 ± 0.04 mm long and 2.6± 0.4 mm wide tube, villous inside, and terminated with five reflexed lobes, each 8.6 ± 0.4 mm long and 3.6 ± 0.4 mm wide. Stamens are five, 5.6 ± 0.4 mm, inserted at the corolla throat, situated between the lobes, exerted, attached to the throat by 0.5-1 mm long glabrous filaments. Anthers are large, 5.6 ± 0.4 mm long, light green, linear, dithecous, shortly apiculate, introrse and dorsifixed. The ovary is small, hemispherical, 2 mm long, bilocular, each locule has 7.52 ± 1.38 (Range 5-10) ovules arranged on axile placentation (Fig. 2h,i). The style is pubescent, columnar 4 mm long, and extended into fusiform and papillate grooved erect stigma (Fig. 2g).

Floral biology

The flowers open during dusk hours from 16:00-18:00 h. The petals unfold exposing the stigma and stamens which stand at the same height (Fig. 2e). The stamens are protandrous

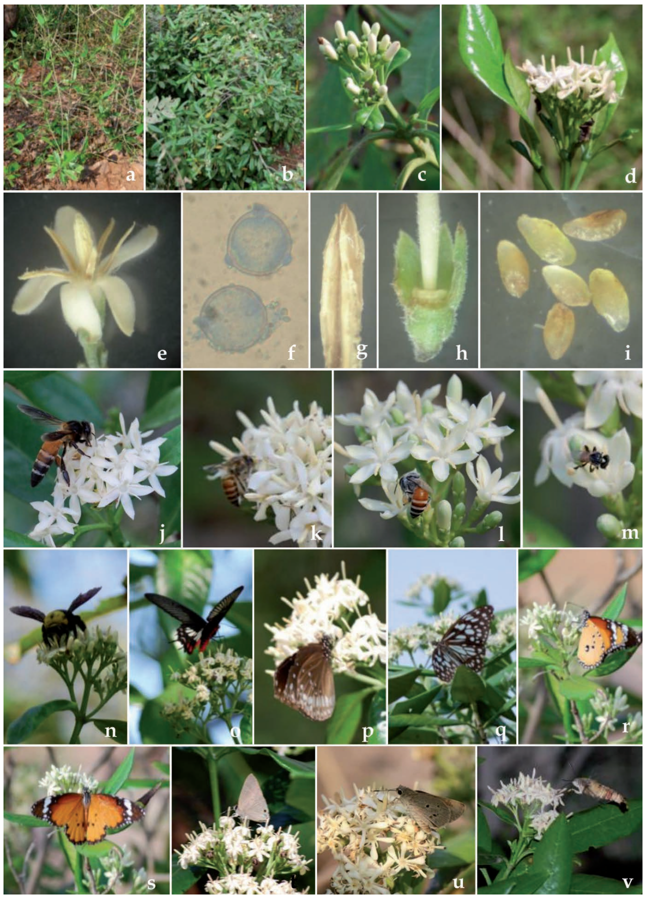

Fig. 2. *Tarenna asiatica*: a. Leaf flushing from old plants, b. Flowering phase, c. Buds, d. Flowers, e. Flower with stamens and pistil, f. Pollen grains, g. Stigma, h. Ovary, i. Ovules, j-v. Insect foragers – j. *Apis dorsata*, k. *Apis cerana*, l. *Apis florea*, m. *Trigona iridipennis*, n. *Xylocopa pubescens*, o. *Pachliopta aristolochiae*, p. *Euploea core*, q. *Tirumala limniace*, r. & s. *Danaus chrysippus*, t. *Jamides celeno*, u. *Suastus gremius*, v. *Cephonodes hylas*.

and anther dehiscence occurs during mature bud stage by longitudinal slits. They gradually bend downwards in a time span of 3-4 hours and move away from the stigma along with the reflexing corolla lobes. The style and stigma remain erect throughout flower life. The dehisced anthers are spreading and twist to the left. Individual anthers produce 13790.2 ± 579.4 pollen grains. A flower produces an average number of 68,951 ± 126 pollen grains. The pollen grains are monads shed as single grains, they are creamy white, tricolporate, circular, powdery and 26.145 ± 2.96 µm in size (Fig. 2f). The pollen-ovule ratio is 9169**:** 1. The stigma is wet during receptive period; the receptivity starts three hours after anthesis and ceases by the noon of the next day. Nectar disc present around ovary produces nectar in minute amount and is collected at the base of corolla tube. The nectar sugar concentration is 22-29%. The flowers fall off at the end of the second day.

