PSYCHOPHILY AND ANEMOCHORY IN WENDLANDIA TINCTORIA (ROXB.) DC. (RUBIACEAE), A DRY SEASON BLOOMING TREE SPECIES IN THE DRY DECIDUOUS SOUTHERN EASTERN GHATS FOREST, ANDHRA PRADESH, INDIA

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Wendlandia tinctoria, a semi-evergreen tree species is a massive bloomer for about a month during March-April. The floral characteristics such as white colour of the flower, lack of odour, short-tubed corolla with deep seated hexose-rich nectar having 15-18% sugar concentration conform to psychophily. The nectar is also a source of two essential amino acids, arginine and histidine, and eight non-essential amino acids for butterflies. A variety of butterflies, especially nymphalids visit the flowers for nectar and in doing so, they pollinate them. Other foragers include bees, a fly and wasps. Wasps are occasional nectar foragers and effect pollination. Bees are consistent foragers of pollen and/or nectar. *Apis* bees collect pollen and nectar while *Trigona* and *Ceratina* bees collect only pollen due to their short tongue length. The fly is an occasional pollen feeder. The intense pollen collection activity of bees has been considered to be detrimental for the reproductive success of the plant. Therefore, *W. tinctoria* is primarily psychophilous and serves as a key forage source also for other insects at the study site where floral nectar sources are scarce during summer season. The plant shows high fruit and seed set rate; it is anemochorous but it is not effective due to seed maturation during rainy season.

Keywords: *Wendlandia tinctoria*, butterflies, psychophily, bees, wasps, nectar source.

INTRODUCTION

Wendelia is a genus of Rubiaceae with over 90 species distributed in tropical and sub-tropical Asia; a single species of this genus is distributed in Africa (Misra and Bellwood, 1985). The literature does not provide any information on the pollination biology of this genus. Chetty et al. (2008) reported that *W. tinctoria* and *W. glabra* occur in Seshachalam hill range of southern Eastern Ghats. Mishra et al. (2006) reported that *W. tinctoria* flowers during September-October in Similipal Biosphere Reserve in Eastern Ghats. In the present study, field investigations carried out in the entire stretch of Eastern Ghats showed that these two tree species do not grow together. *W. tinctoria* is confined to the southern Eastern Ghats while *W. glabrata* has scattered distribution throughout the Eastern Ghats of Andhra Pradesh, India. Further, it is also found that both the species flower at the same time during March-April, show similar flower morphologies and play a crucial role in the nourishment of insects during dry season when floral resources are scarce. These two species have also not been investigated for their pollination biology despite their key role in the nourishment of local insect species. Therefore, the present study is contemplated to describe the pollination biology of *W. tinctoria* and discuss the same in the light of relevant information on the role of local insects in pollination and the attendant reproductive success.

MATERIALS AND METHODS

Wendlandia tinctoria trees occurring at the Seshachalam Hills of southern Eastern Ghats of Andhra Pradesh were used for the study during the summer season of 2009. Twenty five tagged mature buds were followed for recording the time of anthesis and anther dehiscence; the mode of anther dehiscence was also noted by using a 10x hand lens. The details of flower morphology such as flower sex, shape, size, colour, odour, sepals, petals, stamens and ovary were described. Ten mature but undehisced anthers of staminate flowers were collected from five different plants and placed in a Petri dish. Later, each time a single anther was taken out and placed on a clean microscope slide (75 x 25 mm) and dabbed with a needle in a drop of lactophenol-aniline-blue. The anther tissue was then observed under the microscope for pollen, if any, and if pollen grains were not there, the tissue was removed from the slide. The pollen mass was drawn into a band, and the total number of pollen grains was counted under a compound microscope (40x objective, 10x eye piece). This procedure was followed for counting the number of pollen grains in each anther collected. Based on these counts, the mean number of pollen produced per anther was determined. The mean pollen output per anther was multiplied by the number of anthers of a flower for obtaining the mean number of pollen grains per flower. The characteristics of pollen grains were also recorded. Ten fresh flowers were used to measure the total volume of nectar/flower. The nectar sugar concentration was measured by using a Hand Sugar Refractometer (Erma, Japan) as per Dafni et al. (2005). Nectar analysis for sugar types was done as per the Paper Chromatography method of Harborne (1973). Nectar analysis for amino acid types was done as per the Paper Chromatography method of Baker and Baker (1973). The stigma receptivity was tested with hydrogen peroxide from mature bud stage to flower drop as per Dafni et al. (2005). Regular observations were made on the insect species visiting the flowers for forage. The insects were observed for their foraging behaviour such as mode of approach, landing, probing behaviour, the type of forage they collect, contact with essential organs to result in pollination, inter-plant foraging activity in terms of cross-pollination, etc. Three to five specimens of each butterfly species collected at different times of the day were brought to laboratory for examining their proboscis under microscope for the presence of pollen grains in order to assess their role in pollen transfer and pollination. Casual observations were also made on fruit, seed and seedling aspects.

