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# REPRODUCTIVE ECOLOGY OF AN EVERGREEN DRY SEASON-BLOOMING TREE SPECIES, *WALSURA TRIFOLIATA* (A. JUSS.) HARMS (MELIACEAE)

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**Abstract:** *Walsura trifoliata* is an evergreen dry season-blooming hermaphroditic tree species. The flowers are nectariferous and characterized by urceolate androecium, strong protandry and secondary pollination mechanism, protruded bifid stigma displaying receptivity, self-compatibility and facultative xenogamy without the function of spontaneous autogamy. The floral traits indicate generalist pollination syndrome and adaptation for entomophily, with bees effecting mostly geitonogamy and wasps and butterflies effecting mostly xenogamy. Fruit-set is highest in xenogamy. Fruit is a globular drupe with 1-2 seeds embedded in fleshy aril. Seed dispersal modes include zoochory, barochory and hydrochory. The study shows that the function of generalist pollination syndrome, entomophily, facultative xenogamy and polychory enable this tree species to achieve highest fruit-set, maintain genetic variation through cross-pollination, and disperse its seeds to different distances in the forest ecosystem.

**Keywords:** Hermaphrodite, secondary pollination mechanism, facultative xenogamy, entomophily, zoochory, barochory, hydrochory.

## Introduction

Meliaceae is a large family with approximately 50 genera comprising some 620 known species. It is distributed primarily in tropical areas and extends into temperate areas also [5,33]. Many species in this family are commercially important as high-quality timber sources [40]. Several general taxonomic works and local Floras dealing with the Meliaceae [16,20,21,26,29] have stated that the flowers are always hermaphrodite. However, White and Styles [55] documented that hermaphroditism is not fully functional in most of the species of this family. Styles [51] also stated that the structure of Meliaceous flowers suggests that they are entomophilous. Pennington and Styles [39] reported that the variability in floral structure in Meliaceae is most likely to reflect adaptations for specific insect pollinators. Christenhusz and Byng [9] noted that Meliaceae has some duodichogamous species. Rebeca et al. [44] reported that the flowers of Meliaceae are typically provided with a staminal tube, formed by partially or totally fused filaments. This family displays a wide diversity of floral and fruit characteristics, sexual systems and pollination syndromes indicating various evolutionary processes that might have occurred over the course of their natural history. Mabberley and Pannell [32] reported that most species of Meliaceae appear to be insect-pollinated, the agents possibly being bees,

stingless sweat bees or syrphids. In *Trichilia* genus, *T. havanensis* is pollinated by hymenopterans [39] and *T. lepidota* by butterflies, flies, wasps and bees [31]. *Guarea* and *Cedrela* species are pollinated by moths [2, 4] and *Swietenia mahagoni* by thrips [1, 23]. In *Chisocheton* and *Dysoxylum,* some species are purportedly adapted for pollination by moths in the New World and by bats in the Old World [28]. *Dysoxylum spectabile* is pollinated by birds, honeybees and bumblebees [18], *Cabralea canjerana* subsp. *canjerana* by nocturnal moths [17], *Toona ciliata* by insects [58]. In the genus *Turraea*, most species have the style-head acting as a pollen presenter; several species present features of typical hawkmoth pollination syndrome. In *T. vogelioides*, the temporal separation of male and female phases and pollen deposition in the proximal portion of the pollen presenting style-head promote out-crossing and it is pollinated by moths. In *T. floribunda,* the strongly scented petals and staminal tube are more elongated and the style is prominently exserted; the fringe of appendages on the staminal tube enables pollinating hawkmoths to locate visually the narrow entrance to access the nectar [57]. In *Carapa*, most species bear three types of nectaries – extrafloral, petaline and pericarpial. Ants effect pollination while feeding on the exudates produced by the nectaries in these species [27]. Different workers reported on floral sexuality in *Melia azedarach*; it is reported to be hermaphrodite [3, 15, 19] or it produces functionally bisexual and staminate flowers [59] or is monoecious [11]. It is pollinated mostly by moths and bees [34, 59] and mainly by bees [3]. *M. toosendan* is hermaphrodite and pollinated by insects, mainly bees [3].

In India**,** Meliaceae family is represented by 20 genera and 70 species. Chaudhuri [6] reported that Meliaceae has a high degree of endemism. A few studies have been made on the reproductive ecology of members of Meliaceae. *Azadirachta indica* is functionally hermaphrodite and pollinated by honeybees and small carpenter bees [48], wind and insects [43]. *Melia composita* is hermaphrodite, self-compatible, predominantly self-pollinating and frequently pollinated by insects [25]. *Dysoxylum malabaricum* and *Toona ciliata* are hermaphrodite; the former is probably insect-pollinated [24] while the latter is pollinated by thrips and bees [47]. *Xylocarpus granatum* and *X. mekongensis* are monoecious, pollinator-dependent and pollinated by hawkmoths and additionally by bees and butterflies [49].

*Walsura* is a tropical genus of Meliaceae, represented by 15 species in Indo-Malaysia [56] and by 10 species in India [22], of which *W. piscidia* Roxb., now known as *W. trifoliata* (A. Juss.) Harms, is often cultivated for ornamental and medicinal purposes. Chen et al. [7] stated that *Walsura*, comprising 30–40 species, is distributed primarily in mainland China, India, Malaysia and Indonesia. In the Catalogue of Life and the Plants List, 16 species are listed which include *W. bonii, W. candollei, W. decipiens, W. dehiscens, W. gardneri, W. monophylla, W. oxycarpa, W. pachycaulon, W. pinnata, W. poilanei, W. robusta, W. sarawakensis, W. trichostemon, W. trifoliata, W. tubulata* and *W. villosa*. Botanical Survey of India documented that *Walsura* is an Indo-Malesian genus with 10 species but only 7 are distributed in India. They include *W. robusta, W. tubulata, W. candollei, W. perrottetii, W. trifoliata, W. hypoleuca* and *W. oxycarpa* (http://efloraindia.nic.in). Clark [10] reported that most species of *Walsura* are hermaphrodite but certain species such as *W. trifoliata, W. pinnata* and *W. chrysogene* are dioecious. Roubik et al. [45] reported that *Walsura* is visited by *Apis koschevnikovi* in Sarawak. Sosef et al. [50] reported that *Walsura pinnata* is probably insect-pollinated and its fruits are dispersed by birds and gibbons which feed on the fruit pulp. *W. trifoliata* is a small to moderate-sized evergreen tree distributed widely in the tropical dry deciduous forests of Asia such as in

Southern China, India, Malaysia and Indonesia [41]. It is highly reputed in traditional systems of medicine and used by tribal people to treat various diseases like skin allergies, astringent and diarrhoea [8, 41]. Its timber is used for light construction work [46]. The fruit is used in hair washes to kill lice and cure itch, and also as a fish poison [37]. This species is now greatly subject to over-exploitation due to its use in traditional medicine and for timber. In effect, its population is now gradually diminishing in the Eastern Ghats of Andhra Pradesh. Keeping the gradually declining population size of *W. trifoliata* and the lack of reproductive ecology information on this species in view, the present study was initiated to provide details of reproductive ecology of this species to enable the foresters to take measures for the protection of its population in its natural areas in the Eastern Ghats forests of Alluri Sitharama Raju District in Andhra Pradesh State. The aim of this study is to know the floral morphological and functional traits that characterize the pollination syndrome, assess the sexual system and breeding systems to understand their role in the promotion of pollination and fruit-set rate, identify the pollinator fauna and their role in self- and/or cross-pollination, and record fruit/seed aspects and seed dispersal agents of *W. trifoliata*.

