# Reproductive ecology of *Mesua ferrea*, a tropical evergreen tree species from India

**Samareddy Sravan Kumar & Aluri Jacob Solomon Raju**

Department of Environmental Sciences, Andhra University, Visakhapatnam 530 003, India, e-mail: solomonraju@gmail.com (corresponding author)

Received: July 21, 2020 ▹ Accepted: February 26, 2021

**Abstract.** *Mesua ferrea* is an evergreen climax tree species and has a single large population across the Eastern Ghats forests of Andhra Pradesh, India. Leaf fall and leaf flushing occur all year long but are especially distinct in January-February. Flowering occurs in February-September, while intense flowering is confined to February-April. The flowers are large, fragrant, hermaphroditic, slightly protogynous. They open in the early morning and close up completely by the noon of the next day. The mating systems involve spontaneous autogamy, vector-mediated autogamy, geitonogamy and xenogamy, indicating functionality of facultative xenogamy by which the tree is able to produce the highest fruit and seed set. Entomophily involves thrips and bees which rather promote autogamous and geitonogamous than xenogamous pollination. Fruits produce 1–4 seeds and seed weight varies according to the number of seeds produced. Fruit dispersal mode is barochory. Seed germination is fast in seeds of 2–4 seeded fruits but germination rate is the highest in seeds of one-seeded fruits. Almost all parts of the tree have traditional and commercial value. Besides, the entire population is still intact as it is treated as a "sacred grove" and protected by local tribes.

**Key words:** barochory, entomophily, facultative xenogamy, *Mesua ferrea*, sacred grove

---

## Introduction

*Mesua ferrea* L. (*Calophyllaceae*) is an evergreen tree species of ecological, medicinal and commercial value. It is widely distributed in Asia's tropical countries, namely, India, Burma, Thailand, China, and New Guinea (Rajalakshmi & al. 2019). The species epithet was derived from the Latin word for 'iron' to refer to the very heavy, hard and durable wood of the tree, which is so dense that even dried wood sinks in water (Orwa & al. 2009). *M. ferrea* is distributed in the mountains of East Bengal and Eastern Himalayas, Assam, Burma, Andaman, and the evergreen rain forests of Uttara Kannada and South Konkan of India (Das & al. 2018). This evergreen climax tree species is found in the tropical rain forests of Northeast India, Western Ghats and Andaman in India, where it is widely cultivated in gardens and avenues for its attractive foliage and flowers. Outside India, it is also distributed in Bangladesh, Myanmar and Sri Lanka (Arunachalam & al. 2003). *M. ferrea* is a characteristic canopy component in the *Myristica dactyloides-Palaquium ellipticum-Olea glandulifera* vegetation type in the evergreen forests of the Western Ghats of India (Ramesh 1989). This species is one of the most famous hardwoods in tropical Asia. Its introduction and cultivation could be traced back to more than 500 years in China (Ming & al. 2015). *M. ferrea* occurs naturally in the northeast and southern parts of India and also in the tropical regions of Cambodia, Malaysia, Myanmar, Philippines, Singapore, Sri Lanka, Thailand, and Vietnam (Khanduri & Kumar 2017). *M. ferrea* grows naturally at low altitudes and has long been cultivated in Tropical Asia (Byrne & al. 2018).

*M. ferrea* has many uses almost across its entire distribution range. The heart wood is very strong and is mainly used for heavy construction, railway sleepers, boat building, agricultural implements, and tool handles. Trunks are often used to make power transmission and telegraphic posts. The flowers, leaves, seeds and roots are used in herbal medicine and as ingredients in incense sticks. The root is used as an antidote for snake bites and scorpion stings. The fresh flowers are prescribed for excessive thirst, excessive perspiration, cough, and for indigestion. The dried flowers are used to stuff pillows and cushions for bridal beds and also for making dyes, cosmetics and soaps. Seeds are powerhouse of energy and proteins. They yield nearly 80 % of oil, which is extracted for lighting and perfumery. In India, *M. ferrea* seeds have been traditionally used for lighting at night for everyday use before the introduction of kerosene (Min & al. 2006), while its fragrant stamens are used as genuine Ayurveda medication to cure bleeding piles (Jadhav & Deodhar 2015). *M. ferrea* flowers, especially petals, emit a sweet aroma and the essential oil extracted from the entire flower is most suitable for body creams and hair oils, as it masks the base odour of cosmetic products. However, a rather large amount of such extracted essential oil is required for the latter procedure. The oil is also incorporated into massage oils for fragrance (Jadhav & al. 2016). Also, the species is used for treatment of various diseases in the Ayurveda, Siddha and Unani systems of medicine (Khanduri & Kumar 2017). Its wood is one of the hardest woods found in Asia and is used for construction work, railway sleepers and in boat building. Oil from the seed is used in soap-making and flowers and flower buds are applied in cosmetics and perfumery (Byrne & al. 2018). The seed oil is used as a substitute for petroleum-derived gasoline. Its other uses are in cosmetics, as firewood, while the polymer obtained from seed oil is applied in the preparation of resins (Chahar & al. 2013). *M. ferrea* is a multipurpose tree, best known for its biodiesel properties with a potential for high oil-seed production and added benefit of growing on marginal lands. The tree species is emerging in the near future as a species with maximized potential for sustainable biodiesel production. The tree is well adapted to a wide range of ecological conditions, which indicates its considerable genetic variability to be exploited for realization of its potential (Das & al. 2018).

*M. ferrea* flowers are partially self-incompatible and the species breeds by spontaneous and vector-mediated pollination, with the lowest fruit set in the former and the highest fruit set in the latter (Khanduri 2016). Its pollen is airborne and provides a scope for anemophily, though it is pollinated by *Apis cerana* and *Xylocopa latipes* (Khanduri & Kumar 2017). *M. ferrea* displays staggered blooming periods and is pollinated by *Xylocopa* bees (Appanah 1985), by lepidopterae (Duara & Kalita 2013) and by *Thrips hawaiiensis* and *Thrips* sp. (Appanah & Chan 1981). With such a backdrop, the present study was aimed at providing comprehensive details on the reproductive ecology of *M. ferrea*, growing as a single large population on an area of about 20 acres in the tropical deciduous forest of the northern part of Eastern Ghats of Andhra Pradesh, India.

## Material and methods

**Study area.** The population is large and consists of 1347 trees growing on an area of about 25 acres located at Uppa, which is about 5 km away from Hukumpeta (Latitude 16°58'12.4716" N, Longitude 81°47'53.9592" E and 1050 m a.s.l) in Visakhapatnam District, Andhra Pradesh, India. The species is a large evergreen climax tree, called locally *Uppachettu*, which forms a unique continuous stretch of population, with a few flowering plant species inside, where open gaps exist. Since it forms a single extensive population, it is called locally the Uppa Forest (Fig. 1a, b) and is an integral part of the tropical deciduous forest of Eastern Ghats of Andhra Pradesh. The entire population is extending along a perennial stream that flows from the uphill forest and along the ridges with shallow soil of the area. Other plant species inside the Uppa Forest include: *Aristolochia tagala* Cham. (*Aristolochiaceae*), *Ficus auriculata* Lour., *Ficus palmata* Forsskal (*Moraceae*), *Mallotus philippensis* (Lam.) Muell. Arg. (*Euphorbiaceae*), *Mangifera indica* L. (*Anacardiaceae*), and *Dregea volubilis* (L.f.) Benth. ex Hook.f. (*Apocynaceae*). In addition to these, the invasive species *Lantana camara* L. (*Verbenaceae*) and *Chromolaena odorata* (L.) R.M. King & H. Rob. (*Asteraceae*) are growing profusely in the open gaps of this forest. These species bloom all year long as the soil is always wet and attract butterflies of various species also right through the year. *C. odorata* also attracts bees to its flowers. *M. indica* flowers early in the dry season and has a partial overlap in flowering with *M. ferrea*. In this area, the annual mean temperatures range from 25 °C to 33 °C, with the maximum in May and the minimum in January. The minimum temperature ranges from 16 °C to 23 °C. The area receives a normal rainfall of 1303 mm, in which the contribution of the southwestern monsoon accounts to 70 %, while the northeastern monsoon contributes up to 24 %. The remaining percentage of rainfall occurs in summer and winter. The soils are red and red sandy. The fieldwork was carried out from December 2017 to May 2019.

**Phenological aspects.** Prior to collecting the data, field visits were made to the Uppa Forest site to record the leaf flushing and flowering times. Prominent leaf flushing, total flowering season and fruiting seasons were recorded during visits to the tree site at fortnight intervals. The flowers were solitary and their place of occurrence on the tree was noted down.

**Anthesis and anther dehiscence.** The flower-opening stage was initially recorded by observing some marked mature buds on the tree. Then the five observations were made on five different days to provide an accurate anthesis schedule. The same mature buds were used to record the time of anther dehiscence. The presentation pattern of pollen was also recorded by observing how anthers dehisced, and subsequently was confirmed by using a 10× hand lens.

**Flower morphology.** The flower morphology details such as flower sex, shape, size, colour, odour, sepals, petals, stamens, and ovary were recorded. The stamens were described in respect of their position, exposed or hidden during the open state of the flower. Duration of the open state of flowers, time of initiation and complete closing of the flowers were recorded. The time of corolla fall was also noted down. These details were collected prompted by the ambiguity and incorrect descriptions of the earlier workers.

**Pollen production.** Ten mature but undehisced anthers were collected from different trees and kept in


**Fig. 1.** *Mesua ferrea:* The Uppa Forest near Hukumpeta in the northern part of Eastern Ghats of Andhra Pradesh.
**a.** Overall view of the population, **b.** Close-up of the population, **c.** Young tree on the periphery of the population.

a Petri dish. A single anther was taken out each time and placed on a clean microscope slide (75×25 mm), crushed with a glass rod and a small drop of lactophenol-aniline blue was added to disperse the pollen grains evenly over the fixed area on the slide. The pollen grains were counted under a compound microscope (40× objective, 10× eyepiece). This procedure was followed for counting the number of pollen grains in all ten anthers. Based on the pollen counts of each anther, the mean number of pollen grains produced per anther was determined. The stamens were numerous and variable and, hence, the total pollen production per flower was not calculated. The pollen grains characteristics were recorded.

