



Mutualistic Pollination Ecology of *Swietenia mahagoni* (L.) Jacq. and Thrips: A Reproductive Interdependence

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ABSTRACT

Swietenia mahagoni (L.) Jacq., of the family Meliaceae, is economically important for its high-quality timber. *S. mahagoni* produces very small, pale greenish-yellow, crypto-unisexual flowers arranged in axillary panicles. The male and female flowers are visually identical. The sepals are green, very small, and inconspicuous. The petals are spatulate and pale greenish-yellow in color. The stamens are monadelphous; the flat filaments are laterally fused to form a pitcher-like structure. The female flowers have empty anther lobes, whilst the male blooms carry pollen grains. The carpels have a stumpy style, a disc-shaped stigma, and are syncarpous. The carpel of the female flower contains functional ovules, whereas ovules, if present, are non-functional in the male flower. A large population of a Thysanopteran insect visits and lays eggs inside the flowers. During oviposition in different flowers, these insects facilitate the transfer of pollen grains from the male to the female flower's stigma. The reproductive ecology and the mutual reproductive dependence between this tree species and the insect have been thoroughly studied in this work.

Keywords: Inflorescences, Thysanoptera, Volatile organic compounds (VOCs), β -caryophyllene

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INTRODUCTION

Swietenia mahagoni (L.) Jacq. (family Meliaceae) It is a tree that can reach heights of over 30 meters. The trunk of a fully grown tree is at least 1 meter in diameter, with a large canopy composed of dense branches and leaves. The plant is native to Cuba, Florida, the Cayman Islands, the Bahamas, and Jamaica. However, it has been introduced to almost every part of the world, including foothills up to 3000 ft, due to its high-quality timber (Rolfe, 1919). Mahogany is a big-bang species (Gentry, 1974), meaning the majority of its flowers bloom simultaneously, typically only once a year. The flowering season lasts for 15-20 days, from late April to early May. The blossoming season may, however, last an extra seven to ten days within a population. Male and female *S. mahagoni* flowers are nearly identical in appearance, making them crypto-unisexual (Jabbour *et al.*, 2022). Approximately 92% of all flowers are male, with the remaining 8% being female (Lee, 1967). Axillary and sub-terminal panicles with two to six flowers are produced by each terminal branch. The inflorescences are unisexual, i.e., all the flowers in a single inflorescence are of the same sex. *S. mahagoni* exhibits a unique mode of pollination involving oviposition by a species of Thysanopteran insect, *Priesneriella*, first reported by Basu *et al.* in 2013. Before this discovery, the only known example of ovipositional pollination was in figs,

pollinated by fig wasps (Galil & Meiri, 1981; Bronstein, 1987). Zhang and Yang (2017) found that several species of *Eupristina*, *Diaziella*, and *Lipothymus* wasps visit and lay eggs in the hypanthodium of different species of *Ficus*. Another well-known example is the Yucca moth, *Tegeticula*; at least 15 species of this moth pollinate *Yucca* species through oviposition (Pellmyr & Huth, 1994; Pellmyr *et al.*, 1996). More recently, it has been found that gall midges (*Resseliella* sp.) oviposit in the flowers of *Kadsura*, *Schisandra*, and *Illicium* (Luo *et al.*, 2017). Therefore, the details of the pollination ecology and the mutual reproductive relationship between Mahogany and *Priesneriella* have been studied in this work.