## Materials and Methods

**Flowering season and floral biology:** *Walsura trifoliata* trees growing at Modakondamma Padalu (Latitude 18.0795°N and Longitude 82.6621°E) and Lambasingi forest locations (Latitude 17.8186°N and Longitude 82.4922°E) in Alluri Sitharama Raju District, Andhra Pradesh, India, were used for the present study from June 2021 to December 2022. Field observations were made to record flowering period, floral biology, foraging activity and pollination, breeding systems, and fruiting and seed dispersal aspects. Fifty flowers from ten trees were collected to describe morphological aspects of flowers briefly because of reports of inconsistencies on these aspects in the literature. Fifty mature buds tagged on ten trees were followed for recording the timing of anthesis and anther dehiscence. A 10x hand lens was used to confirm the dehiscence time and mode. Stigma receptivity was observed by using $H_2O_2$ test described in Dafni et al. [12]. In this test, the period of release of bubbles from the stigma surface following application of $H_2O_2$ was recorded as the total duration of stigma receptivity during flower life.

**Nectar analysis**: The presence of nectar was determined by gently pulling a flower from its calyx and firmly pressing its base against a hard surface. Twenty-five mature buds which were about to open were bagged before sunrise and removed at midday to measure total nectar produced by each flower by inserting a micropipette into the flower base. Since nectar was not secreted after noon, the flowers were not monitored thereafter during the entire period of their lifespan. The average volume of nectar produced by all these flowers was taken as the total volume of nectar/flower and expressed in µl. The nectar produced in these flowers was used for measuring nectar sugar concentration and then for calculating the mean sugar concentration. Hand Sugar Refractometer (Erma, Japan) was used for measuring nectar sugar concentration.

Nectar analysis for sugar types was carried out using the Paper Chromatography method described in Dafni et al. [12]. Nectar was spotted on Whatman No. 1 filter paper along with the standard samples of glucose, fructose and sucrose. The paper was run ascendingly in chromatography chamber for 24 hours with a solvent system of n-butanol-acetone-water in the ratio of 4:5:1 sprayed with aniline oxalate spray reagent and dried at 120$^{o}$C in an electric oven

for 20 minutes for the development of spots from the nectar and the standard sugar samples. The spots thus developed were compared with those of the standard sugar samples to record sugar types present in the nectar.

Paper chromatography method described in Dafni et al. [12] was followed for identifying the amino acid types present in the nectar. Nectar was spotted on Whatman No. 1 filter paper along with the standard samples of 21 amino acids, namely arginine, tyrosine, alanine, aspartic acid, amino butyric acid, cysteine, cystine, glutamic acid, glycine, histidine, hydroxy-proline, isoleucine, leucine, lysine, methionine, phenylalanine, proline, serine, threonine, tryptophan and valine. The paper was run ascendingly in a chromatography chamber for 24 hours with a solvent system of n-butanol-acetic acid-water in 4:1:5 ratio. The chromatogram was detected with 0.2% ninhydrin reagent and dried at 85$^{o}$C in an electric oven for 15 minutes for the development of spots from the nectar and the standard amino acids. The developed nectar spots were compared with those of the standard amino acids to record the amino acid types present in the nectar.

**Pollen analysis**: The protocols described by Mondal et al. [36] were followed for identifying amino acid types present in the pollen. Pollen was collected from mature anthers and filtered through sieving using meshes of different size (100, 200 and 300 µm) to remove the debris. Then, the pollen was rapidly dried over silica gel at 30°C and stored. Free amino acids were extracted from the pollen using the method of Bieleski and Turner described in Mondal et al. [36]. Later, the extract thus obtained was used for the qualitative analysis of the free amino acids of pollen using thin layer chromatography.

**Foraging behavior and pollination:** Field observations were made on the foraging activity of insects before sunrise, after sunset and during daylight hours. The foraging schedule, forage collected and the flower probing behaviour of each insect species was recorded. The number of foraging visits made by each insect species was recorded for 15 minutes at each hour during the entire length of the observation period to examine the pattern of foraging activity according to the availability levels of nectar and pollen. This field observation on foraging activity of insect species was repeated on four clear sunny days and the data thus collected were used to calculate the average number of visits made by each species at each hour of the day and the percentage of foraging visits by each category of insect species to record the foraging rate of individual insect species and each insect category. The foraging behavior of each insect species was observed with reference to its approach, landing, probing behavior employed for pollen collection and contact with essential organs in effecting pollination.

**Breeding systems and fruit set in open-pollinations:** Breeding systems were tested for different modes of self-pollination, and cross-pollination. Spontaneous autogamy was tested by bagging individual flowers without hand-pollination. Mature buds were bagged, opened the next day after the occurrence of anthesis, anther dehiscence and stigma receptivity; the stigma was pollinated with the pollen of the same flower using a brush and bagged again to test hand self-pollination. Mature buds were bagged after emasculation, opened the next day after the commencement of stigma receptivity; the stigma was pollinated with the fresh pollen of a different flower of the same plant using a brush and again bagged to test geitonogamy. Mature buds were bagged after emasculation, opened the next day after the occurrence of stigma receptivity; the stigma was pollinated with the fresh pollen from the flowers of a different plant using a brush and again bagged to test xenogamy. The bagged flowers were followed for 30 days for fruit-set. Based on the flowers that produced fruits, the percentage of fruit-set was calculated.

Five flowers each from ten trees were tagged prior to anthesis and followed for fruit set in open-pollinations. The percentage of fruit set was calculated based on the number of fruited flowers. Fruits are 1- to 2-seeded but seed-set rate was not calculated in any mode of pollination.

**Fruit and seed characters and seed dispersal:** Fruit and seed characters were described in view of the reports of inconsistencies on these characters. Field observations were made on fruit dispersal agents and the role of dispersal agents was briefly described. Brief field observations were made on the production of new plants from seed to record vegetative growth and development.