**Nectar production.** The presence of nectar was determined by observing the mature buds and open flowers. It was also noted down whether the secreted nectar was in measurable amounts. Since the nectar was secreted in traces, it could not be measured and analyzed for chemical composition.

**Stigma receptivity.** Stigma receptivity was tested with hydrogen peroxide from the mature bud stage to the noon of the 2$^{nd}$ day, by which time the flowers closed back. When applied to a peltate stigma, hydrogen peroxide did not stain but produced bubbles as a result of catalase (peroxidase). This test was widely followed, although it did not indicate the exact location of the receptive area (Dafni & al. 2005). In this study, the period of bubbles release from the stigma surface following application of hydrogen peroxide was adopted as total duration of the stigma receptivity during the flower life.

**Breeding systems.** Breeding systems were tested for apomixis, self-pollination and cross- pollination. For self-pollination, spontaneous autogamy and hand-pollinated autogamy, and hand-pollinated geitonogamy modes were tested. For cross-pollination, xenogamy was tested by hand-pollination. The number of selected mature buds were 20 for each mode of pollination, followed for 45 days for fruit and seed set. Based on the flowers that produced fruits and seeds, the percentage of fruit and seed set was calculated. Some mature buds were emasculated and bagged to test apomoxis. Other mature buds were bagged without emasculation and pollination to test spontaneous self-pollination (autogamy). Thus, some mature buds were bagged, opened on the next day after the occurrence of anthesis, anther dehiscence and stigma receptivity; the stigma was pollinated with pollen of the same flower by a brush and bagged to test hand self-pollination (autogamy). Other mature buds were bagged after emasculation, opened on the next day after the occurrence of anthesis, anther dehiscence and stigma receptivity; the stigma was pollinated with fresh pollen of a different flower from the same tree by a brush and bagged to test hand self-pollination (geitonogamy). And finally, mature buds were bagged after emasculation, opened on the next day after the occurrence of anthesis, anther dehiscence and stigma receptivity; the stigma was pollinated with fresh pollen from flowers of a different tree by a brush and bagged to test hand cross- pollination (xenogamy).

**Fruit and seed set in open pollinations.** Seventy-five solitary flowers, five flowers each from fifteen trees were tagged prior to anthesis and followed for fruit and seed set. Based on the flowers that produced fruits, the percentage of fruit set was calculated. According to the seed-set rate, the fruits were classified into 1-, 2-, 3- and 4-seeded fruits and, accordingly, percentage of the seed-set rate was also calculated.

**Airborne pollen and pollination.** Microscopic slides were coated with petroleum-jelly, fastened horizontally to the top of a 2.5 m long pole erected in the vicinity of the flowering trees and exposed to the air. The slides were placed at 07:00, 09:00, 11:00, 1300, 15:00, and 17:00 h for two successive days during the intense flowering period in the dry season to trap the airborne pollen of the tree. The number of pollen grains per slide was counted on 1 $cm^2$ under the microscope. The pollen was not airborne during 15:00–17:00 h, while at the other times of sampling it was airborne. The pollen trapped by the slides belonged to *M. ferrea* only.

**Flower visitors and pollination.** Mature buds were opened to record whether thrips use them as residents for breeding and feeding. After finding thrips in mature buds, follow-up observations were carried out during the flower-opening period to record the movement and foraging activity of thrips within and between flowers of the same and nearby conspecific flowering trees. Their forage collection activity was noted down with reference to nectar and pollen taken by them, and their role in pollination.

Flowers were observed from morning to evening for five days in the dry season, and for two days in the rainy season to record the flower visitors. The visiting insect species included bees and beetles only during the dry and rainy season. Bees were identified but beetles could not be identified. The approach of flower visitors to the flowers, flower-probing, forage collected by them and the contact of the body parts of the flower visitors with the stigma and stamens were carefully observed by standing close to the flowering tree and also by using a field binocular to record their pollination role. The number of foraging visits made by these insects were recorded at each hour for ten minutes from morning to evening for four days during the dry season and for one day during the rainy season (sunny day), on twenty profusely flowering branches. The consistency and regularity of these insect visits to the flowers were the same during the dry and the rainy season. Data collected on the foraging visits of these insects was tabulated and the mean number of foraging visits at each hour was calculated to understand the foraging pattern of insects across the time. The same data were also used to calculate the percentage of foraging visits made by bees and beetles separately. Ten individuals of each insect species were collected at noontime, killed and brought to the laboratory. In case of bees, the pollen load in the corbiculae was removed prior to their body washings for pollen. In case of beetles, the entire body was washed for pollen. Each insect specimen was thoroughly washed in glycerine with aniline-blue stain on a microscope slide and observed under microscope for counting the number of pollen grains. After counting the pollen from all collected specimens, the range, mean and standard deviation of the pollen grains recovered from each insect species were recorded to evaluate their pollen carryover efficiency.

**Fruit and seed aspects.** Thirty mature buds were tagged and followed for a period of six months to record the fruit growth, development and maturation period. Fruit dehiscence mode and seed dispersal aspects were observed carefully. Fruit and seed morphological characteristics were described to evaluate their role in seed dispersal and germination. Fifty mature and dry fruits fallen under the parental trees were collected to examine whether the vestigial parts of ovules and ill-developed seeds indicating abortion of both fertilized ovules and developing seeds existed or not.

**Seed dispersal and seedling ecology.** One hundred and ten fruits fallen under the parental trees were collected and classified according to the seed number per fruit. Fruits with 1-, 2-, 3- and 4 seeds were separated and then the seeds of each fruit category were individually measured and sown in polythene bags for germination in separate rows in the experimental plot of the Department Garden. The time taken for germination of 1- to 4-seeded fruits was noted and, accordingly, the percentage of germination was calculated to know whether any relationship existed between the seed weight and germination time and percentage. Seedling survival rate of the seeds germinated from 1–4-seeded fruits was visually observed at the tree population site to see the establishment rate, with reference to seed weight.

**Sacred, ecological and medicinal values**. The local tribes living in the nearby tribal hamlet were interviewed about the various uses of *Mesua ferrea* . The information revealed by them was classified into two classes: sacred and medicinal. In terms of the sacred status of the tree population, the locals were interviewed to explain how the tree grove was used for worship and whether any festivals were organized to celebrate some goddesses in this tree grove. In terms of the medicinal values, the locals were interviewed about which parts of the plants were locally used and for what purpose, in order to understand the uses of this tree species in traditional medicine and for other purposes. Field observations were made to see if this tree species was used as a larval host by any lepidopteran species.

## Results

**Flowering phenology.** *Mesua ferrea* is a large, evergreen climax tree growing naturally in the tropical dry deciduous forest of Eastern Ghats. Young trees grow outside the population area as there is plenty of sunlight and comparably little competition for nutrients (Fig. 1c). The trunk is straight, cylindrical and fluted at base; it is usually colonized by lichens (Fig. 2a, b). The bark surface is smooth and irregularly fissured; the outer bark is ash-grey in color, while the inner bark is red to pink. The bark exudes sparse drops of clear whitish to yellow aromatic substance, which eventually darkens upon exposure to sunlight. The leaves are opposite, simple, entire, elliptic, glabrous, and pendulous. Leaf


**Fig. 2.** *Mesua ferrea:* **a. & b.** Trunk with lichen growth, **c. & d.** Leaf flushing stages: purple to creamy, brown to light-green to dark-green in January.

flushing is prominent in January–February and displays different colors. New leaves emerge purplish-red, and turn creamy-brown to light-reen and dark-green with age (Fig. 2c, d). Flowering occurs in February–September, and is intense in February-April (dry season). It is asynchronous within and between the individual trees. In individual trees, sunlit branches display flowering earlier to shaded branches. In this population, the trees facing sunlight most of the day flowered earlier than those exposed to sunlight only part of the day. Individual trees flower profusely for 30–45 days during the dry season and sparsely for 15–20 days during the rainy season. A sub-branch of the tree produces 43.75 ± 2.26 flowers.

**Flower morphology.** The flowers are large, solitary, short-stalked, fragrant, 4.5 ± 0.47 cm long, 9.4 ± 0.51 cm across, born in the leaf axils (Fig. 3a) and also terminal (Fig. 3b). The calyx is green with four large, green suborbicular sepals, and each sepal is 3.5 ± 0.27 cm long, and 3.4 ± 0.19 cm wide. The sepals exude drops of whitish substance, which gradually turns black (Fig. 4a-c). The corolla is large, with four large, white, free, fleshy, retuse, spreading, and wavy petals; each petal is 4.24 ± 0.48 cm long and 4.48 ± 0.27 cm wide. The basal part of the corolla is tinged yellowish on the inner side. The petals surround a central core of yellow-orange filamentous stamens. The stamens are 797.1 ± 43.2 in number long (range 685–864 in number), free, but