Breeding systems

In mature buds, especially during the process of anthesis, the unreceptive stigma is mostly likely to be brushed by the lateral sides of the just dehisced anthers, due to which the papillate, wet stigma is certain to capture pollen. Since the stigma is not receptive at this time, the stigma-pollen interaction does not exist. But, the pollen could germinate on the stigma following the attainment of the receptivity of the latter and hence there is certainty of self-pollination without pollen vector. Keeping this in view, the mature buds were bagged and followed for fruit set. The bagged flowers indicated the formation of fruits and seeds as well suggesting that the flowers are self-compatible and set fruit through autogamy. Fruit set rate is 30% in autonomous autogamy, 40% in hand-pollinated autogamy, 48% in hand-pollinated geitonogamy, 84% in hand-pollinated xenogamy, and 52% in open-pollinations (Table 1). Individual inflorescences produce 9.2 ± 2.3 fruits which account for 37% of the average number of flowers produced.

Table 1. Results of breeding systems in Tarenna asiatica.

Pollination mode	No. of flowers pollinated	No. of fruits formed	Fruit set (%)
Autogamy (un-manipulated and bagged)	50	15	30
Autogamy (hand-pollinated and bagged)	50	20	40
Geitonogamy	50	24	48
Xenogamy	50	42	84
Open-pollination	400	208	52

Pollinator guilds and pollination

The flower buds contain thrips and emerge out as soon as the flower are open. Since nectar is produced in bud stage, the thrips feed on it as soon as it is available. The thrips also feed on pollen following anther dehiscence during mature bud stage. The flowers were not visited by foragers at and after anthesis throughout the night but they were foraged on the following day during day time by honey bees for pollen and nectar while carpenter bees, butterflies and hawk moths for nectar only. The honey bees were *Apis dorsata* (Fig. 2j), *A. cerana* (Fig. 2k), *A. florea* (Fig. 2l) and *Trigona iridipennis* (Fig. 2m). The carpenter bees were *Xylocopa pubescens* (Fig. 2n) and *X. latipes*. The butterflies were *Pachliopta aristolochiae* (Papilionidae) (Fig. 2o), *Euploea core* (Fig. 2p), *Tirumala limniace* (Fig. 2q), *Danaus chrysippus* (Nymphalidae) (Fig. 2r,s), *Jamides celeno* (Lycaenidae)

(Fig. 2t), *Suastus gremius* (Hesperiidae) (Fig. 2u) and *Cephonodes hylas* (Sphingidae) (Fig. 2v). The honey bees and carpenter bees approached the flowers in upright position and held the probing flower with their legs. They accessed nectar located at the flower base with a bit difficulty due to narrow corolla tube. The butterflies also approached the flowers in upright position, landed on the flowers and then probed the flowers with their proboscis for nectar. The bees, papilionid and nymphalid butterflies recorded here were found at the flowers throughout the flowering season but these insects displayed consistent and intense foraging activity during peak flowering phase. The daily foraging activity pattern of the insects indicated that the foraging visits to the flowers were more during 08:00-10:00 h in case of bees (Fig. 3), during 10:00-12:00 h in case of butterflies (Fig. 4) and during 05:00-08:00 h and 16:00-19:00 h (Fig. 5). Overall, the foraging activity of these insects except the hawk moth was intense during forenoon period and gradually decreased towards early evening. The foraging activity ceased at 16:00 h in case of bees and at 15:00 h in case of butterflies. The data of foraging visits made during day time by insects showed that honey bees made 38%, carpenter bees 19%, butterflies 31% and hawk moths 12% of the total visits (Fig. 6).