## Results

**Phenology:** It is a moderate-sized evergreen tree with pale brown slightly fissured brittle bark. Leaves are imparipinnate, tri-foliate, spirally arranged, glabrous, ovate to elliptic and shiny. Leaf fall and flushing events occur simultaneously throughout the year and this pattern contributes to evergreen status of the tree. Initiation of floral buds occurs in the 1$^{st}$ week of January while flowering commences in the 2$^{nd}$ week of February at population level. Further, peak flowering appears in the 1$^{st}$ week of March and termination of flowering takes place in the 2$^{nd}$ week of April at population level (Fig. 1a,b). This pattern of flowering at population level characterizes almost synchronous flowering. The inflorescence is corymbosely branched, of dense heads of flowers borne at the ends of secondary rachides, 8.84 ± 1.94 cm long with 182.4 ± 62.4 flowers (Fig. 1c) and stands out prominently above the foliage to display the flowers to the intended foragers.

**Floral morphology:** Flowers are mildly fragrant and hermaphrodite. The stamens have connate filaments to about half of their actual length forming a staminal tube basally while the upper half is free and bi-dentate at apex in which the bi-locular short-beaked creamy-coloured anthers are inserted (Fig. 1g). The connate and free portion of the stamens is hairy inside. The nectary disk is annular, shallow, fleshy and well developed; it is seated above the ovary around the style base between the connate portion of the stamen tube and the creamy white pistil and its inner surface is lined with a large number of trichomes. The ovary is 2-celled, each with 2 collateral ovules (Fig. 1i,j). The style is short and capitate to conical in shape with 2 protruded, vertical wet and shiny stigmatic lobes.

**Floral biology:** Mature buds are open during 0800–1000 hrs (Fig. 1d). The process of bud opening involves only the unfolding of petals exposing the urceolate staminal tube with anthers inserted in the apical bi-dentate filamentous sheath, which almost lie on the rim of capitate style-head throughout the flower life (Fig. 1e,f). The anthers dehisce by longitudinal slits shortly before the petals unfold and the pollen from anthers is brushed to the rim of capitate style-head which is unreceptive to pollen during the entire period of flower life. The bi-lobed stigma protrudes from the centre of the capitate style-head about 4 hours after anthesis displaying instantaneous receptivity to pollen; the stigma receptivity ends by the evening of the next day. The pollen grains are monads, slightly sticky, light yellow, prolate-spheroidal, 29.05 ± 4.3 µm, tetra-colporate with smooth exine and thickened at apertures (Fig. 1h). The pollen has 5 essential amino acids which include threonine, methionine, leucine, lysine and arginine, and 5 non-essential amino acids which included alanine, amino-butyric acid, cystine, glycine and hydroxy proline (Table 1). Individual flowers produce 0.8 ± 0.29 µl of nectar with sucrose, glucose and fructose sugars; the total sugar concentration stands at 27 ± 2%. The nectar contains

6 essential amino acids namely threonine, valine, leucine, isoleucine, histidine and arginine, and 9 non-essential amino acids namely, alanine, amino-butyric acid, cysteine, cystine, glutamic acid, glycine, hydroxy proline, proline and serine which are required for flower-visiting insects (Table 1).

**Table 1: Essential and non-essential amino acids present in the pollen and nectar of *Walsura trifoliata***

| Amino acid type | Essential amino acids | | Amino acid type | Essential amino acids | |
|---|---|---|---|---|---|
| | Pollen | Nectar | | Pollen | Nectar |
| Threonine | + | + | Alanine | + | + |
| Valine | - | + | Amino butyric acid | + | + |
| Methionine | + | - | Aspartic acid | - | - |
| Leucine | + | + | Cysteine | - | + |
| Isoleucine | - | + | Cystine | + | + |
| Lysine | + | - | Glutamic acid | - | + |
| Phenylalanine | - | - | Glycine | + | + |
| Histidine | - | + | Hydroxyproline | + | + |
| Arginine | + | + | Proline | - | + |
| Tryptophan | - | - | Serine | - | + |
| + = Present; - = Absent | | | Tyrosine | - | - |


**Fig. 1: *Walsura trifoliata*:** a. & b. Flowering phase, c. Flowering inflorescence, d. Anthesis initiation, e. Position of stamens and pistil, f. Pistil enveloped by staminal column, g. Insertion of anthers in the teeth of staminal sheath, h. Pollen grain, i. Pistil, j. Ovules.

**Secondary Pollen Presentation Mechanism:** In open flowers, the style-head is capitate without any projection from its centre and this portion is non-receptive to pollen. However, bifid stigma springs out from the centre of capitate style-head about 4 hours later to anthesis. The stigmatic lobes commence receptivity to pollen instantaneously and continue to be receptive until the evening of the following day, although the flowers remain in place for another two days showing signs of fading and withering. The anthers lie on the capitate style-head throughout the flower lifespan and in this situation, the pollen released upon anther dehiscence becomes attached automatically to the rim of the capitate style-head and this portion of the style-head simply acts as pollen presenter facilitating the occurrence of cross-pollination until the time of protrusion of bifid stigma in the presence of foraging activity by insects which remove/collect most of the self-pollen by the time of commencement of stigma receptivity and limit the

occurrence of vector-mediated autogamy. Further, the temporal separation of male and female phases for a brief period displayed by protandry and secondary pollen presentation largely facilitate the occurrence of geitonogamy.