**Fig. 3.** *Mesua ferrea:* **a.** Budding stage, **b.** Flowering phase.

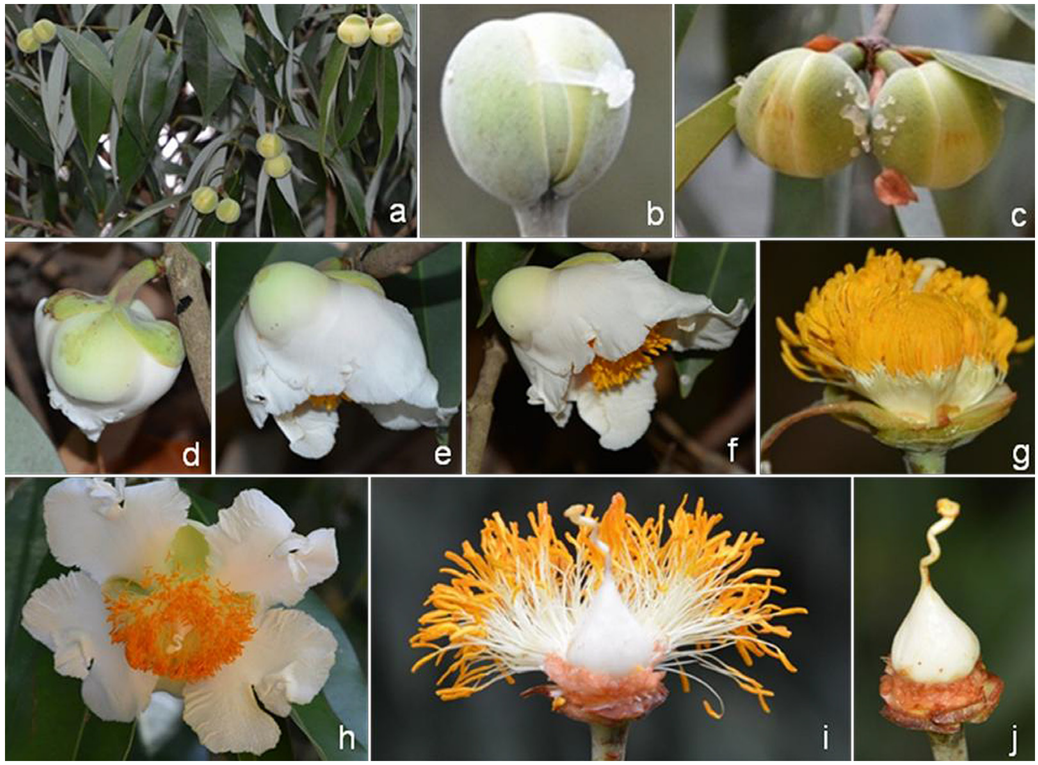


**Fig. 4.** *Mesua ferrea:* **a.** Buds, **b. & c.** Maturing bud with resin secretion from sepals, **d-f.** Anthesis stages, **g.** Position of stamens and stigma, **h.** Fully open flower, **i.** Closely spaced stamens and style and stigma at the same height, **j.** Ovary with style and stigma.

connate at base; the filaments are white, soft, brittle and 1.6 ± 0.12 cm long, while the anthers are golden-yellow, linear, 0.38 ± 0.07 cm long and basifixed. The ovary is globose, 1.1 ± 0.12 cm long, bicarpellary, bilocularly syncarpous, with two anatropous erect ovules in each locule. The style is 1.01 ± 0.11 cm long, slender, subulate, and tipped with a peltate to 4-lobed stigma (Fig. 4j).

**Floral biology.** Mature buds begin to bulge gradually from late evening onwards and open at 04:00–05:00 h, but the corolla becomes widely open at sunrise (Fig. 4d-f). In bud stage, the stamens curve inwards, while style and stigma are twisted (Fig. 4g). During mature bud and flower-opening stage, the corolla gradually unfolds exposing the stamens and stigma (Fig. 4h). By the time the mature bud opens, the style is still in slightly to moderately twisted state, while the stigma stands slightly above the anthers and becomes very distinct against the background of golden-yellow anthers (Fig. 4i). At this stage, the stigma is receptive and remains so until noon of the next day; thereafter, it withers and turns brown and eventually black. The anthers dehisce by longitudinal slits about an hour after anthesis. The pollen grains per anther are 3789 ± 45.69; they are monads, yellow, spheroidal, tricolporate, with long colpi, densely perforated, 21–68 μm on polar axis and 15–62 μm on equatorial axis. The time gap between the commencement of stigma receptivity and dehiscence of anthers is very narrow and facilitates overlapping of male and female phases within the flowers. Nectar is secreted in traces and is available in the open state of the flowers. The corolla closes back gradually, enclosing the stamens and stigma; this process commences around 16:00 h on the day of anthesis (Fig. 5a, b) and is completed at noon of the $2^{nd}$ day (Fig. 5c). The closed flowers remain so permanently, while the corolla drops off either on the evening of the $3^{rd}$ day or before noon of the $4^{th}$ day (Fig. 5d). The stamens gradually wilt and either fall off or remain squeezed between the calyx and growing fruit. The style and stigma are persistent and cast off later. The calyx is persistent, enlarged and thickened during fruit growth and development.

**Breeding system.** Hand-pollination tests have shown that the flowers do not set fruit through apomixis. Fruit set occurs through self- and cross-pollination: 15 % in spontaneous self-pollination, 55 % in hand self-pollination, 75 % in geitonogamy, and 90 % in xenogamy. The corresponding seed set rates for these modes of pollination are 33 %, 48 %, 67 %, and 93 %, respectively. The fruit set is 83 % and seed set is 87 % in open pollinations (Table 1). The results of hand-pollinations hasindicated that the plant is facultatively xenogamous.


**Fig. 5.** *Mesua ferrea:* **a**-**d.** Stages of flower closure in time: **a.** Initiation of flower closure with corolla intact on the evening of the day of anthesis, **b.** Advanced stage of flower closure at forenoon of the 2$^{nd}$ day, **c.** Completely closed flower at noon of the 2$^{nd}$ day, **d.** Corolla drop in late evening of the 3$^{rd}$ day/forenoon of the 4$^{th}$ day.

**Table 1. Results of the breeding systems in *Mesua ferrea*.**

| Treatment | Number of flowers sampled | Number of flowers set fruit | Fruit set (%) | Seed set (%) |
|---|---|---|---|---|
| Apomixis | 20 | 0 | 0 | 0 |
| Spontaneous self-pollination (mature buds just bagged) | 20 | 3 | 15 | 33 |
| Hand self-pollination (flowers hand-pollinated and bagged) | 20 | 11 | 55 | 48 |
| Geitonogamy (flowers hand-pollinated and bagged) | 20 | 15 | 75 | 67 |
| Xenogamy (flowers hand-pollinated and bagged) | 20 | 18 | 90 | 93 |
| Open pollination (flowers tagged) | 75 | 62 | 83 | 87 |

**Airborne pollen and anemophily.** Microscopic slides coated with petroleum jelly were placed at 2.5 m height around the trees and exposed during 07:00–09:00 h and 13:00–15:00 h periods for airborne pollen from the flowers of the plant. During the dry season, the pollen was airborne but the pollen load too small. The pollen load consisted of 27–35 pollen grains per cm$^2$ during the 07:00–09:00 h period and of 37–56 per cm$^2$ during the 13:00–15:00 h period. Occurrence of pollen of this tree in the air indicated that wind has played its role in pollen dispersal. However, field observations have shown that there was a limited scope for pollen dispersal, even if the pollen was airborne, because of the closed canopy structure of the tree population with umbrella-like branches and dense foliage. Therefore, anemophily was almost non-functional.

## Foraging activity and pollination

**Thrips pollination**. The thrips species *Frankliniella schultzei*, *Scirtothrips dorsalis* and *Thrips hawaiiensis* (Thysanoptera: Thripidae) ovi-posited in the early bud stage. The larvae emerged from the eggs in synchrony with flower opening. These species were observed feeding on pollen and nectar as well. Individual thrips were dusted with pollen in their random movements inside the corolla and within anthers, and between anthers and stigma. The pollen surface facilitated the thrips to carry 289 to 531 pollen grains on their body setae, wings and legs. They transported the pollen from anthers and to the peltate stigma; their abdomen was rubbed against the spacious stigmatic surface, and they cleaned their bodily parts with their hind legs and also by their wing combing mechanism. In the tree population, individuals were closely spaced and thrips could fly easily between flowers of the same and of different trees. Such regular and random movements could effect autogamous, geitonogamous and xenogamous pollination. The thrips were resident foragers and diurnal in their activity effecting pollination in open flowers. They also entered the closed flowers easily due to their tiny size and effected pollination, as the stigma was receptive until the noon of the next day.

**Bee pollination**. The flowers were foraged by honey bees *Apis dorsata* (Fig. 6a, b), *A. cerana* (Fig. 6b) and *A. florea*, and the sweat bee *Nomia* sp. (Fig. 6c) in the dry and wet seasons (Table 2). All these bee species foraged for both nectar and pollen during daytime, from 07:00 to 17:00 h, with maximum visits from 10:00 to 13:00 h in the dry season (Fig. 14). They were consistent and regular foragers during the dry season, due to then intense flowering, and inconsistent and irregular foragers during the wet season, when the flowering was not prolific. While collecting pollen, all bee species did


**Fig. 6.** *Mesua ferrea:* **a.** *Apis dorsata* collecting pollen, **b.** *Apis dorsata* (bottom) and *A. cerana* (top) collecting pollen simultaneously on the same flower, **c.** *Nomia* sp. collecting pollen, **d.** Unidentified beetles collecting pollen.