MATERIALS AND METHODS

The study was based on Mahogany populations from different parts of West Bengal, India. Samples were collected from the districts of Kolkata, Hooghly, Burdwan, Cooch Behar, and Alipurduar, covering a vast geo-climatic area. Flowers from different locations were collected during the flowering season and examined under microscopes. Various developmental stages of insects were collected alive from the flowers, preserved in 70% alcohol and 0.01% formaldehyde solution, and observed under a 10× hand lens and microscope. Insect eggs were collected from the nectar discs of male flowers using a stereo-binocular microscope and mounted in 0.01% formaldehyde solution. All microphotographs were taken using a WILD M3B Leica (Switzerland) stereo-binocular microscope

and a Leitz Laborlux S (Germany) bright-field microscope, both equipped with a Leica DFC 295 digital camera. A Nikon D5000 digital SLR camera was used to take field photos. Ten male flowers' nectar discs were soaked and crushed in 1 ml and 2 ml of distilled water to determine the nectar's carbohydrate content. The solutions were filtered through Whatman filter paper no. 1. Then, 1 ml of each filtrate was taken in separate test tubes, Fehling A and Fehling B solutions were added, and the mixtures were observed for the formation of brick-red precipitate (Negreiros *et al.*, 2024; Omokunle *et al.*, 2024)

RESULTS AND DISCUSSION

Floral architecture

The flowers of *S. mahagoni* are very small, measuring 3-4 mm in length and 9-10 mm in breadth, and are pale greenish-yellow in color (**Figures 1a and 1b**). The calyx whorl is inconspicuous and difficult to distinguish from the pedicel and corolla. It consists of five leathery, round sepals approximately 0.8-1 mm in diameter. The corolla whorl comprises five small, straw-yellow, polypetalous petals. Each petal is oval-spatulate in shape, measuring approximately 4.2-4.4 mm in length and 1.6-1.7 mm in breadth. In all flowers (both male and female), both sexual organs are present (**Figures 1c and 1l**), though ovules are absent in the male flowers and pollen grains are absent in the female flowers (Pisano *et al.*, 2023). The androecial whorl consists of ten monadelphous stamens. The filaments are flat and laterally fused to form a pitcher-like structure called the androecial urceolus (Basu *et al.*, 2013). The tips of the filaments are free, forming ten tooth-like structures, and the urceolus itself measures approximately 3.4 mm in length and 2.7 mm in breadth (**Figure 1c**). The anthers are bilobed, brown, about 0.7 mm long and 0.3 mm broad, and are located subterminally at the junction of two teeth. In male flowers, the anther lobes bear a white mass of pollen (**Figure 1d**). The anthers of the female flowers are visibly different and lack pollen grains (**Figure 1e**). The gynoecium is pentacarpellary and syncarpous, with a five-chambered pitcher-shaped ovary (**Figure 1e**), each chamber containing five to six ovules (♀ pistil length $\pm$ 2.6 mm and breadth $\pm$ 2.1 mm; ♂ pistil length $\pm$ 2.2 mm and breadth $\pm$ 1.2 mm). The ovary is larger and contains fertile ovules in the female flower (**Figures 1f and 1i**), whereas in the male flower, it is smaller, slender, and less conspicuous, with no or abortive ovule(s) (**Figure 1g**). The stigma is discoid with five faint radiating ridges, indicating the fusion of five carpels (**Figures 1j and 1k**). The style is short and broad, and even shorter and broader in female flowers compared to male flowers (**Figures 1f and 1g**). The free tips of the androecial urceolus almost touch the periphery of the discoid stigma, leaving window-like openings between every two tooth-like tips of consecutive filaments (**Figures 1j and 1k**). The upper surface of the stigma remains exposed during the open-flower stage (**Figures 1j and 1k**). At the base of the gynoecium, there is an orange, disc-like structure that contains an Fehling-positive (sugary) fluid or nectar (**Figures 1f and 1g**). In male flowers, as the ovaries are slender, the nectar discs are broader, providing a larger secretory surface than in female flowers (**Figure 1g**). Overall, the internal space within the urceolate structure of a male flower is much greater than that of a female flower.