RESULTS

Wendlandia tinctoria is a semi-evergreen tree species with scattered distribution in the forest (Figure 1a). Field surveys in the entire forest area covering an extent of 50 sq. km showed that the population of this species is limited to about 25 trees only. The leaves are glabrous and elliptic-lanceolate borne opposite to each other. Leaf flushing occurs during rainy season adding bright green look to the foliage. The flowering occurs from 3rd week of March to 3rd week of April. The flowering is almost synchronous in all individuals. The flowers are borne in clusters of terminal paniculate inflorescences (Figure 1b). The flowers open at 0600 h. The petals unfold exposing the stigma and stamens beyond the length of the corolla tube (Figure 1c-e). The flowers are small, 6-7 mm long, tubular, white with yellow tinge, odourless, regular and bisexual. The calyx is very small with five light green fused sepals; it is persistent and transforms into fruiting calyx after fertilization. The corolla is tubate tipped with five lobes, 5 mm long, white and conceals nectar. The stamens are five each with dithecous anthers having versatile fixation, very small and situated below the stigma; the anthers appear star-like at mature bud stage but take different postures after anthesis. The stamens are protandrous and anther dehiscence occurs during mature bud stage by longitudinal slits. A flower produces an average number of 38,850 pollen grains. The pollen grains are monads, tricolporate, reticulate, circular, powdery and 16.6µm in size (Figure 1f). The ovary is well seated in the calyx, bicarpellary, syncarpous with a total of 95-100 ovules (Figure 1g); the style is erect and terminated with spathulate bifid stigma. The stigma attains receptivity about two hours after anthesis by the gradual unfolding of the stigmatic lobes and the receptivity remains so until the evening of 2nd day. The stigmatic lobes gradually turn brown indicating the loss of receptivity. The same duration was evidenced in the hydrogen peroxide test also. Nectar is produced in minute amount which stands at 0.6 ± 0.12 µl per flower and is collected at the base of corolla tube. The nectar sugar concentration ranged from 15% to 18%; the sugar types include sucrose, fructose and glucose but the last is more dominant. The nectar contains both essential and non-essential amino acids. The essential amino acids are arginine and histidine while non-essential amino acids are alanine, aspartic acid, cysteine, glysine, hydroxyproline, tyrosine, glutamic acid and serine. The flowers remain in place for four days and fall off subsequently.