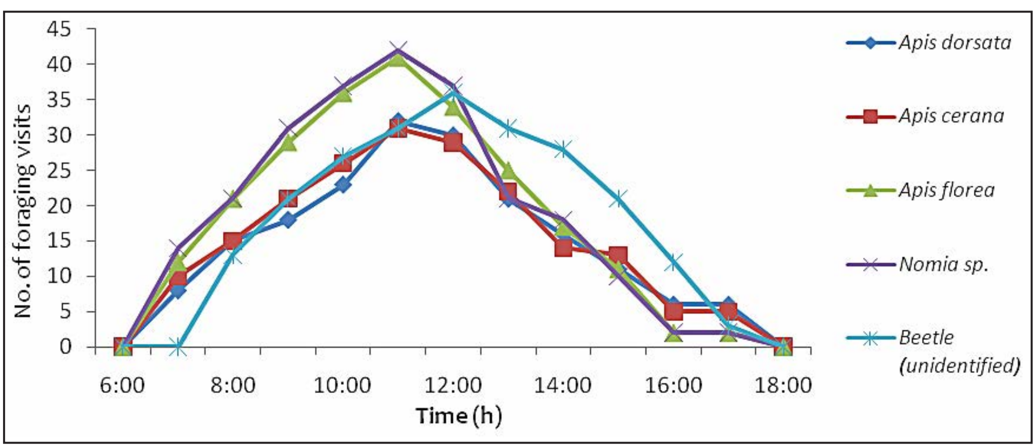


**Fig. 14.** Hourly foraging activity of bees and the beetle (unidentified) on *Mesua ferrea* in the dry season.

**Table 2.** List of insect foragers on *Mesua ferrea*.

| Order | Family | Genus | Species | Common name | Forage sought |
|---|---|---|---|---|---|
| Hymenoptera | Apidae | *Apis* | *dorsata* F. | Rock Honey bee | Pollen + Nectar |
| | | *Apis* | *cerana* F. | Indian Honey bee | Pollen + Nectar |
| | | *Apis* | *florea* F. | Dwarf Honey bee | Pollen + Nectar |
| | Halictidae | *Nomia* | sp. | Sweat Bee | Pollen + Nectar |
| Coleoptera | | Beetle (unidentified) | – | – | Pollen |

not discriminate between the stigma and the anthers and contacted the stigma, while collecting pollen and nectar. The *Apis* bees spent on each flower they visited more than 6–7 minutes, while the *Nomia* bees spent on each flower more than 910 minutes for collecting both pollen and nectar. The long-time visits of each flower by all these bees were considered to be favouring rather autogamy and geitonogamy than xenogamy. Since nectar was available in traces, these bees concentrated more on pollen collection and the collected pollen was transferred to the pollen comb on the hind legs and then combed, compacted and transferred to the corbicula on the outside surface of the tibia of the hind legs. Since each flower produces huge quantity of pollen from numerous anthers, these bees still had considerable number of pollen grains left on their bodies, especially on the ventral side, even after loading the collected pollen into their corbiculae. The mean number of pollen grains recorded on the bodies of these bees varied from 146.6±43.05 to 261.6±68.31: 261.6±68.31 in *A. dorsata*, 248.5±56.73 in *A. cerana*, 208.1±50.83 in *A. florea*, and 146.6±43.05 in *Nomia* sp (Table 3). The number of pollen grains carried by these bees was found to be related to the size of their body and efficiency in forage collection. Individuals of all these bees foraged simultaneously on the same flower for pollen collection without clashing with each other. As the flowers closed back preventing the bees to visit them, the bees collected fresh nectar and pollen from the newly opened flowers daily. Apart from bees, swarms of one beetle species (unidentified) (Fig. 6d) also visited the flowers for pollen during the dry season. This beetle voraciously fed on pollen and also damaged the style and stigma; it collected fresh pollen daily due to closing of the flowers from sunset onwards. It also carried on its body a mean number of pollen grains 111.5±31.5. However, its pollen-feeding activity was considered to be drastically reducing the availability of pollen for pollination purposes and, hence, that beetle species was treated as a pollen robber. Of the total foraging visits made by bees and beetles, the former accounted for 79% and the latter accounted for 21% (Fig. 15), but only the bees were the pollinators.

**Fruiting ecology.** Fertilized flowers initiated fruit development immediately and continued it until maturation. Individual fruits matured within 4–5 months,

**Table 3. Pollen recorded in the body washings of bees and the beetle on *Mesua ferrea*.**

| Insect species | Sample size (N) | Number of pollen grains recorded | | |
|---|---|---|---|---|
| | | Range | Mean | S.D. |
| *Apis dorsata* | 10 | 133–408 | 261.6 | 68.31 |
| *Apis cerana* | 10 | 121–343 | 248.5 | 56.73 |
| *Apis florea* | 10 | 106–302 | 208.1 | 50.83 |
| *Nomia* sp. | 10 | 73–246 | 146.6 | 43.05 |
| Beetle (unidentified) | 10 | 45–168 | 111.5 | 31.50 |

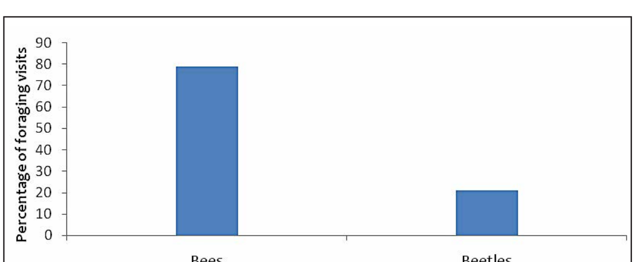


**Fig. 15.** Percentage of foraging visits of bees and the beetle (unidentified) on *Mesua ferrea* in the dry season.

but flowers fertilized during the dry season matured later than those fertilized during the wet season, depending on the soil nutrient and moisture during these seasons. The fruit of *Mesua ferrea* was a capsule, ovoid to ellipsoid, with a conical point, woody, 5–6.5 cm long and 2.5–3 cm in diameter, with a tough pericarp and persistent woody sepals (Fig. 7a-d; Fig. 8a-c). Each fruit contained 1–4 seeds and, accordingly, the fruits were classified as 1-seeded (Fig. 8d), 2-seeded, 3-seeded, and 4-seded. The fruits with one seed accounted for 19%, with two seeds for 31%, with three seeds for 43%, and with four seeds for 7% (Fig. 16). The production of 3-seeded fruits was the highest, followed by 2-seeded, 1-seeded and 4-seeded, respectfully. Fruits were 2–4 valved and dehisce along the valves to expose or disperse seeds, which characteristically occurred during the dry season. However, fruits also detached from the parent-tree without dehiscence during the dry season. In dehiscent fruits, passive seed dispersal was effective in 4- and 3-seeded fruits, while seeds were just exposed and retained in the 1- and 2-seeded fruits. In the rainy season, fruits were usually indehiscent and fell off by gravity, after which gradually decomposed and exposed seeds for subsequent germination. Seeds were glossy-brown, woody and oily; they were egg- shaped in 1-seeded fruits and flattened or irregularly-shaped in 2- to 4-seeded fruits (Fig. 8e, Fig. 9a-c). Selective abortion of ovules in fertilized flowers and of maturing seeds within the fruits occurred commonly. Vestigial parts of aborted ovules and seeds were found in mature fruits.

**Seed germination and seedling establishment.** The 1-seeded fruits were the heaviest and the 4-seeded fruits were the lightest (Table 4). The seed size for 1–4 seeded fruits (SF) was in this order: 1SF>2SF>3SF>4SF, indicating the size of the seed as a direct function of the number of seeds per fruit. Seeds that germinated fast soon produced seedlings, irrespective of the

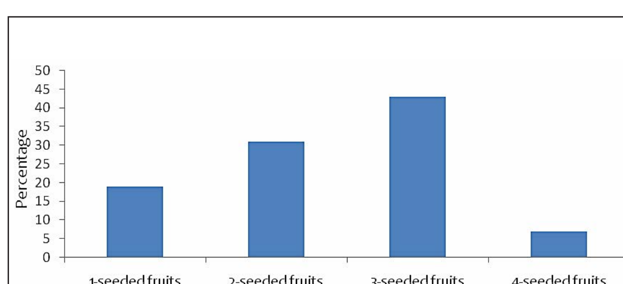


**Fig. 16.** Percentage of 1–4-seeded fruits in *Mesua ferrea*.


**Fig. 7.** *Mesua ferrea:* **a-d.** Stages of fruit development (stamens persistent in withered form).


**Fig. 8.** *Mesua ferrea:* **a. & b.** Mature and dry fruits, **c.** Close-up of dry fruits, **d.** One-seeded fruit, **e.** 2-seeded fruit.


**Fig. 9.** *Mesua ferrea:* **a.** 2-seeded fruit, **b.** 3-seeded fruit, **c.** 4-seeded fruit.

**Table 4. Fresh seed weight and *ex-situ* germination rate from the seeds of 1–4-seeded fruits of *Mesua ferrea*.**

| 1-4-seeded fruits | Fresh seed weight (g) | Rate of seed germination |
|---|---|---|
| Seed from 1-seeded fruit | 6.10–9.10 | 73 |
| Seed from 2-seeded fruit | 4.10–5.70 | 61 |
| Seed from 3-seeded fruit | 2.40–3.90 | 50 |
| Seed from 4-seeded fruit | 1.40–2.30 | 39 |

nutrient status of the soil. However, their further growth was found to be dependent on the availability of nutrients in the soil environment. In the case of seeds of 1-seeded fruits, they germinated slowly and produced seedlings, which got established successfully by utilizing the nutrient reserves sufficiently available within the seed. In the case of seeds of the 2–4 seeded fruits, the amount of nutrients within the seeds was related to the number of seeds produced by the fruits and, accordingly, their success rate in seedling establishment was evidenced in the habitat of the plant (Fig. 10a-f). In the habitat of the plant population, there have been found numerous wilted seedlings formed from 2–4 seeded fruits (Fig. 10 g, h), while wilted seedlings from 1-seeded fruits have been very rare in occurrence. In the *ex-situ* experimental plots, seeds from 2–4 seeded fruits germinated from the 15$^{th}$ day after sowing, while those from 1-seeded fruits germinated from the 24$^{th}$ day after sowing (Fig. 11a-e). Subsequently, seeds from 1-seeded fruits have shown a higher percentage of germination than those from 2–4-seeded fruits. The germination percentage of seeds from 1–4 seeded fruits was as follows: 1SF>2SF>3SF>4SF.

**Ecological, sacred and medicinal value.** The tree population with individuals with umbrella-like branches growing along a perennial stream that flows from the uphill parts and along the ridges with shallow soil at the Uppa Forest is highly suitable for roosting by bats. Locally, there are frugivorous bats *Pteropus giganteus* and *Cynopterus sphinx* but they never use these trees for roosting. During the rainy season, the larvae of a noctuid moth, *Aegilia describens* was found to feed on the leaves of the trees, especially on the young leaves (Fig. 12a-e).