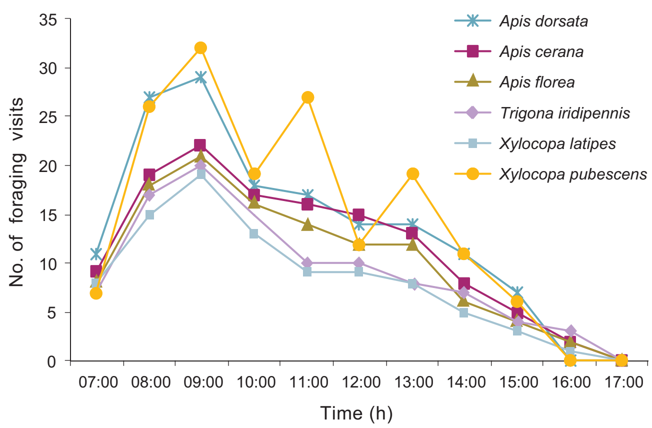

Fig. 3. Hourly foraging activity of bees on *Tarenna asiatica.*

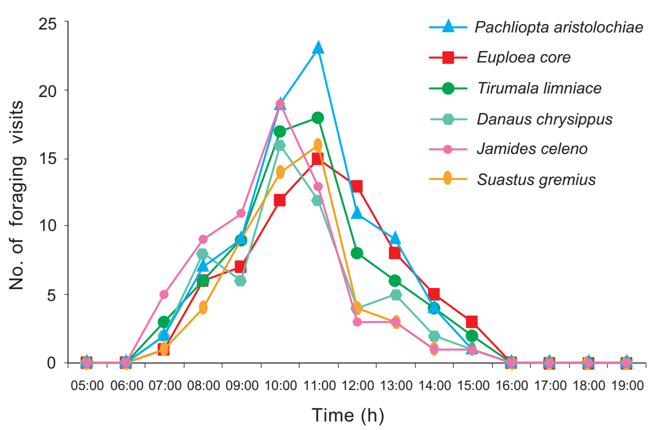

Fig. 4. Hourly foraging activity of butterflies on *Tarenna asiatica.*

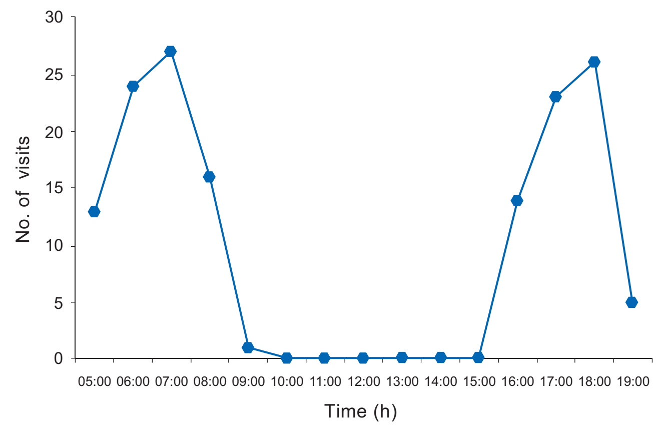

Fig. 5. Hourly foraging activity of the hawk moth, *Cephonodes hylas.*

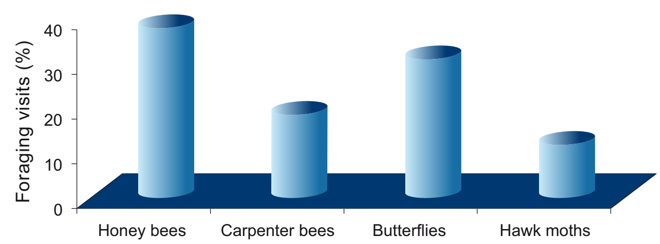

Fig. 6. Percentage of foraging visits of different categories of insects on *Tarenna asiatica.*

The honey bees probed the dehisced anthers for pollen collection; while doing so they invariably contacted the papillate stigma due to its placement in the center of the flower above the corolla throat. Further, these bees and also carpenter bees while collecting nectar had definite contact with the stigma during probing of the corolla tube. The pollen and nectar collecting behavior of honey bees and nectar collecting behavior of carpenter bees were found to be contributing to pollination. The quest for pollen and/or nectar by several individuals of each bee species made them to pay visits to different conspecific individual plants and such visits were considered to be important in effecting and promoting cross-pollination.

The butterflies and hawk moths while collecting nectar had contact with the stigma with their proboscis and with dehisced anthers with the underside of their body. The short corolla tube of the flower facilitated the butterflies and hawk moths to reach nectar location with their long proboscis with great ease. Their nectar collection activity was found to be contributing to pollination. The aggregated arrangement of flowers enabled both bees, butterflies and hawk moths to probe several flowers of the same and/or different inflorescences on the same plant in each visit in succession for nectar before their departure. The insects tended to spend more time at the same flower during forenoon period while they gradually displayed swift movement from flower to flower during the afternoon period. Such a differential length of foraging visits during forenoon and afternoon periods was considered to be related to the levels of standing crop of pollen and/or nectar available in the flowers.