The mature buds contain thrips. Each mature bud/flower showed a minimum of 3-4 thrips. The presence of thrips in flowers prior to anthesis showed that the thrips use the plant species for breeding. They partly feed on nectar before anthesis and hence the flowers offer only minute amount of nectar after opening to nectar foragers. Insects began foraging at the flowers soon after anthesis; they included butterflies, bees, wasps and a fly species. Butterflies foraged throughout the day while all other insects during forenoon only. The butterflies included 25 species representing Papilionidae, Pieridae, Nymphalidae, Lycaenidae and Hesperiidae (Table 1). The Papilionidae and Pieridae each was represented by 2 species, Lycaenidae by 5 species, Nymphalidae by 15 species, and Hesperidae by a single species (Figure 11). The Papilionids were *Pachliopta hector* (Figure 1h) and *Papilio clytia* (Figure 1i). The Pierids were *Catopsilia pyranthe* (Figure 1j) and *C. pomona*. The Nymphalids were *Danaus genutia* (Figure 1k), *D. chrysippus, Euploea core* (Figure 2a), *Tirumala septentrionis* (Figure 2b), *T. limniace* (Figure 2c), *Hypolimnas* *bolina* (Figure 2d), *H. misippus* (Figure 2e), *Precis iphita* (Figure 2f), *Phalanta phalantha* (Figure 2g), *Neptis hylas* (Figure 2h), *Junonia lemonias* (Figure 2i), *J. hierta, Ariadne merione, Acraea violae* and *Parantica aglea* (Figure 2j). The Lycaenids were *Jamides celeno* (Figure 2k), *Arhopala amantes* (Figure 2l), *Lampides boeticus* (Figure 2m), *Spindasis vulcanus* (Figure 2n) and *Everes lacturnus*. The Hesperiid was *Borbo cinnara* (Figure 3a). Of these, the individuals of Nymphalid butterflies were more than those of other families at the flowers throughout the flowering season. The foraging activity of these butterflies gradually increased from morning to noon and gradually decreased towards the evening (Figure 5-10). This foraging trend was observed almost throughout the flowering season for butterflies of all families recorded in this study. The data collected on the foraging visits of butterflies of each family showed that Nymphalids made 63%, Lycaenids 18%, Papilionids 9%, Pierids 7%, and Hesperiids 3% of total visits (Figure 12). The aggregated arrangement of flowers provide comfortable landing place for butterflies and also this arrangement enable them to probe several flowers in each visit in succession for nectar before their departure. The clusters of paniculate inflorescences borne terminally stand out prominently and the butterflies were found to be attracted to them even from a long distance. A sample of 3-5 specimens of all butterfly species was used to examine the pollen carrying capacity of their proboscides. The results indicated that the proboscides invariably contained pollen grains ranging from 23-156 in Papilionids, 15-89 in Pierids, 35-213 in Nymphalids, 22-69 in Lycaenids and 31-93 in Hesperiids. All these butterflies probed the flowers with their proboscis to reach the nectar located at the flower base; while doing so the proboscis invariably contacted the stigmatic lobes and the exposed dehisced anthers effecting pollination. The butterflies frequently moved between individual plants of *W. tinctoria* which occur scattered in the forest; this inter-tree foraging activity was considered to be promoting cross-pollination. Further, the diurnal hawkmoth, *Cephonodes hylas* (Figure 3b) also foraged for nectar but its foraging activity was confined to dawn hours when flowers just open and offer fresh nectar. The bees visiting the flowers were consistent foragers of pollen and/or nectar. They were *Apis dorsata* (Figure 3c), *A. cerana* (Figure 3d), *A. florea* (Figure 3e), *Trigona iridipennis* (Figure 3f) and *Ceratina* sp. (Figure 3g). Of these, *Apis* bees collect pollen and nectar while the other bees collect only pollen due to their short tongue length. The wasps foraging at the flowers were *Stizus* sp. (Figure 3i), *Eumenes petiolata* (Figure 3j), *Eumenes conica* (Figure 3k), *Scolia* sp. (Figure 3l), *Campsomeris annulata* (Figure 3m) and *Vespa cincta* (Figure 3n) while the fly was *Helophilus* sp. (Figure 3h). Both wasps and the fly were occasional foragers only; the former collect only nectar while the latter only pollen. The intense pollen feeding activity of bees was considered to be limiting the pollen availability for seed set while wasps during nectar collection were found to be contacting the stigma as well as the dehisced anthers thereby contributing to pollination.

The fruit growth and development begins immediately after pollination and fertilization (Figure 4a-c). A sample of ten tagged inflorescences consisting of 2987 flowers showed 7% fruit set in open-pollinations. The fruit is a small globose capsule, light green initially and brown when mature. Each fruit produces 45-53 seeds out of which viable seeds range from 34 to 46 (Figure 4d-f) while the remaining ones are either half-filled or ill-formed (Figure 4g). Fruits mature in about 5 months and then split apart releasing the tiny seeds into the air. This occurs during rainy season. The time of seed dispersal was found to be unfavourable for the establishment of new populations. During the period of seed dispersal, the seasonal herbaceous vegetation and grass cover reach to their peak growth limiting the space for the newly emerging seedlings. Further, the vegetation also does not allow sunlight to hit the ground. These factors were considered to be responsible for the limited population size of *W. tinctoria* in the study areas.