Inside the Uppa Forest, a small temple constructed long ago (Fig. 13a) has been in use for worship by the local tribes during a festival called locally *Gangamma Jatara* and organized in May every year. This temple is an abode of snakes, especially of the venomous Indian cobra, *Naja naja* L. (Order Squamata and family

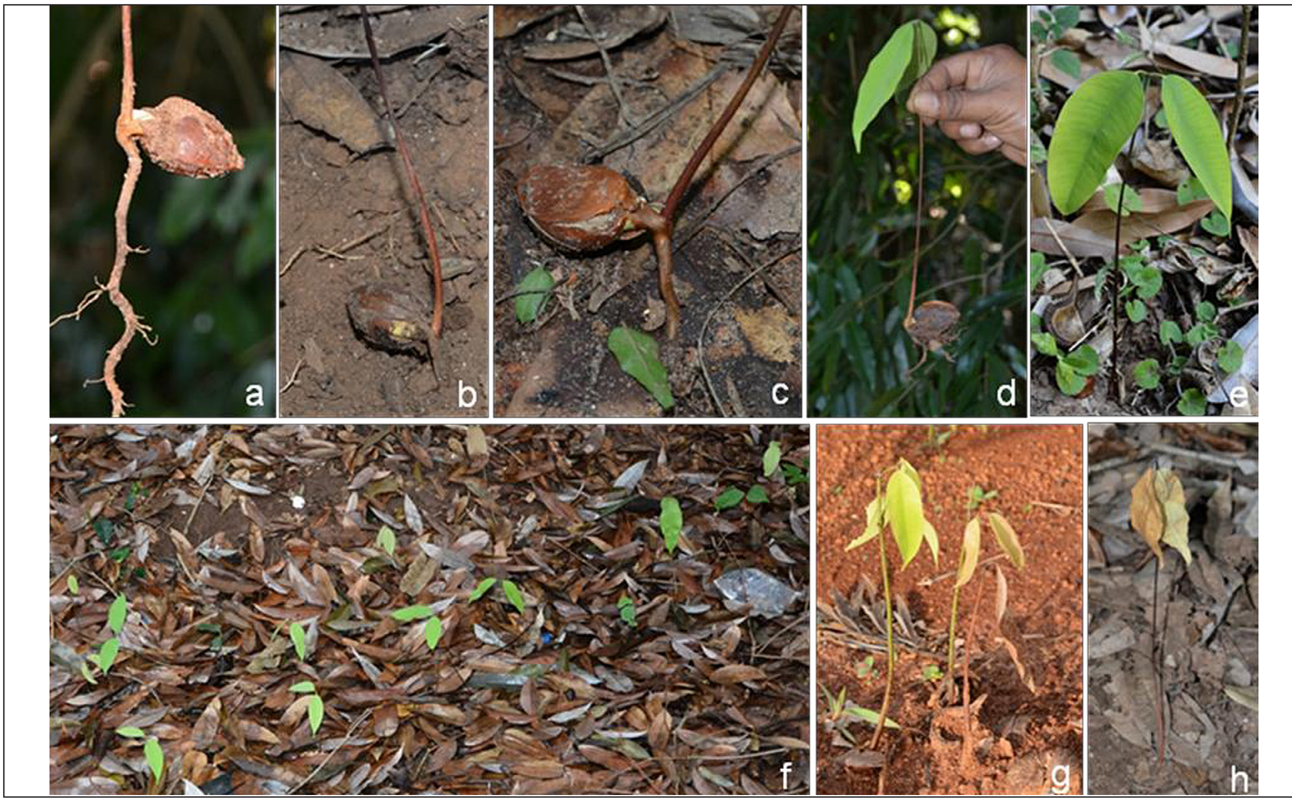

**Fig. 10.** *Mesua ferrea. In-situ* self-recruitment: **a-e.** Stages of seed germination and formation of seedling from 2-seeded fruits, **f.** Seedlings near parental trees, **g.** Initiation of withering of seedlings of the 3–4-seeded fruits, **h.** Complete withering of seedling of the 3–4-seeded fruits.

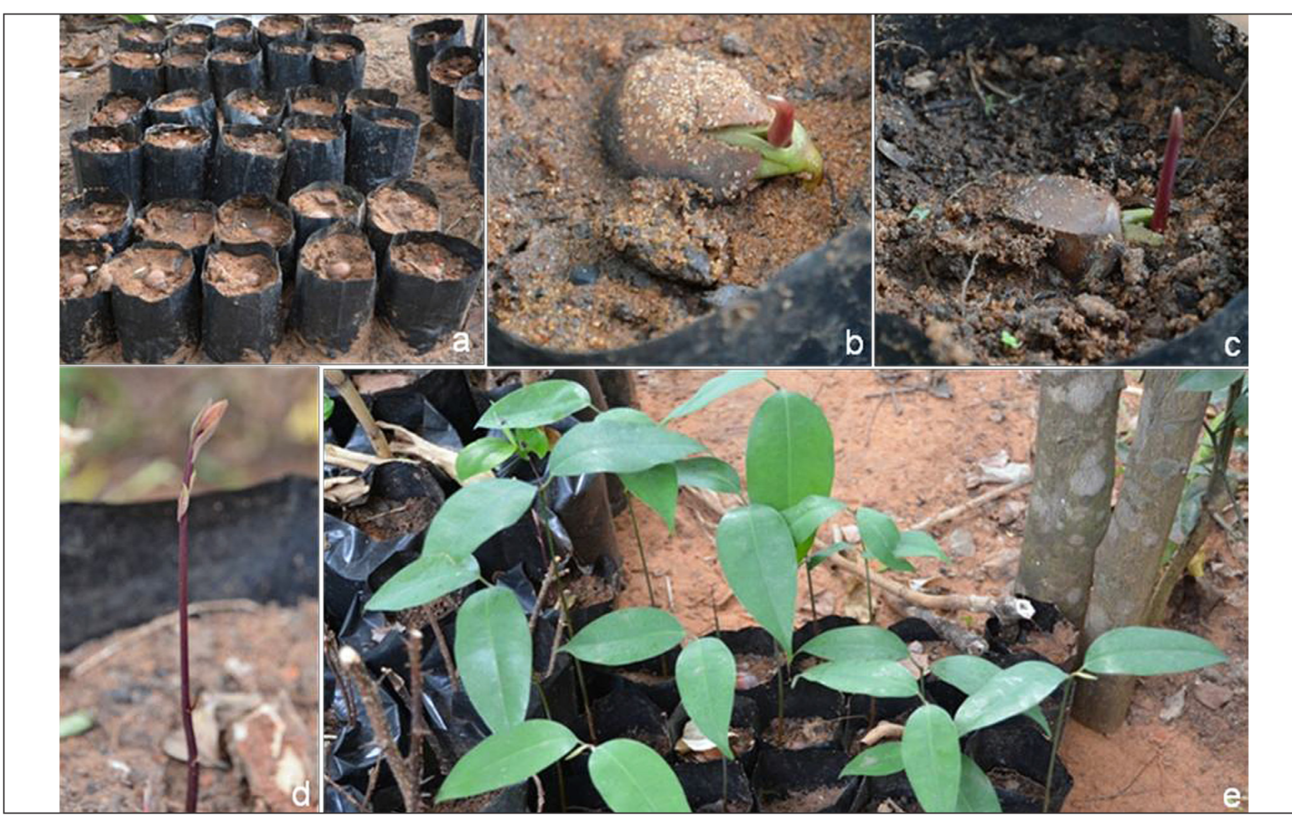

**Fig. 11.** *Mesua ferrea. Ex-situ* seed germination and seedling production: **a-e.** Stages of seed germination and formation of seedlings from the seeds of 1–4-seeded fruits.


**Fig. 12.** *Mesua ferrea:* **a-e.** Larval host plant for the noctuid moth *Aegilia describens*


**Fig. 13.** *Mesua ferrea:* **a.** Temple within the population used for worship by local tribes. Population is treated as a "sacred grove" (Temple is the abode for Indian Cobra, *Naja Naja*), **b-d.** Flowers soaked in pure water produce fragrant colored water used in perfume-making and massages, **e.** Oil produced from seeds is used traditionally for treating skin diseases, for massages and against hair fall, **f. & g.** Traditional use of seeds for lighting at night in the local tribal hamlet.

Elapidae). The locals consider the Uppa Forest "sacred" and do not allow any cutting of the *M. ferrea* trees, hence, the place is regarded as a Sacred Grove. Furthermore, the forest was declared part of the Forest Reserve by the local Forest Department.

The flowers were procured by locals to non-locals for use in perfume-making and massages (Fig. 13b-d). Tribal women were found to use the flowers and leaves for decorating their hair. Seeds were crushed to extract oil for lighting and for treating skin diseases, hair fall and massages by the locals (Fig. 13e). At night, seeds stringed on a long wire burned for lighting (Fig. 13f, g). Interestingly, but the tribes have never indulged in tree felling there for timber or fuel wood, despite its high heat and commercial value.

## Discussion

In India, *M. ferrea* has been reported to be distributed in the evergreen forests of the Western Ghats where it is a characteristic canopy component in the *Myristica dactyloides-Palaquium elliptium-Olea glandulifera* vegetation type (Ramesh 1989), in the tropical rain forests of Northeast India, Western Ghats and Andamans (Arunachalam & al. 2003), in the northeastern and southern parts (Khanduri & Kumar 2017) and in the mountains of East Bengal and Eastern Himalaya, Assam and the Andaman Islands, and also in the evergreen rain forests of Uttara Kannada and parts of South Konkan (Das & al. 2018). There have been no earlier reports of *M. ferrea* being distributed in the Eastern Ghats of Andhra Pradesh. The present study reports first time that *M. ferrea* has naturally a large population spread in an area of about 20 acres of land in the northern parts of the Eastern Ghats of Andhra Pradesh. The forest area where *M. ferrea* population is situated is of the tropical deciduous forest type. The entire population of *M. ferrea* there is treated as sacred by locals. Inside the population of *M. ferrea*, a small temple was constructed long ago for worship by local tribes during a local festival Gangamma Jatara andorganized in May every year. The temple is an abode for snakes, especially of the Indian cobra, *Naja naja*. The study has found that the population of this tree species exists as a side-effect of the "sacredness" attributed to it by the locals and because of being an integral part of the Forest Reserve declared by the local Forestry Department.