**Foraging activity and pollination**: Bees, wasps and butterflies visited the flowers as soon as they are open. They do not visit flowers opened on previous days. However, it was not clear whether they were able to distinguish between virgin and mature flowers after the occurrence of anthesis. The bees included 6 species, namely *Apis dorsata* (Fig. 2a), *A. cerana* (Fig. 2b), *A. florea* (Fig. 2c), *Trigona iridipennis*, *Ceratina* sp. (Fig. 2d) and *Xylocopa* sp. (Fig. 2e). The wasps included only 2 species, *Stilbum superbum* (Fig. 2f) and *Eumenis conica* (Fig. 2g). The butterflies included 3 papilionid species, 1 pierid species, 6 nymphalid species, 2 lycaenid species and 2 hesperiid species (Table 2). The papilionids were *Pachliopta hector* (Fig. 3a), *Graphium agamemnon* (Fig. 3b) and *G. sarpedon* (Fig. 3c). The pierid was *Delias eucharis* (Fig.3d). The nymphalids were *Euploea core* (Fig. 3e,f), *Junonia lemonias* (Fig. 4a), *Neptis hylas* (Fig. 4b), *Parantica aglea* (Fig. 4c), *Phalanta phalantha* (Fig. 4d) and *Tirumala limniace* (Fig. 4e). The lycaenids were *Jamides celeno* (Fig. 4f) and *Leptotes plinius* (Fig. 4g). The hesperiids were *Hasora chromus* (Fig. 4h) and *Pelopidas mathias* (Fig. 4i). All these insects visited the flowers during daytime from 0900 to 1700 hrs with peak foraging activity at 1000–1100 hrs (Fig. 6,7). All bee and butterfly species visited the flowers sporadically only in the afternoon period while the wasp species ceased their foraging activity at 1500 hrs. All these insects collected nectar, but the bees collected pollen also. They approached the flowers in an upright position, landed on the petals and then probed the flowers for nectar by inserting the tongue/proboscis through the narrow gap between the appendages of the staminal tube and the style-head. Since the staminal tube is short, these insects accessed the nectar location with great ease. All these insects collected pollen and/or nectar during unreceptive and receptive stigma phases of flowers; pollen was carried away without pollination effect by them during unreceptive phase of the style-head while pollen transfer and pollination occurred during receptive phase of the bifid stigma of the style-head. The insects approached the flowers in an upright manner, landed on the urceolate staminal tube and inserted their tongue/proboscis through the narrow gaps between the staminal tube and style-head to collect the nectar seated at the ovary base. In flowers with the unreceptive phase of the style-head, the forehead and tongue/proboscis/ventral side of abdomen of insects invariably made contacted with the rim of style-head lined with pollen. In consequence, the pollen was transferred to these parts of the insects and the pollen thus carried away by the insects was transferred to other conspecific flowers in their successive foraging visits for nectar and/or pollen collection. Pollination occurred only when they visited the flowers with receptive style-head. In flowers with a receptive style-head, the insects first contacted the protruded bifid stigma portion of the style-head with their forehead and the ventral side of their body; then pollen transfer to the receptive bifid stigma of style-head occurred if the insect had visited the flowers previously and carried pollen on their dorsal side. As a result, either self- or cross-pollination occurs depending on the pollen source. In flowers with unreceptive style-head, this bee gathered pollen from the rim of the capitate style-head and in this act, the bees packed pollen into the pollen basket. The pollen basket is a particular arrangement of hairs that occur on the tibia of the hind legs of the bees. The packed pollen was then easily carried away by the bee and transferred to the receptive bifid stigma of the style-head.

**Table 2: List of Insect foragers on *Walsura trifoliata***

| Order | Family | Insect species | Common name | Forage sought |
|---|---|---|---|---|
| Hymenoptera | Apidae | *Apis dorsata* F. | Rock honey bee | Pollen + Nectar |
| | | *Apis cerana* F. | Asiatic honey bee | Pollen + Nectar |
| | | *Apis florea* F. | Dwarf honey bee | Pollen + Nectar |
| | | *Ceratina* sp. | Small carpenter bee | Pollen + Nectar |
| | | *Xylocopa* sp. | Large carpenter bee | Nectar |
| | Chrysididae | *Stilbum superbum* L. | Cuckoo wasp | Nectar |
| | | *Eumenes conica* F. | Mason wasp | Nectar |
| Lepidoptera | Papilionidae | *Pachliopta hector* L. | Crimson Rose | Nectar |
| | | *Graphium agamemnon* L. | Tailed Jay | Nectar |
| | | *Graphium sarpedon* L. | Common Bluebottle | Nectar |
| | Pieridae | *Delias eucharis* Drury | Indian Jezebel | Nectar |
| | Nymphalidae | *Euploea core* Cramer | Common Crow | Nectar |
| | | *Junonia lemonias* L. | Lemon Pansy | Nectar |
| | | *Neptis hylas* L. | Common Sailor | Nectar |
| | | *Parantica aglea* Stoll | Glassy Tiger | Nectar |
| | | *Phalanta phalantha* Drury | Common Leopard | Nectar |
| | | *Tirumala limniace* Cramer | Cramer | Nectar |
| | Lycaenidae | *Jamides celeno* Cramer | Common Cerulean | Nectar |
| | | *Leptotes plinius* F. | Zebra Blue | Nectar |
| | Hesperiidae | *Hasora chromus* Cramer | Common Banded Awl | Nectar |
| | | *Pelopidas mathias* F. | Small Branded Swift | Nectar |


**Fig. 2: *Walsura trifoliata*:** a-e. Bees – a. *Apis dorsata*, b. *Apis cerana*, c. *Apis florea*, d. *Ceratina* sp., e. *Xylocopa* sp., f. & g. Wasps – f. *Stilbum superbum*, g. *Eumenes conica*.


**Fig. 3: *Walsura trifoliata:* Butterflies:** a-c. Papilionids – a. *Pachilopta hector*, b. *Graphium agamemnon*, c. *Graphium sarpedon*, d. Pierid, *Delias eucharis*, e. & f. Nymphalid, *Euploea core*.

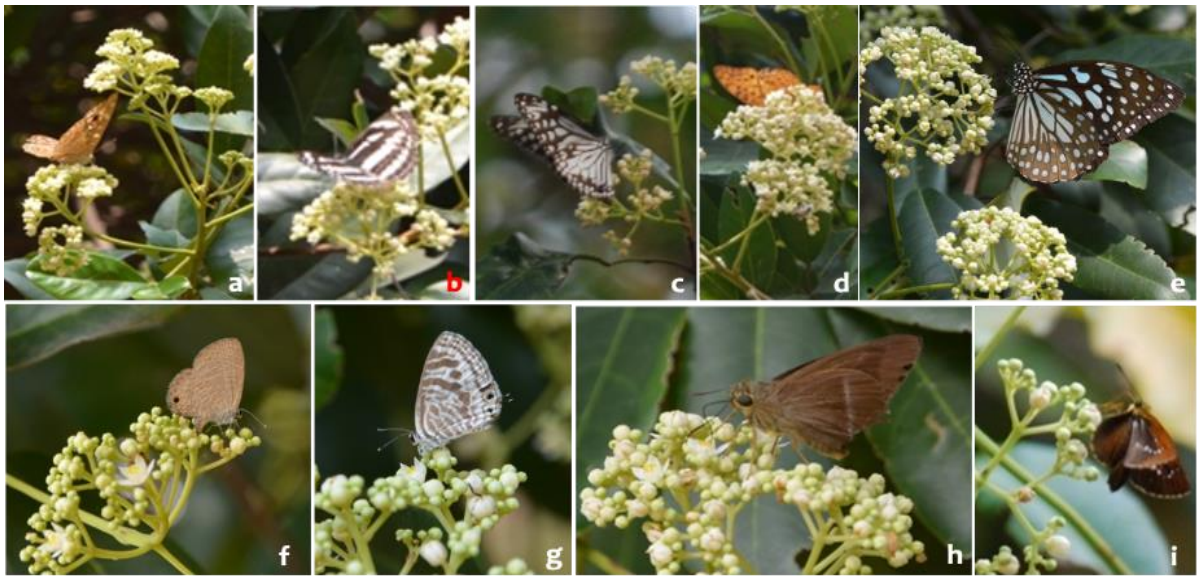


**Fig. 4: *Walsura trifoliata:* Butterflies:** a-e. Nymphalids – a. *Junonia lemonias*, b. *Neptis hylas*, c. *Parantica aglea*, d. *Phalanta phalantha*, e. *Tirumala limniace*, f-g. Lycaenids – f. *Jamides celeno*, g. *Leptotes plinius*, h-i. Hesperiids – h. *Hasora chromus*, i. *Pelopidas mathias.*