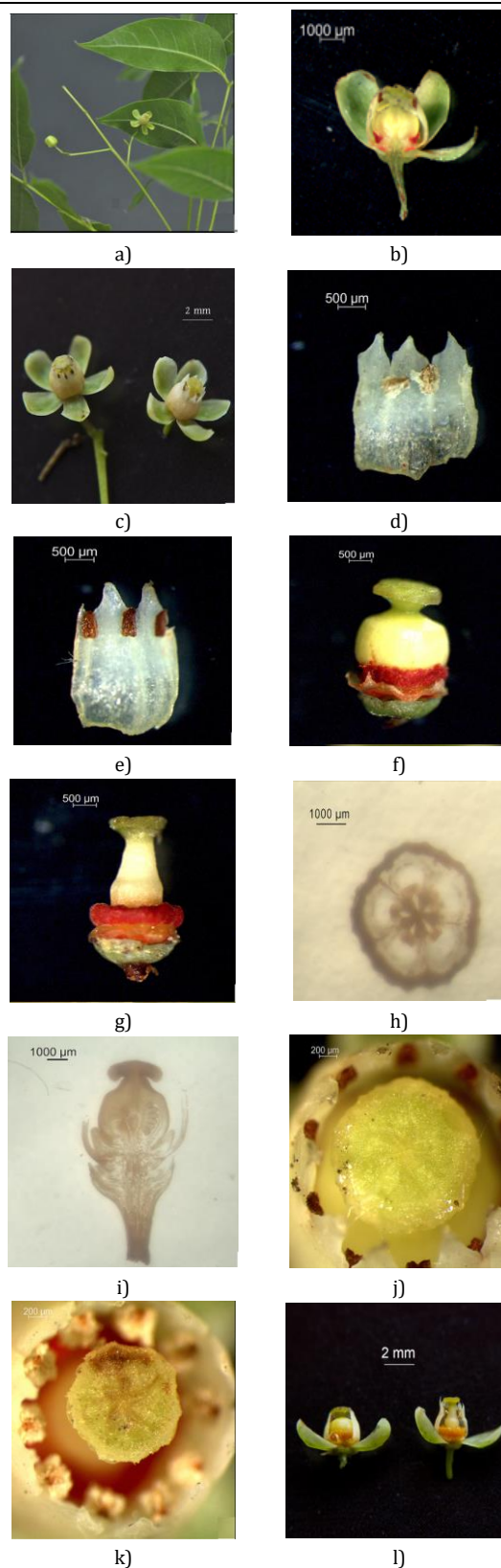


Figure 1. a). A male *Swietenia mahagoni* flower and a flower bud; b). Longitudinal section of a female flower showing the floral construction; c). Morphological comparison of a male and a female flower, showing

polypetalous petals and androecial urceolus; d). A portion of the androecial urceolus from a male flower showing fused filaments, free tips, and anther lobes with pollen grains; e). A portion of the androecial urceolus from a female flower showing fused filaments, free tips, and empty anther lobes; f). An isolated gynoecium from a female flower showing a larger ovary, short style, discoid stigma, and an ill-developed nectar disc; g). An isolated gynoecium from a male flower showing a slender ovary, longer style, discoid stigma, and a well-developed nectar disc with a larger surface area; h). Transverse section of a gynoecium from a male flower showing five chambers and abortive ovules; i). Longitudinal section of a gynoecium from a female flower showing six ovules in each chamber; j). Enlarged view of a wet stigmatic surface from a female flower showing five faint ridges; k). Enlarged view of a stigmatic surface from a male flower. The openings for insect movement and masses of pollen grains in their path are also visible in the image; l). Partially dissected female (left) and male (right) flowers showing differences in the space inside the androecial chambers, sizes of the gynoecia, and the shape and size of the nectar discs.