Orwa & al. (2009) have reported that *Mesua ferrea* blooms during the dry season and flushing of leaves occurs in the rainy season. Khanduri & Kumar (2017) have reported that *M. ferrea* grows naturally in the northeastern hill region of the Mizoram State, blooms in March-July and the flowering is asynchronous within and between the individuals in a population. Khan & al. (2002) have reported that the sunlit branches of *M. ferrea* engage in heavy flowering because sunlight is highly intensive, which is instrumental for the increase of bud temperature and concentration of growth regulators, particularly of gibberellins. In this study, *M. ferrea* in the tropical deciduous forest of the Eastern Ghats displays leaf fall and flushing across the year, but leaf fall and flushing are especially distinct in January-February and the latter is displayed by a quick shift in leaf colors from purple to creamy-brown, light-green and dark-green, which aesthetically is very appealing to the human eye. The flowering starts in February and continues until September. However, intense flowering occurs in February-April, which coincides with the dry season. The flowering is asynchronous within and between trees of the population which is attributed to the extent and duration of sunlight striking the branches. The sunlit branches flower early and display intense flowering, while shaded branches flower late and display less intense to sparse flowering, depending on the intensity of sunlight striking them. This finding is in agreement with Khan & al. (2002) who have stated that in *M. ferrea* the sunlit branches exhibit heavy flowering. Orwa et al. (2009) have reported that *M. ferrea* produces bisexual flowers, anthesis occurs during 03:00–04:00 h and the flowers close back around sunset. Khanduri & Kumar (2017) have noted that *M. ferrea* flowers open in the forenoon and the anthers dehisce gradually during the day. The flower life span extends to two and a half days in warmer locations and three and a half days in cooler locations. However, the above authors did not provide any details on the floral parts that fall off or remain attached during the fruiting phase.

In the present study, *M. ferrea* flowers have been found to be hermaphroditic and exhibit anthesis during 04:00–05:00 h, irrespective of their position on sunlit or shaded branches. Furthermore, the corolla commences its closure in the evening of the day of anthesis and completes it by the noon of the next day. The closed flowers are persistent, except for the corolla which falls off by the noon of fourth day. The calyx, also persistent, enlarges and thickens, thus providing basal protection to the fruit until maturation. Khanduri & Kumar (2017) have reported that the stigma is slightly protogynous because the stigma becomes receptive at anthesis and the anthers dehisce an hour after anthesis. These authors also mentioned that the stigma remains receptive for two days, indicating the overlapping of both male and female phases. The present study supports the findings of Khanduri & Kumar (2017) that the stigma of *M. ferrea* is slightly protogynous, but there is a long period of overlapping of the male and female phases. During the open state of the flower, the centrally located erect stigma is surrounded by numerous dehisced stamens and the placement of anthers at the height of the stigma facilitates contact with the latter, effecting spontaneous or autonomous self-pollination. However, the extent at which this pollination mode occurs is attributed to the ambient temperature, relative humidity and wind speed. All these three environmental factors are highly favorable for spontaneous pollination during the dry season and less favorable during the rainy season. During the process of corolla closing from the evening of the day of anthesis to the noon of the next day, the inward folding of the corolla enables the stamens to lean towards the stigma, which is still receptive, and make it possible for self-pollen to get onto the peltate stigma surface. Therefore, spontaneous self-pollination occurs structurally, if the stigma is compatible with self-pollen (Cruden & Lyon 1989). The function of self-compatibility and occurrence of spontaneous self-pollination has been carried out by the fruit and seed set in bagged flowers. However, the fruit and seed set rates are the lowest in this pollination mode. Similarly, Khanduri (2016) has also reported that *M. ferrea* flowers are partially self-incompatible and the plant breeds through spontaneous self-pollination with lowest fruit and seed set.

Khanduri (2016) has reported that *M. ferrea* breeds also through vector-mediated pollinations with the highest fruit and seed set rates. Hand self-pollination within (autogamy) and between flowers of the same tree (geitonogamy) and cross-pollination between flowers of different trees (xenogamy) occur, of which the first mode produces the least, the second mode somewhat higher and the third mode the highest fruit and seed set rates. The same author has also stated that high fruit and seed set rates in geitonogamous selfing indicate a possibility for a high rate of inter-flower selfing in the natural pollination, which could be mostly due to pollination by *Apis* and *Xylocopa* bees, weak protogyny and asynchronous flowering among the trees within the population. In the present study, the fruit and seed set rates in *M. ferrea* have been also in the same order in the hand-pollinated autogamy, geitonogamy and xenogamy tests. However, the rates of both fruit and seed set have varied in each mode of pollination. *M. ferrea* with the lowest self-compatibility for spontaneous selfing moderate self-compatibility for geitonogamous selfing, and the highest cross-compatibility for xenogamy displays the facultative xenogamous mating system. This mating system enables the plant to maintain a balance between self- and cross-pollination through pollinator activity. Autogamy, particularly the spontaneous mode, provides reproductive assurance in the absence of pollinators, or when pollinators are unreliable. Such a mating system primarily occurs in climax or other stable communities (Cruden & Lyon 2019). Therefore, being a climax tree species in a stable forest unit at the study site, with a facultative xenogamy mating system, *M. ferrea* is able to produce the highest fruit and seed set as evidenced in the open-pollination mode.

Khanduri & Kumar (2017) have reported that individual flowers of *M. ferrea* contain numerous anthers, which vary from 948 to 1202 in number, and each anther produces 3204–4409 pollen grains. In this study, it has been found that *M. ferrea* flowers produce a mean number of 797 pollen grains and each anther produces a mean number of 3789 spheroidal, tricolporate, monad pollen grains. Cruden & Lyon (2019) have reported that the pollen-ovule ratios of facultative xenogamous species are intermediate between those of xenogamous and facultative autogamous species. Cruden (1977) had come out with an outcrossing index, taking into consideration the breeding system and the pollen-ovule ratio. In this index, he mentioned that the mean pollen-ovule ratio is 796.6 ± 87.7 for facultatively xenogamous species, and 5859 ± 936.5 for xenogamous species. In the present study, the facultatively xenogamous *M. ferrea* with numerous stamens produces huge amounts of pollen, which exceeds the ratio of even xenogamous species as specified by Cruden (1977). The plant might be requiring such a huge amount of pollen to compensate for the pollen loss due to pollen release into the air and the voracious collection of pollen by thrips, bees and beetles, and ensure availability of pollen for pollination when the flower is in open state.

Resins are complex mixtures of substances composed of lipo-soluble volatiles and non-volatile terpenoids and/or other secondary metabolites (Lamgenhein 2003). They are commonly found in vegetative organs but have seldom been reported for floral structures. In *Clusia* of Clusiaceae, the resins produced by vegetative organs attract bees, which inflict injuries on the plant in the process of resin collection for construction of their nests. In the course of time, the wounded flowers might have leaked out resins, which eventually have become a reward to pollinating bees (Gustafsson & Bittrich 2002; Gustafsson & al. 2007). The resins are non-nutritive rewards for certain groups of solitary bees that use them to build their nests (Armbruster 1984; Bittrich & Amaral 1996). These resins are waterproof and have antimicrobial, antifungal, and antiviral properties, which reduce the risk of pathogens in nests and help protecting the bee larvae (Armbruster 1984; Porto & al. 2000). In the present study, it was found that *M. ferrea* sepals secrete or exude a white sticky resinous substance, which turns brownish-black upon drying. However, the flower-visiting bees and beetles have never attempted to collect resins from the sepals, thus suggesting that its secretion has no role in attracting pollinators and, hence, resin secretion is a residual trait still in function from the plant.

Appanah & Chan (1981) had reported that *Thrips hawaiiensis* and *Thrips* sp. acted as pollinators of *Mesua ferrea* flowers between the periods of general flowering of dipterocarps in Malaysia. The present study has testified that different thrips species, *Frankliniella schultzei, Scirtothrips dorsalis* and *Thrips hawaiiensis*, all belonging to the Thripidae family, have used *M. ferrea* flowers for breeding and feeding. Their larvae emerged during the process of anthesis and fed on both nectar and pollen. They were short-distance fliers and their feeding activity within and between flowers of the same tree or nearby trees effected autogamy, geitonogamy and also xenogamy. Since the flowers were solitary, they frequently made visits to different flowers, thus promoting geitonogamous pollination. As the individual trees of *M. ferrea* population were closely situated to each other, thrips easily flied and visited the flowers of different trees and affected xenogamy as well. Therefore, thrips plaid an important role in both self- and cross-pollination, and, hence, thripophily was functional.

Khanduri & Kumar (2017) have reported that *M. ferrea* pollen is airborne and is in circulation in the air almost all day long, but the pollen load recovered from the microscopic slides exposed to the air at plant height has been too small and, hence, anemophily has not been effective. Furthermore, these authors have stated that a strong relationship exists only between the pollinator visitations and pollen deposition on stigmas, indicating that *M. ferrea* is primarily entomophilous. The present study has also indicated that *M. ferrea* pollen is airborne and anemophily is ineffective. Also, the dispersal of airborne pollen by wind is restricted by the closed canopy structure of the tree population and umbrella-like branches with dense foliage of the individual trees. Therefore, with numerous stamens and copious pollen exposed to sunlight, *M. ferrea* in principle is not adapted for anemophily, although there is a scope for its occurrence.