Fruiting behavior

The fruit growth and development begins immediately after pollination and fertilization. The fruits mature within 3-4 weeks depending on the availability of nutrients in the soil. The fruit is small (6 mm across), globose, 2-celled berry; it is green initially and black with a crown of calyx when ripe (Fig. 7a-c). Individual fruits produce 6.02 ± 1.31 (Range = 4–10) kidney-shaped brown seeds which are 3.6 ± 0.4 mm long and 2.3 ± 0.2 mm wide (Fig. 7d). A scan of seeds indicated filled and unfilled ones, the filled ones were considered healthy and viable while the un-filled ones unhealthy and in-viable. The percentage of viable seeds is 76% and that of in-viable ones is 24%. The in-viable seeds could be attributed to those produced from the self-fertilized ovules and to the preferential supply of nutrients to the cross-fertilized ovules by the plant. The seeds germinate soon after seasonal rains that start in June and produce new plants. Seedlings wither away if there is a long dry spell within the rainy season.

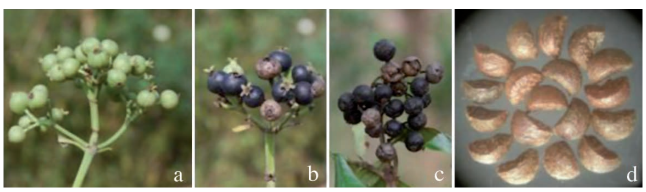

Fig. 7. *Tarenna asiatica*. a-c: different stages of fruit maturation, d: seeds.

Discussion

T. asiatica sporadically distributed in the deciduous and scrub jungle forest ecosystem of southern Eastern Ghats of Andhra Pradesh (India), is evergreen with leaves intact in moisture-rich locations and semi-deciduous with leaf fall in dry locations. Such a situation is indicative of the role of moisture to enable the shrub as evergreen or semi-deciduous one (Chetty et al. 2008). Flowering phenology indicated that the plant flowers throughout the year with profuse flowering during December-April. Such a flowering schedule appears to have evolved as an adaptive response to compete for the available pollinators in order to set fruit to the extent possible, especially through cross-pollination.

In India, Nayak & Davidar (2010) in a study on tropical dry evergreen forest in southern region noted that *Tarenna asiatica* exhibits moth-pollinator syndrome but is visited by honey bees and syrphid flies. These authors however did not provide any further details. In the present study, *T. asiatica* appears prominently because of its creamy white flowers borne in corymbose cymes which are produced at the terminal portion of the branches. Chetty et al. (2008) reported that it flowers and fruits most part of the year in the southern Eastern Ghats of Andhra Pradesh. The present study conducted in the same region showed that its flowering period is largely confined to December-April only. In *T. asiatica*, the dusk anthesis, creamy white and odoriferous flowers suggest that it is adapted for moth-pollination. But, field observations indicated that the flowers were not foraged either by moths or by other insects at or after anthesis throughout the night. The flowers with dehisced anthers during mature bud stage and nectar availability at anthesis are rewarding for insects from anthesis onwards. Since there is no insect activity on the flowers from the dusk time to the morning of the following day, the pollen and nectar remain unutilized and is available throughout 2nd day for day-active foragers. The flowers being protandrous facilitate pollen deposition on the unreceptive stigma during anthesis but the rate of pollen deposition varies depending on the synchrony or asynchrony in the unfolding of all five petals and also relatable to the distance level between dehisced anthers and the centrally situated stigma. The flowers in which the self-pollen deposition occurs on the unreceptive stigma during anthesis and in which self-pollination occurs following the attainment of stigma receptivity end up in fruit set but the percentage of fruit set does not exceed 30%. The fruit set in the absence of insect activity is surely an adaptation for the plant to set fruit in isolated areas where other individuals of this plant species do not occur. The flowers with pollen and nectar unutilized on the day of anthesis attract day-active bees and butterflies on the following day. The short-tubed corolla of *T. asiatica* exposes the nectar due to which the sucrose sugar breaks down into hexose sugars. As a result, the nectar tends to be hexose-rich (Baker & Baker, 1983a,b). The sugar concentration in the nectar is at moderate levels and suitable for utilization by both bees and butterflies (Cruden et al., 1983). Since the flowers produce minute amount of nectar, it is not energetically rewarding for the visiting insects. But, the clustered state of flowers born in corymbose cymes is advantageous for insects to minimize search and flight times in order to get net energy gain. Such a situation stands valid in 2nd day flowers for the forenoon period due to the availability all unvisited flowers and accordingly the foraging activity is very intense during this period. In the afternoon period of the same day, the insect activity is not intense as in the forenoon period; this could be attributed to the extent of availability of standing crop of pollen and nectar. This state of floral rewards compels the foraging insects to do a more laborious search for nectar from a greater number of flowers either on the same or different plants. Since the pollen and nectar requirements of bees are high, they visit conspecific plants to collect the forage as much as possible; the inter-plant foraging activity is further amplified by the foraging visits of honey bees in large groups. This foraging behavior promotes cross-pollination rate. Nayak & Davidar (2010) also reported that *T. asiatica* despite having a moth-pollinator syndrome has not been pollinated by moths following dusk anthesis but has been visited the next day by honey bees and syrphid fly. Westercamp (1991) reported that honey bees are known to be less efficient pollinators compared to other bee species since they are more generalists and collect forage from various floral resources. The authors also noted that considering their abundance and visitation frequencies, the honey bees contribute significantly to pollination especially in degraded habitats.