Flowering phenology

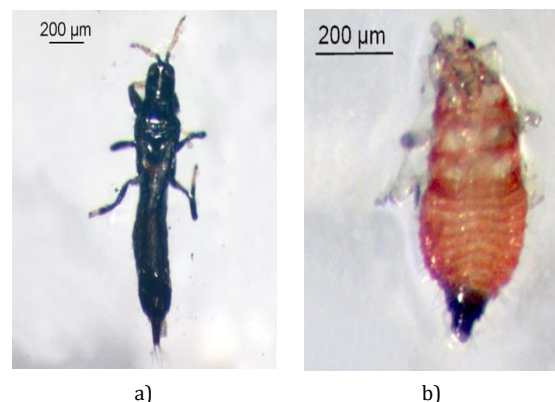
The plant produces two-day flowers with a floral longevity of 38-40 hours. Flower opening begins in the morning around 5:00-5:30 a.m. with the partial divergence of petals, followed by the separation of the teeth of the androecial urceolus. Maximum petal divergence, along with complete opening of the androecial chamber due to further divergence of the urceolus teeth into a vertical position, is achieved by 7:30-8:00 a.m. The stigma is of the wet type, and in a freshly bloomed female flower, it is already receptive, as indicated by its pronounced, juicy, and lustrous appearance. On the following day, between 7:00-7:30 a.m., the tips of the erect teeth of the androecial urceolus begin to curve inward slightly. By approximately 9:30 a.m., the stigma of the female flower starts to lose its receptivity, as evidenced by visible dryness and slight shrinkage. Around noon (11:30 a.m.), the stigmatic disc becomes somewhat pentagonal in outline, and its margins, along with the radiating surface ridges, turn brown. This condition marks the end of stigma receptivity. Anthers of a male flower begin to dehisce early in the morning of the first day, around 5:30 a.m., coinciding with the flower opening. The dehiscence slit of a freshly opened anther is barely visible, and the initiation of dehiscence can be identified by the oozing of loose pollen. Full anther dehiscence is achieved approximately one hour after flower opening. By 1:00-1:30 p.m. on the second day, the anther lobes are almost devoid of pollen grains. Nectar secretion from the disc begins simultaneously with flower opening, i.e., around 6:30-7:00 a.m., and continues until the afternoon of the following day. By the end of the second day, the nectary tissue shows signs of disorganization, and the teeth of the androecial urceolus turn brown and appear somewhat irregular. The termination of floral longevity is marked by the withering of all floral parts except the gynoecium. None of the floral organs undergo abscission. Therefore, with respect to stigma receptivity, anther dehiscence, and pollen dispersal, the flowers are homogamous, exhibiting a prolonged male phase in comparison to the female phase.

Anthesis

Anthesis begins at approximately 7:30 a.m. on the first day of flower opening, when pollen grains from freshly dehiscent anthers of male flowers are transferred to the already receptive stigmas of female flowers. It ends around 1:30 p.m. on the second day of flower opening, by which time the anthers of male flowers are nearly depleted of pollen. Thus, the duration of anthesis extends from approximately 7:30 a.m. on the first day to around 1:30 p.m. on the second day of flower opening.

Pollinators and their activity

A species of insect, *Priesneriola oneillae* Ananthakrishnan (**Figure 2a**), belonging to the order Thysanoptera and family Thripidae (Ananthakrishnan, 1964; Rasool et al., 2023), was found to visit Mahogany flowers (Basu et al., 2013). It was observed that almost all the adult insects visiting the flowers were females, identified by their ovipositors (**Figure 2a**). The adult insects land on the stigmatic discs of first-day male flowers and crawl into the chamber of the androecial urceolus through the window-like openings to lay eggs (**Figures 1c, 1j and 1k**), while also feeding on the pollen grains and nectar. The adult *Priesneriola oneillae* carry pollen grains from the male flowers on their bodies and unintentionally brush them against the receptive stigmas of first-day female flowers, which are visually identical to the male flowers, as the insects exit and visit the subsequent bloom for the same purpose. Eggs are laid on the nectar discs of male flowers. After hatching, the larvae (hatchlings) emerge from second- or third-day male flowers and take shelter inside the androecial urceolus of first-day male flowers to feed on nectar and pollen grains, eventually metamorphosing into the nymph stage (**Figure 2b**). During the metamorphosis process—from larva to nymph to adult (**Figures 2a-2d**)—they continue visiting flower after flower, facilitating the transfer of pollen from male to female flowers. Since adults are more active and capable of longer flights, they are primarily responsible for both geitonogamy and xenogamy in a dense population of Mahogany trees. However, the less active nymphs are only capable of geitonogamy. Larvae, being relatively immobile, do not contribute significantly to pollen transfer except for occasional accidental contact.