Different authors have reported flower visitors and pollinators of *Mesua ferrea*. It is reported to have been pollinated by *Xylocopa* bees in the climax rain forests of Southeast Asia (Appanah 1985), by lepidopterans in Nambor Doigrung Wildlife Sanctuary, Assam, India (Duara & Kalita 2013), and by *Apis* and *Xylocopa* bees in the northeastern hill region, Mizoram, where the former insects favour the occurrence of self-pollination, while the latter favour the occurrence of both geitonogamy and xenogamy (Khanduri & Kumar 2017). Apart from these reports, Abdullah & al. (2018) have noted that *M. ferrea* is the nectar host plant for several butterflies in the Tasik Kenyir Forest, Terengganu, Malaysia. In the present study, as a climax evergreen tree species in the tropical deciduous forest of the Eastern Ghats, *M. ferrea* has been pollinated exclusively by honey bees and sweat bees. Both classes of bees mostly favour autogamy and geitonogamy due to their long stay on each flower for pollen collection, because pollen is their chief floral reward, while nectar is a minor floral reward offered by the plant. Furthermore, beetles also collect pollen, reducing voraciously the extent of availability of pollen for pollination and by damaging the style and stigma, and thus affecting the fertilization of ovaries. Their feeding activity on floral parts has a negative impact on the fertilization rate of flowers in open pollinations. Nevertheless, *M. ferrea* utilizes thrips and bees as principal pollinators and, hence, the species is entomophilous, involving thripophily and melittophily.

Khan & al. (2002) have reported that *M. ferrea* generally produces more 1-seeded fruits on sunlit branches than on shaded branches. Arunachalam & al. (2003)

have stated that *M. ferrea* produces 1–4-seeded fruits in a varied proportion: the production of 3-seeded fruits is the highest, followed by 2-seeded fruits, while the production of 1- and 4-seeded fruits is much smaller. The present study shows that in *M. ferrea* the production of 3-seeded fruits is the greatest, followed by that of 2-, 1- and 4-seeded fruits, and thus supports the report by Arunachalam & al. (2003).

Uma Shaanker & al. (1988) had pointed out that intra-fruit abortion of fertilized ovules or developing seeds is a common phenomenon in flowering plants. Bawa & Buckley (1988) had stated that many plant species with multi-ovulated ovaries display brood reduction by showing a wide variation in the number of ovules that mature into seeds. Uma Shaanker & al. (1988) viewed brood reduction as a manifestation of genetic load, predation or maternal regulation of offspring quality. In this study, *M. ferrea* with 4-ovuled ovaries has shown distinct variation in the seed weight of 1–4 seeded fruits: the seed weight is the highest in 1-seeded fruits and the lowest in 4-seeded fruits, thus reflecting the accumulation levels of the food reserves.

In other words, seeds from 1-seeded fruits accumulate larger reserves of food than those from 2-, 3- and 4-seeded fruits. Variation in seed-setting rate in fertilized flowers is an indication of selective abortion of fertilized ovules or maturing seeds within the fruits, and it can be attributed to the genetically inferior pollen, particularly the self-pollen that fertilized the ovule(s) of flowers. The aborted fertilized ovules and maturing seeds remain as vestigial and visible in mature fruits. The selective abortion process has been reported to be a common feature in wind-dispersed (Mohan Raju & al. 1996; Uma Shaanker & Ganeshaiah 1988), animal-dispersed (Herrera 1984; Janzen 1982) and explosively dispersed species (Bawa & Buckley 1988; Mitchell 1977). Brood reduction by selective abortion of fertilized ovules and maturing seeds is more frequent in species, whose fruits are dispersed by wind, water or animals than in those species in which the fruit seeds are passively dispersed (Uma Shaanker & al. 1988). Khan & al. (1999) reported that *M. ferrea* disperses the seeds through explosion of the fruit capsule and the seeds produced in the fruits show an equally effective probability of dispersal. Hence, brood reduction as a function of maternal strategy to gain seed dispersal advantage is ruled out. The present study has found that *M. ferrea* fruits do not explode but dehisce exposing the seeds, which subsequently reach ground by gravity. This is especially true for the dry season because the fruits then are indehiscent and fall to the ground during the rainy season. In the observed population, the ambient environmental conditions have not been sufficiently warm to enable the mature fruits to dry up and explode dispersing the seeds, hence, only *in situ* seed dispersal is functional. Joshi & al. (1993) stated that the ovule position within the ovary entiles competition among the siblings for resources. However, in *M. ferrea*, the ovary has two locules with two symmetrically positioned erect ovules in each and, hence, the positional effect that drives siblings to compete for resources is totally ruled out.

Khan & al. (1999) had reported that in *M. ferrea* the percentage of germination, germination time and survival of seedlings is influenced by seed size. Being the lightest, the seeds from 4-seeded fruits germinate faster and achieve a higher germination rate than the seeds from 1-, 2- and 3-seeded fruits. The heavier 1-seeded fruits germinate slower and achieve a lower germination rate but the vigour of their seedlings is greater than of the earlier germinated lighter seeds. This indicates that the greater initial reserves within the seeds play a greater role in the early growth of seedlings than the pre-emption of resources through early germination. Arunachalam & al. (2003) have reported that 1-seeded fruits of *M. ferrea* contain higher carbon reserves sufficient for initial seedling establishment and allocate relatively more vegetative biomass in favour of leaf components and low root-shoot ratio. These food reserves in the 1-seeded fruits give them a competitive reproductive advantage in the habitats, where competition among seedlings of different species exists. Khan & al. (1999) reported that *M. ferrea* with its explosive mode of seed dispersal have scattered seeds under or near the crown edge, thus rendering heavy intra-specific competition for seedling growth. In this study, seeds of 1-seeded fruits have germinated after the germination of seeds of the 2- to 4-seeded fruits but the germination rate of seeds of 1-seeded fruits was the highest. For that matter, the seedlings from seeds of 2–4-seeded fruits wilted quickly, if the soil was deficient in nutrients and moisture. Therefore, the seedlings produced from the seeds of 1-seeded fruits have had the advantage of greater initial reserves and a temporal advantage in reducing competition among the sibling seedlings produced from 2–4-seeded fruits. Although seedlings from 1-seeded fruits had competitive and temporal advantage, they also had to struggle to establish and produce new plants due to low sunlight penetration through the canopy of the tree population.

Kostermans (1980) and Ashton & al. (1997) reported that *M. ferrea* was a slow-growing tree, which developed along streams and on ridges with shallow soil. The present study has also found that the individuals of the population of *M. ferrea* grow along a perennial stream that receives water from an uphill forest and along the ridges with shallow soil of the Eastern Ghats. The root system of this tree is associated with endomycorrhiza, which captures atmospheric nitrogen to benefit the tree in such soil environment (Ashton & al. 1997). In the Xishuangbanna region of Southwest China, *M. ferrea* is used by frugivorous bats, *Rousettus leschenaulti* and *Cynopterus sphinx,* as a feeding roost (Zhan-Hui & al. 2008). In the present study, although there were frugivorous bats, *Pteropus giganteus* and *Cynopterus sphinx*, they never used *M. ferrea* population as a feeding roost. Holloway (1985) had noted that the noctuid moth *Aegilia describens* uses *Mesua ferrea* as its larval host plant. In the present study it has been also found that *A. describens* uses *M. ferrea* as its larval host plant and the larvae feed voraciously on the leaves, preferably the young ones, during the rainy season.

Different authors have reported that different parts of *M. ferrea* have been used across its distribution range in traditional medicine for the treatment of asthma, cough, fever, snake bite, scorpion sting, excessive thirst, excessive perspiration, cough, and indigestion (Min & al. 2006; Teh & al. 2016), as well as to cure various human ailments in Ayurveda, Siddha and Unani systems of medicine (Jadhav & Deodhar 2015; Khanduri & Kumar 2017). The aromatic oil extracted from the flowers is used in body creams, as hair oil, massage oil, for soap-making, in cosmetics and perfumery industries (Jadhav & al. 2016; Byrne & al. 2018). The leaves and flowers are used as hair decorations by women (Byrne & al. 2018). Roots, leaves, flowers, and seeds are used as a source of oil for incense sticks (Min & al. 2006). *M. ferrea* produces very hard wood used for heavy construction, railway sleepers, boat building, agricultural implements, tool handles, power-transmission and telegraphic posts. Dried flowers are used to stuff pillows and cushions for bridal beds (Min & al. 2006; Byrne & al. 2018). Seed oil of *M. ferrea* is the best source for biodiesel and resin production (Chahar & al. 2013). In India, the raw seeds or the oil extracted from them have been traditionally used for lighting until the introduction of kerosene (Min & al. 2006). It has been found in the present study that *M. ferrea* flowers procured by non-locals are used for perfume making and massages. The fruit shell is used as fuel wood. Seed oil of this species traditionally extracted by locals is used for treating skin diseases, for massages, against hair fall and for lighting at night even now. Local tribes do not indulge in tree felling of *M. ferrea* for timber/fuel wood, despite its high commercial value. These various uses indicate that this tree species ensures ecological, medicinal and commercial services. The collection of flowers, fruits and seeds has a great negative impact on the success of sexual reproduction and on the buildup of *M. ferrea* population. Therefore, it is imperative to regulate the collection of these plant products of *M. ferrea,* in order to enable the plant to further build up its population on its own, since this is the only population represented by this tree species that exists in the Eastern Ghats of Andhra Pradesh, India.