The temporal separation of male and female phases within the flowers does not facilitate the occurrence of both self- and cross-pollination until the time of commencement of receptivity of the bifid style-head but thereafter with the protrusion of bifid stigma of the style-head, both self- and cross-pollination occur in the evening hours of day 1 flowers and day-long in day 2 flowers. However, the insects made a few visits to flowers during the receptivity period of the bifid stigma in day 1 flowers indicating that the day 1 flowers largely act as pollen donors while day 2 flowers principally act as pollen recipients. Such a strikingly protandrous condition appeared to prevent the occurrence of autogamy and allows geitonogamy and xenogamy.

Among the insects recorded at the flowers, wasps and butterflies were found to be visiting the flowers across conspecific trees in quest of more nectar collection and such inter-tree foraging activities by them appeared to be promoting cross-pollination and reducing geitonogamous pollination. The bees being pollen and nectar foragers tended to spend more time at individual flowers and on the same tree, and such a foraging behavior was considered to be promoting geitonogamous pollination rather than cross-pollination. Of the total foraging visits made by all insect species, butterflies made 57%, bees 39% and wasps 4% (Fig. 8). Body washings of insects which were collected at 1100 hrs for assessing pollen carry-over efficiency showed that the mean number of pollen grains carried by individual species ranged from 8 to 324. The bees carried 64 to 324 83.8 pollen grains, wasps from 25 to 102 and butterflies from 8 to 104 (Table 3). These values indicated that the bees had high pollen-carrying capacity when compared to wasps and butterflies but the bees are important for effecting mostly geitonogamous pollination. Wasps had moderate pollen-carrying capacity but their frequent inter-tree foraging activity is important for effecting mostly xenogamous pollination. Butterflies are also important for promoting xenogamous pollination but they had low pollen-carrying capacity compared to wasps and bees. Therefore, wasps and butterflies were found to be important for cross-pollination while the bees for self-pollination.

**Table 3: Pollen recorded in the body washings of insects on *Walsura trifoliata***

| Insect species | Sample size (N) | Number of pollen grains | | |
|---|---|---|---|---|
| | | Range | Mean | S.D |
| *Apis dorsata* | 10 | 125 - 324 | 229.4 | 66.92 |
| *Apis cerana* | 10 | 96 - 315 | 208.3 | 71.85 |
| *Apis florea* | 10 | 72 - 264 | 162.4 | 52.82 |
| *Ceratina* sp. | 10 | 74 - 208 | 146.1 | 37.31 |
| *Xylocopa* sp. | 10 | 64 - 252 | 150.3 | 60.81 |
| *Stilbum superbum* | 10 | 46 - 102 | 72.8 | 18.06 |
| *Eumenes conica* | 10 | 25 - 93 | 59.7 | 22.58 |
| *Pachliopta hector* | 10 | 24 - 104 | 64.7 | 27.66 |
| *Graphium agamemnon* | 10 | 32 - 93 | 62.3 | 19.72 |
| *Graphium sarpedon* | 10 | 21 - 94 | 60.6 | 22.19 |
| *Delias eucharis* | 10 | 19 - 82 | 55.7 | 20.44 |
| *Euploea core* | 10 | 18 - 86 | 53.9 | 21.91 |
| *Junonia lemonias* | 10 | 16 - 73 | 45.2 | 17.93 |
| *Neptis hylas* | 10 | 9 - 43 | 27.8 | 11.22 |
| *Parantica aglea* | 10 | 10 - 76 | 37.8 | 23.43 |
| *Phalanta phalantha* | 10 | 11 - 28 | 20.4 | 5.3 |
| *Tirumala limniace* | 10 | 11 - 82 | 52.2 | 22.39 |
| *Jamides celeno* | 10 | 10-25 | 18.9 | 4.7 |
| *Leptotes plinius* | 10 | 13-38 | 28.7 | 7.0 |
| *Hasora chromus* | 10 | 8-31 | 23.1 | 6.1 |
| *Pelopidas mathias* | 10 | 15-47 | 34.3 | 8.8 |

**Breeding systems:** Hand-pollination tests for breeding systems showed that spontaneous autogamy is not functional. while manipulated autogamy, geitonogamy and xenogamy are functional, but fruit set in manipulated autogamy is negligible as it stood at 10% only. Fruit-set is 45% in geitonogamy, 75% in xenogamy and 86% in open-pollination mode (Table 4). The results of hand-pollination tests showed that the plant has a facultative xenogamous breeding system which is almost completely vector-dependent.

**Table 4: Results of breeding systems in *Walsura trifoliata***

| Treatment | Number of flowers sampled | Number of flowers set fruit | Fruit set (%) |
|---|---|---|---|
| Spontaneous self-pollination (Mature buds just bagged) | 20 | 0 | 0 |
| Hand self-pollination (Flowers hand-pollinated and bagged) | 20 | 2 | 10 |
| Geitonogamy (Flowers hand-pollinated and bagged) | 20 | 9 | 45 |
| Xenogamy (Flowers hand-pollinated and bagged) | 20 | 15 | 75 |
| Open pollination (Flowers tagged) | 50 | 43 | 86 |