In the present study, *T. asiatica* occurs in rocky area with little litter content. Honey bees visit the flowers in abundance and exhibit high visitation frequency; such a foraging activity makes them as efficient pollinators. Further, carpenter bees also visit the flowers and they are known as the most efficient pollinators among insects (Solomon Raju & Rao, 2006). Butterflies also exhibit similar foraging behavior and hence contribute to both self- and cross-pollination. The flowers fall off after the loss of stigma receptivity by the end of the 2nd day suggesting that *T. asiatica* does not extend the life of flowers to enhance attractiveness to the foragers. The study shows that *T. asiatica* is entomophilous but melittophily is the primary mode. Further, the plant serves as a major source of pollen and minor source of nectar for five months to its foragers.

Hand-pollination results in *T. asiatica* indicate that all modes of pollination are functional and hence the plant is facultatively xenogamous. The ability to have compatibility to self and cross-pollen and set fruit through self and cross-pollinations appears to be a fail-safe strategy to assure fruit set even in the absence of insect activity. The high natural fruit set rate indicates that sexual reproduction is a great success in this plant in the study localities. Detailed study was not conducted to find out seed dispersal mode in *T. asiatica*. However, preliminary observations indicate that the fruits mature within a short period and seeds fall to the ground. The fallen seeds germinate following monsoon rains in June-July.

In the study region, most of the plant species display leafless state while a few plant species display flowering during December-April. During the same period, *T. asiatica* displays profuse flowering and attracts honey bees, carpenter bees and some butterflies which are appropriate for forage collection from its flowers. This plant offers both nectar and pollen as floral rewards to these insects. Somerville (2000) reported that the pollen provides most of the proteins, amino acids, fats, lipids, carbohydrates, vitamins, minerals and many other requirements of the diet of insects. It is the major source of protein for bees which use it to feed developing larvae and young bees to provide structural elements of muscles, glands and other tissues. Hence, it is an important food source for honeybees and other pollen collecting bees. Rhoades & Bergdahl (1981) reported that in floral nectars, the sugars, amino acids, lipids, and trace nutrients function as pollinator rewards. The nectar of *T. asiatica* is therefore an important floral reward providing different chemical constituents to the pollinators but nectar analysis has not been done due to its secretion in traces/minute amount. Therefore, the nectar characteristics such as volume, sugar concentration, sugar types, and amino acids may make nectar feeding insects to maintain floral constancy. A dearth of floral resources exists during December-April period; *T. asiatica* with profuse flowering during this period plays a key role to provide pollen and nectar for the probing flower foragers and hence is considered to be a keystone species in the Eastern Ghats Forest.

In *T. asiatica*, the year-long flowering continuously produces seeds in batches and disperses them as and when they are due for dispersal; the fallen seeds remain dormant until the onset of monsoon rains. Therefore, the seeds germinate irrespective of their time of production. The rainfall in June-July is the growth period in the southern Eastern Ghats forest ecosystem during which the local plant species produce their populations and provide floral rewards to local flower-dependent insect fauna.

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