## Conclusions

*Mesua ferrea* has a single large population along the entire length of the Eastern Ghats forests of Andhra Pradesh, India. Leaf fall and leaf flushing occur across the year but are especially distinct in January-February. Flowering occurs in February-September, with intense flowering confined to February-April. The flowers are large, fragrant, hermaphroditic, slightly protogynous. They open in the early morning and close again completely by the noon of the next day. The mating systems involve spontaneous autogamy, vector-mediated autogamy, geitonogamy and xenogamy, indicating the functionality of facultative xenogamy. The plant is entomophilous, involving thrips and bees, which promote rather autogamous and geitonogamous than xenogamous pollination. Fruits produce 1 to 4 seeds and seed weight varies according to the number of produced seeds. Barochory is functional, although the fruits are of the dehiscent type during the dry season. Seed germination is fast in the seeds of 2–4 seeded fruits but germination rate is highest in the seeds of 1-seeded fruits. Almost all parts of the tree have traditional and commercial value. Also, the entire population is still intact because of being treated as a "sacred grove" and protected by local tribes.

**Acknowledgement.** The authors are grateful to the Andhra University, Visakhapatnam, India, for providing the facilities to carry out this research work. The first author is thankful to the Ministry of Tribal Welfare, Government of India, New Delhi, for the award of fellowship to pursue this research work.

## References

**Abdullah, M.T., Mohammad, A., Zalipah, M.N. & Lola, M.S.** 2018. Greater Kenyir Landscapes: Social Development and Environmental Sustainability: From Ride to Reef. Springer, Switzerland, 325.

**Appanah, S.** 1985. General flowering in the climax rain forests of South-east Asia. – J. Trop. Ecol., **1**: 225- 240.

**Appanah, S. & Chan, H.T.** 1981. Thrips: The pollinators of some Dipterocarps. – Malaysian For., **44**: 234- 252.

**Armbruster, W.S.** 1984. The role of resin in angiosperm pollination: ecological and chemical considerations. – Am. J. Bot., **71**: 1149-1160.

**Arunachalam, A., Khan, M.L. & Singh, N.D.** 2003. Germination, growth and biomass accumulation as influenced by seed size in *Mesua ferrea* L. – Turk. J. Bot., **27**: 343-348.

**Ashton, M., Gunatilleke, S., de Zoysa, N., Gunatilleke, N. & Wijesundera, S.** 1997. A Field Guide to the Common Trees and Shrubs of Sri Lanka. Wildlife Heritage Trust, Colombo, 432.

**Bawa, K.S. & Buckley, D.P.** 1988. Seed-ovule ratios, selective seed abortion, and mating systems in leguminosae. Missouri Bot. Gard. Mongr. – Syst. Bot., **27**: 243-262.

**Bittrich, V. & Amaral, M.C.E.** 1996. Flower morphology and pollination biology of some *Clusia* species from the Gran Sabana (Venezuela). – Kew Bull., **51**: 681-693.

**Byrne, C., Parnell, J.A.N. & Chayamari, K.** 2018. Systematics of the Thai Calophyllaceae and Hypericaceae with comments on the Kielmeyeroidae (Clusiaceae). – Thai Forest Bull. Bot., **46**: 162-216.

**Chahar, M.K., Sanjaya Kumar, D.S., Geetha, L., Lokesh, T. & Manohara, K.P.** 2013. *Mesua ferrea* L.: A review of the medical evidence for its phytochemistry and pharmacological actions. – Afr. J. Pharm. Pharmacol., **7**: 211-219.

**Cruden, R. W.** 1977. Pollen ovule ratios: a conservative indicator of breeding systems in flowering plants. – Evolution, **31**: 32-46.

**Cruden, R. W. & Lyon, D. L.** 1989. Facultative xenogamy: examination of a mixed mating system. – In: **J. Bock and Y.B. Linhart** (eds), The Evolutionary Ecology of Plants. Westview Press, Boulder, Colorado, pp. 171-207.

**Dafni, A., Kevan, P.G. & Husband, B.C.** 2005. Practical Pollination Biology. Enviroquest Ltd., Cambridge, 590.

**Das, R., Shelke, R.G., Rangan, L. & Mitra, S.** 2018. Estimation of nuclear genome size and characterization of Ty1-copia like LTR retrotransposon in *Mesua ferrea* L. – J. Plant Biochem. Biotechnol., **27**: 478-487.

**Duara, P. & Kalita, J.** 2013. An investigation on the pollinating insects of medicinally important plants. – Int. J. Life Sci. Biotech. & Pharm. Res., **2**: 318-324.

**Gustafsson, M.H.G. & Bittrich, V.** 2002. Evolution of morphological diversity and resin secretion in flowers of *Clusia* (*Clusiaveae*): insights from ITS sequence variation. – Nord. J. Bot., **22**: 183-203.

**Gustafsson, M.H.G., Winter, K. & Bittrich, V.** 2007. Diversity, phylogeny and classification of Clusia. – In: **U. Luttge** (ed.), *Clusia*: a woody neotropical genus of remarkable plasticity and diversity. – Ecological Studies, Vol. **194**., 95-116.

**Herrera, C.M.** 1984. Selective pressures on fruit seediness: differential predation by fly larvae on the fruits of *Berberis hispanica*. – Oikos, **42**: 166-170.

**Holloway, J.D.** 1985. The moths of Borneo: Part. 14. Noct.: Euteliinae, Stictopterinae, Plusiinae, Panthe inae. – Malayan Nature J., **38:** 157-317.

**Jadhav, N.M. & Deodhar, M.A.** 2015. *In-vitro* propagation of aromatic woody plant *Mesua ferrea*. – Linn. J. Plant Sci., **2**: 120.

**Jadhav, N.M., Thergaonkar, R.S. & Deodhar, M.A.** 2016. Extraction of essential oil from flowers of *Mesua ferrea* Linn. GC-MS analysis and incorporation in cosmetic products. – Int. J. Pharm. Sci. Res., **7**: 5106-5110.

**Janzen, D.H.** 1982. Variation in average seed size and fruit seedlings in a fruit crop of a Gunacaste tree (Leguminosae) *Enterolobium cyclocarpum*. – Am. J. Bot., **69**: 1169-1178.

**Joshi, N.V., Uma Shaanker, R. & Ganeshaiah, K.N.** 1993. The 'neighbour effect' and its role in shaping the positional pattern of seed development in fruits: an illustration from the pods of *Erythrina suberosa*. – Curr. Sci., **65**: 234-238.

**Khan, M.L., Bhuyan, P., Shankar, U. & Todaria, N.P.** 1999. Seed germination and seedling fitness in *Mesua ferrea* L. in relation to fruit size and seed number per fruit. – Acta Oecologia, **20**: 599-606.

**Khan, M.L., Bhuyan, P., Singh, N.D. & Todaria, N.P.** 2002. Fruit set, seed germination and seedling growth of *Mesua ferrea* (Clusiaceae) in relation to light intensity. – J. Trop. Forest Sci., **14**: 35-48.

**Khanduri, V.P.** 2016. Mating system and seedling growth of five tropical tree species. – Scientia Forestalis, **44**: 509-517.

**Khanduri, V.P. & Kumar, K.S.** 2017. Pollen production and release in Mesua ferrea Linn. (Guttiferae): aspatio-temporal pattern. – Aerobiologia, **33**: 13-21.

**Kostermans, A.J.G.H.** 1980. Clusiaceae (Guttiferae). – In: **M.D. Dassanayaka and F.R. Fosberg** (eds), A Revised Handbook to the Flora of Ceylon. Vol. I. Oxford & IBH Publishing Company, New Delhi, pp 107-110.

**Lamgenhein, J.H.** 2003. Plant resins: chemistry, evolution, ecology, and ethnobotany. Timber Press, Portland, 586 p.

**Min, B.C., Omar-Hor, K. & Ou-Yang** 2006. 1001 Garden Plants in Singapore. National Parks Board, Singapore.

**Ming, A.G., Zheng, L., Ma, J., Tao, Y., Lao, Q.X. & Lu, L.H.** 2015. Biomass, carbon stock and allocation characteristics in *Mesua ferrea* plantation. – J. Beijing Univ., **2**: 32-39.

**Mitchell, R.** 1977. Bruchid beetles and seed packaging by Pallo Verde. – Ecology, **58**: 644-651.

**Mohan Raju, B., Uma Shaanker, R. & Ganeshaiah, K.N.** 1996. Intrafruit seed abortion in a wind dispersed tree *Dalbergia sissoo* Roxb.: proximate mechanisms. – Sex. Plant Reprod., **9**: 273-278.

**Orwa, C., Mutua, A., Kindt, R., Jamnadass, R. & Simons, A.** 2009. Agroforestree Database: a tree reference and selection guide. Version 4.0. (http://www.worldagrofrestry. org/sites/treedbs/ treedatabases. asp).

Porto, A.L.M., Machado, S.M.F., Oliveira, C.M.A., Bittrich, V., Amaral, M.C.E. & Marsaioli, A.J. **2000.** Polyisoprenylated benzophenones from *Clusia* floral resins. – Phytochem., **55**: 755-768.

**Rajalakshmi, P., Vadivel, V., Ravichandran, N. & Brindha, P.** 2019. Investigation on pharmacognostic parameters of sirunagapoo (*Mesua ferrea* L.): a traditional Indian herbal drug. – Pharmacogn. J., **2**: 255-230.

**Ramesh, B.R.** 1989. Evergreen forests of Biligiri Rangan Hills, South India – ecology, structure and floristic composition. Ph.D. Thesis, University of Madras, Chennai.

**Teh, S.S., Ee, G.C.L., Mah, S.H. & Ahmad, Z.** 2016. Structure-activity relationship study of secondary metabolites from *Mesua beccariana, Mesua ferrea* and *Mesua congestiflora* for anticholinesterase activity. – Med. Chem. Res., **25**: 1-5.

**Uma Shaanker, R., Ganeshaiah, K.N. & Bawa, K.S.** 1988. Parent-offspring conflict, sibling rivalry, and brood size patterns in plants. – Ann. Rev. Ecol. Syst., **19**: 177-205.

**Zhan-Hui, T., Cao, M., Lian-Xi, S., Xun-Feng, M., Walsh, A. & Shu-Yi, Z.** 2008. Seed dispersal of Morus macroura (Moraceae) by two frugivorous bats in Xishuangbanna, SW China. – Biotropica **40**: 127–131.