**Fruiting ecology:** Fruit growth and development occurs as soon as the flower is fertilized (Fig. 5a). The ovary is initially enclosed completely by the corolla and staminal tube in the initial state of fruit development (Fig. 5b). Later, the fruit gradually bulges out but is still enclosed partially by the unidentifiable form of withered calyx, corolla and reproductive organs. All withered floral parts disappear when the fruit is mature. The duration from fruit initiation to maturation is about 2 months. Mature fruits are quite prominent and displayed above the foliage. Fruit is a globose drupe, 12-15 mm long, 8-19 mm wide and velvety-tomentose; it is initially green, and bright orange-yellow when mature (Fig. 5c). Its pericarp consists of an outer parenchymatous and an inner sclerenchymatous layer. The inner sclerenchymatous layer consists of an outer layer of sclereids and an inner layer of fibres. Each fruit produces 1 or 2 pale brown, smooth seeds which are completely embedded in a thick white sweet fleshy aril (Fig. 5d). The seed is connected to the pericarp via a septum in 1-seeded fruits but the septum divides the fruit cavity into two locules in 2-seeded fruits. The ripe fruits were eaten by the rodent, three-striped squirrel, *Funambulus palmarum* L. (Sciuridae), which is quite common in the study region. This squirrel removed the pericarp of the intact ripe fruit and/or removed the fruit from the tree, then removed the pericarp to eat the fleshy aril part which is very firmly attached to the remaining portion of the seed. In doing so, the seeds were discarded and found their way to the ground around and in the vicinity of the parent tree. The frugivory by this squirrel was found to be involved in the short-distance seed dispersal from the parent trees. The fallen seeds presumably disperse through runoff of rainwater during the rainy season. The seeds germinate during the rainy season and produce new plants depending on the continued presence of moisture and nutrients in the soil.


**Fig. 5:** ***Walsura trifoliata*****:** a. Fruiting phase, b. Initiation of fruit development, c. Mature and ripe fruit, d. Succulent aril.