a)

b)

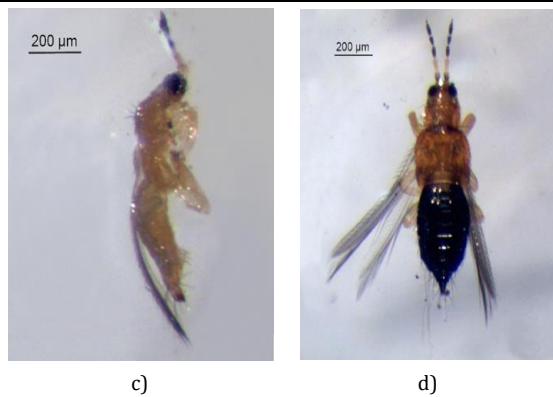


Figure 2. a). An adult female *Priesneriola oneillae* Ananthakrishnan showing the ovipositor; b). A larva (hatchling) of *Priesneriola oneillae*; c). Early-stage nymph of *Priesneriola oneillae*; d). Late-stage nymph of *Priesneriola oneillae*.

Thrips and their host plants: selection strategies and ecological interactions

Insects are small organisms that are closely associated with their host plants through specific cues. Particular host plants transmit distinct signals that stimulate specific insects to engage in foraging and reproduction on those plants (Botelho *et al.*, 2023; Bulusu *et al.*, 2023). However, not all plants can serve as host plants for all insect species. Instead, specific plants are suited to specific insects, leading to competition among insects for high-quality host plants (Bruce *et al.*, 2005). Phytophagous insects have gradually evolved their olfactory and nervous systems to avoid non-specific host plants (Martin *et al.*, 2011). Their decision-making behavior is remarkably efficient; during flight, insects can decide within milliseconds which plant to land on for foraging or reproduction (Carde & Willis, 2008; Baker, 2009; Bruce & Pickett, 2011). Phytophagous insects feed on plant tissues, which can negatively impact food resources. However, insects also play a critical role in pollination, and some plants even exhibit carnivory by directly consuming insects (Renner & Specht, 2013). The coevolution between plants and insects has contributed to the speciation of flowering plants, ultimately enhancing their diversity (Yuan *et al.*, 2013). The behaviors of feeding on plants and acting as pollinators date back approximately 400 million and 250 million years, respectively. Over the course of evolution, plants have gradually modified the signals they emit to attract insects for pollination (Grajales-Conesa *et al.*, 2011; Labandeira, 2013). Volatile organic compounds (VOCs) act as signaling molecules, attracting specific insects to perform particular behavioral patterns. Compounds such as β -caryophyllene, hexan-1-ol, and 2-ethyl hexan-1-yl-butanoate are potent VOCs produced by *E. angolensis*, *E. utila*, and *K. ivorensis*, which attract various moth species (Abraham *et al.*, 2014). Among these, β -caryophyllene is particularly effective in attracting gravid females of *Bactrocera dorsalis*, encouraging them to lay eggs on fruits (Khallaf & Kanaden, 2020). Similar to this, specific volatile organic compounds (VOCs) released by mahogany trees may affect the reproductive behaviour of Thysanoptera. For insects, choosing the best place to lay their eggs is a difficult challenge. They typically prefer unoccupied sites that offer abundant food resources while minimizing intraspecific competition. Marking behavior is often observed in insects, wherein they secrete host-

marking pheromones to signal oviposition sites (Kirby, 1856). For instance, gravid females of *Drosophila melanogaster* can identify secure and suitable sites and communicate with other females to lay eggs at the same location, thereby enhancing the survival of their progeny (Dum  nil *et al.*, 2016). Such strategies and interactions may also occur between Thysanoptera and mahogany, promoting the fitness of both species (Fiodorova *et al.*, 2022; Ogbeide *et al.* 2022).