DISCUSSION

Burkhardt (1964) and Faegri and van der Pijl (1979) characterized butterfly-flowers. Flowers conforming to this type usually possess large, white, pink, red, yellow or blue, narrow, tubular flowers with deep nectaries and often yellow rings or other markings on the petals which function as nectar guides. Baker and Baker (1983) reported that the short-tubed flowers tend to be hexose-rich and if grouped in conspicuous inflorescences provide excellent standing platform for foragers, and attract both butterflies and short-tongued bees. Cruden et al. (1983) also stated that hexose-richness appears to prevail in the nectar of short-tubed flowers. These authors also documented that the nectars of most butterfly-pollinated flowers fall within the range of

15 to 25% sugar concentration. Kingsolver and Daniel (1979) suggested that the nectar sugar concentrations of 20-25% optimize the net energy gain by the butterflies. In *W. tinctoria*, the floral characteristics such as white colour of the flower, lack of odour, short-tubed corolla with deep seated hexose-rich nectar accounting for 15-18% sugar concentration characterize psychophily.

Nectar is a potential source of amino acids for the nutrition of butterflies. Naturally, butterfly nectars are rich in amino acids (Baker and Baker 1983). Butterflies require ten essential amino acids but all of them are not normally found in all nectars. Usually, three to four essential amino acids and several non-essential amino acids are found in floral nectars (Baker and Baker, 1982; 1983). Baker and Baker (1986) reported that the amino acids add taste to the floral nectar and it depends on their concentration. Their presence serves as an important cue for butterflies to make flower visits and in the process effect pollination. In *W. tinctoria*, the nectar contains two essential (arginine and histidine) and eight non-essential amino acids. Its nectar is an important source for two of the ten essential amino acids required by butterflies during adult life for their growth and development (DeGroot, 1953). Non-essential amino acids are metabolized by butterflies from the food they take; however, floral nectar provides some of these amino acids instantaneously. The nectar of *W. tinctoria* provides alanine, aspartic acid, cysteine, glysine, hydroxyproline, tyrosine, glutamic acid and serine. Gardener and Gillman (2002) mentioned that if local soil conditions favour higher amino acids in the nectar then local populations of butterflies may derive certain benefits. Adult feeding on amino acid rich food has been shown to increase longevity and reproductive ability in certain heliconine butterflies (Gilbert, 1972; Dunlap-Pianka et al. 1977). A later study on a temperate species *Euphydryas editha* showed that amino acids in the adult diet led to heavier eggs (Murphy et al. 1983). Jervis and Boggs (2005) reported that the butterflies are agents of selection for higher nectar amino acid production. The requirement of amino acids during adult stage of the butterfly is related to the larval nutritional condition. The larval food plant has a key role in the evolution of the flower-butterfly mutualism, and demonstrates that the importance to butterfly reproduction, and of different nutrient source varies with butterfly nutritional state. Gardener and Gillman (2001) reported that soil conditions can affect the amino acid complement of nectar. This may have implications for plant-butterfly interactions, as local populations of butterflies may benefit from the increased amino acid content of the nectar and preferentially visit plants growing in high nutrient conditions. The fidelity of butterflies to *W. tinctoria* during flowering phase attests the fact that butterflies are in need of amino acids present in this nectar and in the process contributing to pollination.