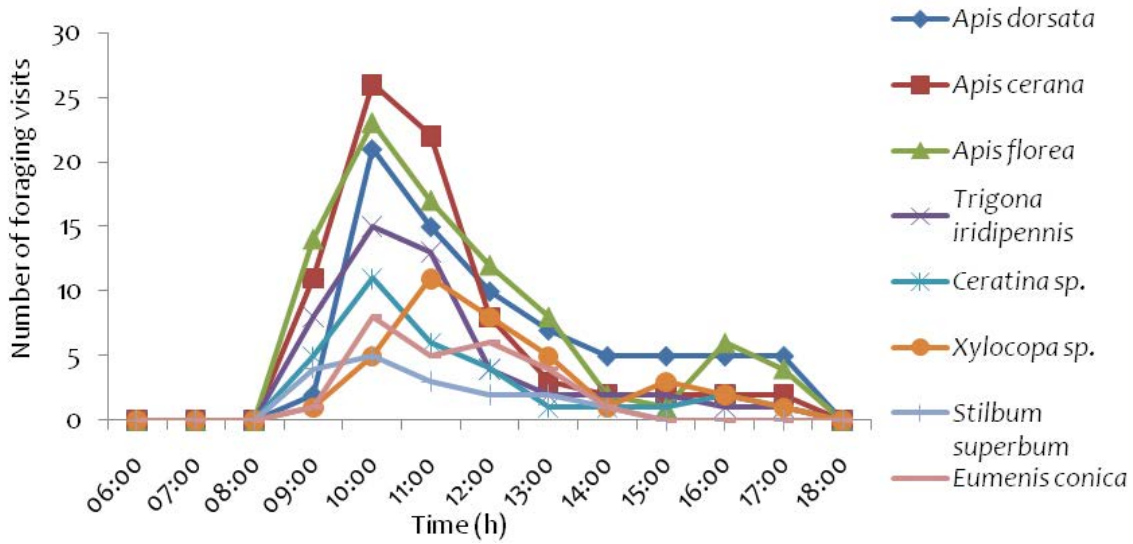


**Fig. 6: Hourly foraging activity of bees and wasps on *W. trifoliata***

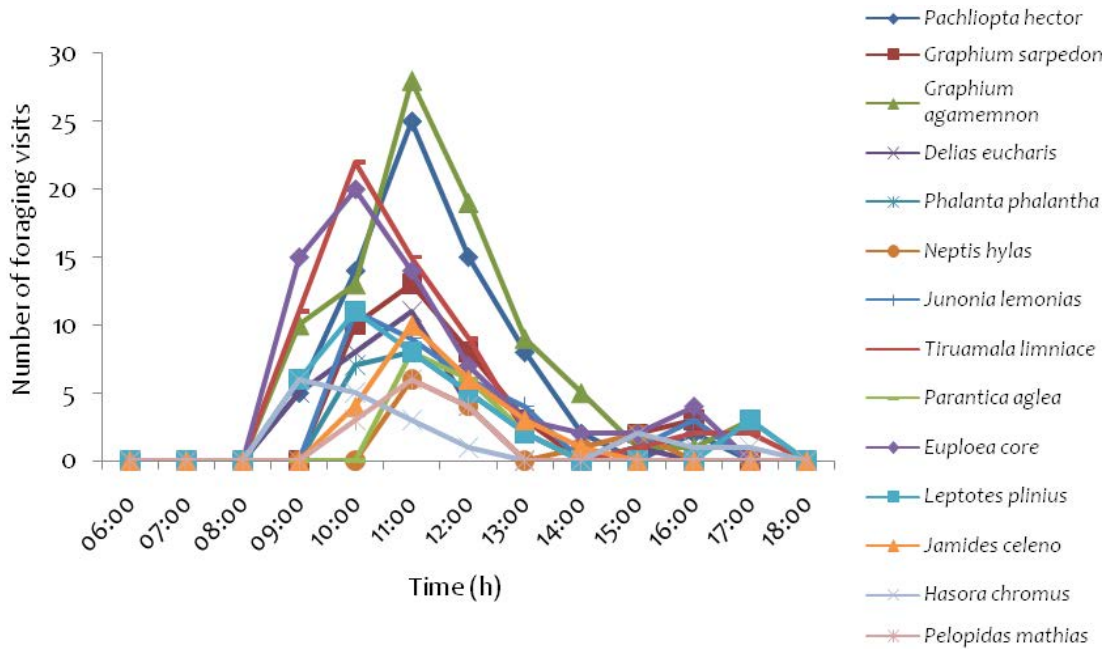


**Fig. 7: Hourly foraging activity of butterflies on *W. trifoliata***

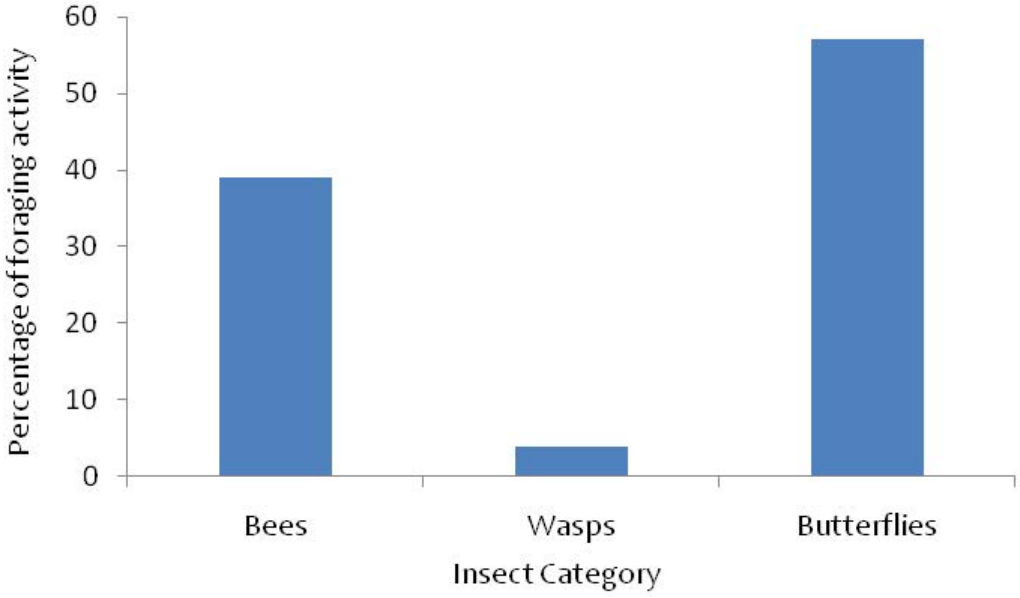


**Fig. 8: Percentage of foraging activity of bees, wasps and butterflies on *W. trifoliata***

**Discussion**

Pullaiah and Sri Ramamurthy [42] reported that *Walsura trifoliata* is common in dry deciduous forests of the Eastern Ghats. The present study found that this tree species is nearly rare in the Eastern Ghats forests of Andhra Pradesh. Clark [10] reported that most species of *Walsura* genus are hermaphroditic but some species such as *W. trifoliata, W. pinnata* and *W. chrysogene* are dioecious. Furthermore, this author also noted that *W. robusta* is either dioecious or hermaphrodite. In this study, it is found that *W. trifoliata*, being an evergreen tree species displaying flowering during the dry season for about 2 months, at population level produces flowers which are morphologically and functionally hermaphroditic and they did not show any change in the sexual expression between two consecutive years of the study period. This finding refutes the report by Clark [10] that this species is dioecious. The inflorescence produces dense heads of flowers at the ends of secondary rachides as reported by Clark [10]. Such a feature is reported to be rare in other *Walsura* species [10]. The flowers are numerous in each inflorescence and collectively stand out above the foliage. Such a placement of inflorescences with numerous flowers is advantageous for the tree to attract the foragers to its flowers even from a long distance in order to achieve reproductive success.

Pennington and Styles [39] reported that the partial or complete fusion of the staminal filaments to form a staminal tube is the characteristic feature in Meliaceae family. The presentation of variable degree of connation of the basal portions of filaments and the variability in the adnation to the petals and to the gynoecium is reported to be unique in the subfamily Swietenioideae of Meliaceae. The origin of the staminal tube might rely on the expansion of the connate zone of the filaments upwards to the whole structure in other species of Meliaceae. Furthermore, these authors also documented that *Pseudocedrela* in the subfamily Cedreloideae of Meliaceae has an urceolate staminal tube with anthers inserted in the middle of deltate teeth of the lobes. In the present study, *W. trifoliata* belonging to the subfamily Melioideae produces flowers with urceolate androecium which is tubular below with discrete filaments above. The

staminal tube is formed by the connation of filaments to the extent of ½ of their length from the base while the other apical half is free with bi-dentate apex in which the short-beaked anthers are inserted. The evolution and variability of urceolate structure of staminal tube could not be evaluated in different sub-families of Meliaceae due to lack of documented information.

Clark [10] reported that all species of *Walsura* possess a shallow cylindrical disk above the ovary around the style base and the ovary is densely covered with bristle-like trichomes. This author also mentioned that *W. chrysogyne* lacks a disk completely. The present study reports that *W. trifoliata* flowers have a shallow nectar disk which is present above the ovary around the style base between connate portion of the stamen tube and the creamy white pistil and its inner surface is lined with a large number of trichomes and the ovary is sparsely covered with bristle-like trichomes.

Clark [10] reported that pollen morphology is nearly uniform in all *Walsura* species he examined. The pollen grains are monads, apolar, 4-5-zonocolporate and prolate-spheroidal. In this study, it is found that *W. trifoliata* also produces monad, apolar, tetra-colporate and prolate-spheroidal pollen grains. Clark [10] noted that pollen grains are smallest in *W. robusta* and largest in *W. pinnata* but this author did not provide the pollen grain size of the *Walsura* species he investigated. Therefore, the present study could not state whether the pollen grains of *W. trifoliata* are the smallest or largest or moderate in size in relation to the pollen grains of other species of *Walsura*.

In this study, it is found that *W. trifoliata* flowers are prominently protandrous as the bifid stigma becomes receptive four hours later to anthesis by protrusion from the center of the capitate style-head. The capitate style-head indicating unreceptive state of stigma acts as pollen presenter because the pollen automatically gets attached to its rim at the time of anther dehiscence due to leaning of anthers around the style-head rim. Such a manner of pollen presentation by the capitate style-head is the characteristic of secondary pollen presentation mechanism. Since pollen is available right from anthesis, the flower-visitors that collect forage, either pollen or nectar or both pick up pollen presented by the capitate style-head until the commencement of stigma receptivity which is displayed by the protrusion of bifid stigma from the style-head and effect cross-pollination in their foraging visits to flowers of different conspecific plants. Furthermore, the self-pollen transferred within and between fresh flowers of the same plant before the commencement of stigma receptivity is ineffective to effect self-pollination but there is a possibility for self-pollination after the stigma attains receptivity. The protandrous condition and secondary pollen presentation mechanism in *W. trifoliata* appear to have an important role to promote cross-pollination and minimize self-pollination. The function of secondary pollen presentation mechanism through the style-head has been reported in most species of the genus *Turraea* [57] and also in *C. baccifera* of the present study.

In *W. trifoliata*, the functional breeding systems include both self- and cross-pollination. In case of self-pollination, spontaneous autogamy is not functional while manipulated autogamy is partially functional indicating that secondary pollen presentation mechanism is efficient in preventing or minimizing self-pollination rate through autogamy. Geitonogamy as an advanced form of self-pollination is highly functional while xenogamy is almost fully functional as fruit set rate is the highest in this mode of pollination. The dual modes of pollination functional in this plant species ensure it to maximize fruit-set rate through pollen vectors. The domination of cross-pollination rate to the extent of 95% and self-pollination to only 5% has been reported in

*Swietenia macrophylla* [30]. Further, the highest fruit set rate in xenogamy and lowest fruit set in autogamy has been recorded in hand-pollination tests in *C. baccifera*. Therefore, the facultative xenogamy with self-compatibility, delayed autogamy and secondary pollen presentation in *W. trifoliata* contribute to the success of its sexual reproduction and increases the heritable fitness that empowers this tree species to grow and withstand adverse environmental conditions.