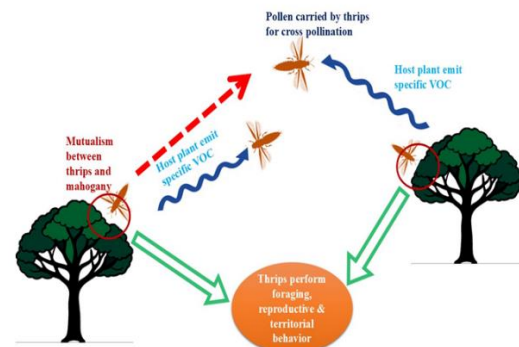


Figure 3. The figure illustrates the probable mechanism of interaction between mahogany and thrips. The mahogany plant releases volatile organic compounds (VOCs), indicated by blue arrows, to attract thrips. Upon arrival, the thrips land on the mahogany flowers, where they engage in egg-laying, foraging, and territorial behaviors. During these activities, pollen from the host plant adheres to their body parts. As the pollen-carrying thrips move to another mahogany flower, they facilitate cross-pollination, represented by red arrows (Ingle *et al.*, 2023).

Swietenia mahagoni (L.) Jacq. And *Priesneriola oneillae* Ananthakrishnan shares a mutual reproductive dependence. It is evident that the plant has coevolved several traits with the insect to maintain this relationship: i) The 'closed-vial test' performed with freshly bloomed flowers showed no positive result, indicating that the primary attractant is visual rather than olfactory. Although the flowers are small, they are produced in terminal thyrse clusters, functioning as long-distance attractants for visitors. The reddish-pink tinge at the base of the androecial urceolus, located just opposite the nectar disc, serves as a nectar guide. Edible pollen grains and nectar constitute the rewards for the visitors. The nearly closed, pitcher-like structure of the androecium lures insects for oviposition (Lassmann *et al.*, 2022; Wilhelmy *et al.*, 2022). The nectar disc at the base of the gynoecium secretes nectar, which provides the growing nymphs with nourishment in addition to shelter. ii) The flowers that are crypto-unisexual display mimicry, particularly Batesian mimicry (Ruxton *et al.*, 2019), where the male flower acts as the model and the female flower as the mimic. This mimicry deceives insects and leads them to visit and pollinate the female flower. iii) The presence of more male flowers than female ones may not appear to be a wise evolutionary strategy from a reproductive perspective—regarding productivity and resource optimization—but it offers the insect an abundance of attractants and rewards, encouraging dependence on the plant and keeping them in proximity. This significantly enhances the chances of pollination for the plant. iv) The access path to nectar and pollen grains is

narrow, enabling the plant to select specific visitors of appropriate size and shape while restricting unwanted visitors, thus preventing nectar and pollen theft. In addition, nectar secretion is minimal and only moistens the surface of the nectar disc. Most of the nectar remains inside the orange nectar gland, compelling insects to consume the nectar disc as food. No insect can externally suck the nectar with a proboscis, thereby preventing Lepidopteran insects from stealing the nectar (Basu, 2019, 2023).

CONCLUSION

This study demonstrates a reproductive dependence between *Swietenia mahagoni* and thrips, indicating a mutualistic relationship. This interaction may be mediated by one or more volatile organic compounds that guide or regulate their association. In the future, such mutualistic reproductive behavior could contribute significantly to the population growth of *Swietenia mahagoni*, while also affecting the abundance and dynamics of thrips populations.

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