In Meliaceae, the majority of species appear to be pollinated by bees and/or flies [32]. Hymenopterans have been reported as pollinators in *Trichilia havanensis* [39], butterflies, flies, wasps and bees in *T. lepidota* ([31], ants in *Carapa* species [27], moths in *Guarea, Cedrela* species, *Cabralea canjerana* subsp. *canjerana* [2, 4, 17], moths and bees in *Melia azedarach* [3, 59, 34], hawkmoths in *Turraea floribunda* [57], thrips in *Swietenia mahagoni* [23], moths and bats in *Chisocheton* and *Dysoxylum* species [28], birds and bees in *Dysoxylum spectabile* [18], insects in *Melia composita* [25], insects, mainly bees, in *Melia toosendan* [3] and *Toona sinensis* [58]. *Walsura pinnata* is speculated to be pollinated by insects [50]. A species of *Walsura* is reported to be visited by *Apis koschevnikovi* in Sarawak [45]. In this study, bees, wasps and butterflies utilize *W. trifoliata* flowers as food source during dry season. Of these, bees are important for self-pollination through geitonogamy while wasps and butterflies are important for promoting cross-pollination. Pollen-carrying capacity of these groups of insects analyzed through their body washings for pollen indicated that the bees are efficient carriers of pollen but they do not make visits between conspecific plants frequently as it is involved in both pollen and nectar collection from individual flowers; such a restricted or limited movement mostly brings about geitonogamous pollinations. Wasps and butterflies with moderate to limited pollen-carrying capacity mostly bring about cross-pollinations due to their swift flying nature and collection of only nectar as a reward. In *W. trifoliata* flowers, the forage characters such as nectar with three common sugars and certain amino acids and pollen with certain amino acids indicate that this plant species is evolved to attract insect pollinators and maximize cross-pollination rate while keeping the option open for self-pollination mostly through vector-mediated pollination. Such a flexible mating system functional in *W. trifoliata* is advantageous for this tree species to achieve genetic variation which is essential for its perpetuation in different forest habitats. Similar situation of production floral nectar sugars and amino acids, and pollen amino acids, and insect pollination has been evidenced in *C. baccifera* also. Therefore, *W. trifoliata* with generalist flowers is pollinated by different insect groups and species and hence is typically entomophilous.

Seed dispersal agents are reported for a few species of Meliaceae. White [54] reported that seed dispersal in *Carapa guianensis* is speculated to be mediated by rodents, monkeys and wild pigs. Miller [35] reported that seed dispersal in *M. azedarach* is mediated by birds and fruit bats. Seed dispersal is reported to be functional also by gravity and water in *M. azedarach* [53, 38]. Bats are reported to be the likely seed dispersal agents in *Azadirachta indica* [53]. *Walsura* species are in generally fleshy with seeds equipped with an arillode or sarcotesta [52]. Seed dispersal in *W. pinnata* is effected by birds and gibbons which feed on the fleshy part of the fruit [50]. In *W. trifoliata*, seeds dispersal is mediated by vertebrates in tropical dry evergreen forest fragments in Puducherry region [14] and by frugivorous birds in the tropical dry evergreen forests of Tamil Nadu and Andhra Pradesh [13]. In this study, it is found that *W. trifoliata* is fleshy globular drupe with 1 or 2 seeds completely embedded in a thick white sweet fleshy aril. The fruits attract only one three-striped squirrel, *Funambulus palmarum*. This squirrel feeds on

fleshy aril part of the drupe and discards the seeds which fall to the ground in the vicinity of parental trees effecting only short-distance seed dispersal. The fallen seeds in parental sites probably disperse through rainwater during the rainy season. The seeds germinate during the rainy season and produce new plants depending on the continued presence of moisture and nutrients in the soil.

*W. trifoliata* is highly valued in traditional systems of medicine and is used by tribal people for treating certain diseases by external application [8, 41]. Further, its fruits are used in hair wash especially by women to kill lice and cure scalp itching. In some areas, the fruit extract is also used as fish poison [37]. However, this tree species shows scattered and sparse distribution in the study region and in the entire extent of the Eastern Ghats forest; it is highly subjected to over-exploitation due to traditional medicinal values. Furthermore, its wood is used as timber for making certain furniture items by local people. As a consequence, it has disappeared in many pockets of the Eastern Ghats of Andhra Pradesh. Therefore, appropriate measures are required to protect the existing trees of this species and to control its uses by locals.

## Conclusions

*W. trifoliata* is a dry season-blooming evergreen hermaphrodite tree species with seed mode of propagation. The flowers are characterized by urceolate androecium, capitate style-head protruded with a receptive bifid stigma, secondary pollen presentation functional through protandry. Facultative xenogamy is functional but spontaneous autogamy occurs only after the stigma becomes receptive for which the possibility for its occurrence is very low due to low insect activity at that time. The floral traits display the function of generalist pollination syndrome adapted for pollination by insects, of which bees are important for geitonogamy while wasps and butterflies are important for xenogamy. Zoochory (*Funambulus palmarum*), barochory and hydrochory are functional.

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## ECOLOGIA REPRODUCTIVĂ A UNEI SPECII SEMPERVIRESCENTE DE ARBORE, CE ÎNFLOREȘTE ÎN SEZONUL SECETOS, *WALSURA TRIFOLIATA* (A. JUSS.) HARMS (MELIACEAE)

**(Rezumat)**

*Walsura trifoliata* este o specie arborescentă, sempervirescentă, hermafrodită, ce înflorește în sezonul uscat. Florile sunt nectarifere și se caracterizează prin androceu urceolat, protandrie puternică și mecanism de polenizare secundară, stigmat bifid proeminent (pentru receptivitate), autocompatibilitate și xenogamie facultativă, fără funcție de autogamie spontană. Trăsăturile florale indică tipul general de polenizare și adaptarea la entomofilie, albinele efectuând în principal geitonogamia, iar viespii și fluturii xenogamia. Numărul de fructe obținute este mai mare în cazul xenogamiei. Fructul este o drupă globulară, cu 1-2 semințe încorporate în arilul cărnos. Modurile de dispersie a semințelor includ zoochoria, barochoria și hidrochoria. Studiul arată că tipul general de polenizare, entomofilia, xenogamia facultativă și polichoria îi permit acestei specii de arbore să obțină cea mai mare cantitate de fructe, să mențină variabilitatea genetică prin polenizare încrucișată și să-și disperseze semințele la diferite distanțe în ecosistemul forestier.

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