In *W. tinctoria*, the inflorescences with clusters of flowers provide excellent platform for foraging by butterflies. The retention of flowers for two more days after the cessation of stigma receptivity appears to be an adaptive trait for the plant to enhance the attractiveness to butterflies and other foragers. With these floral structural and functional characteristics, *W. tinctoria* has been found to be foraged by butterflies of all five families of Lepidoptera and by other insects. The short-tubed flowers facilitate butterflies with any length of proboscis to collect nectar easily. The flowers being small in size with minute amount of nectar compel the butterflies to do a more laborious search for nectar from a greater number of flowers. The reduced standing nectar crop due to nectar feeding by thrips prior to and after anthesis further drive butterflies to visit as many flower as possible either from the same or different individual plants to quench their nectar thirst. But, the clustered state of flowers is energetically profitable for butterflies to reduce search time and also flight time to collect a good amount of nectar. Overall, the search for nectar by butterflies due to the production of minute amount of nectar at flower level contributes to both self- and cross-pollination. The presence of pollen on the proboscides of butterflies substantiates this conclusion. *W. tinctoria* attracts more number of individuals and species of Nymphalid butterflies when compared to those of other families of butterflies suggesting that Nymphalid butterflies play a key role in the pollination. The psychophily is advantageous for the plant because butterflies do not collect pollen for themselves but only carry pollen on their proboscis and effect pollination while collecting nectar.

W. tinctoria also attracts bees, wasps and a fly species. The bees being consistent pollen feeders and the fly being an occasional pollen feeder collect huge amount of pollen; *Trigona* and *Ceratina* bees being exclusive pollen feeders due to their short tongue length further empty the pollen of dehisced anthers quickly. Such an intense pollen feeding activity of bees drastically reduces the pollen availability for pollination though they effect pollination while collecting pollen and nectar. This pollen feeding activity is highly detrimental for the plant as it reduces the availability of pollen for pollination which is to be effected by butterflies. Therefore, bees act as effective pollen thieves of *W. tinctoria*. Wasps being nectar feeders also effect pollination but they are not consistent visitors. The study suggests that butterflies are the prime pollinators while other insects, especially wasps contribute to additional pollinations enabling the plant to slightly enhance seed set rate. *W. tinctoria* with massive flowering is an important nectar and/or pollen source for local insects and hence, it is a keystone tree species for them since it provides them with nectar for a period of about one month during summer season in the dry deciduous forest ecosystem of Seshachalam hills. There are no other plant species in flowering which attract a diversity of butterflies to this extent during the flowering period of *W. tinctoria* and hence this tree species plays a crucial role for the local butterflies for their nutrition for one month during summer season.

In *W. tinctoria,* the low fruit set rate despite pollination by butterflies and other insects suggests that the plant might be either self-incompatible or indication of inadequate pollination due to pollen thievery by bees. Each fruit produces a small percentage of half-filled seeds and these seeds do not germinate to produce new plants. The occurrence of such seeds could be attributable to fertilization of certain ovules with inferior pollen and to poor nutritional environment. It indicates post-zygotic incompatibility. The fruits split apart to disperse seeds into the air and hence it is anemochorous. Seed dispersal occurs during rainy season; anemochory is effective only on clear sunny days during this season. The cloudy and rainy days contribute to a drastic decrease in ambient temperature and a drastic increase in ambient humidity and hence anemochory does not occur. Seeds germinate as soon as they fall to the ground but most of the seedlings soon dry up due to non-penetration of sunlight, over-growth of herbaceous vegetation and space limitation. Therefore, inadequate pollination, post-zygotic incompatibility, ineffective anemochory and poor competitive ability of seedlings and other factors stated above in *W. tinctoria* collectively contribute to the small population size and hence it attains the status of "rare" plant in the southern Eastern Ghats.

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Table 1. List of Hymenopteran insects on *Wendlandia tinctoria*

Family	Scientific Name	Common Name
Papilionidae	*Pachliopta hector*	Crimson Rose
	Papilio aglea	Common Mime
Pieridae	*Catopsilia pyranthe*	Mottled Emigrant
	C. pomona	Common Emigrant
Nymphalidae	*Danaus genutia*	Striped Tiger
	D. chrysippus	Plain Tiger
	Junonia lemonias	Lemon Pansy
	Junonia hierta	Yellow Pansy
	Precis iphita	Chocolate Pansy
	Euploea core	Common Indian Crow
	Ariadne merione	Common Castor
	Acraea violae	Tawny Coster
	Tirumala septentrionis	Dark Blue Tiger
	T. limniace	Blue Tiger
	Hypolimnas bolina	Great Eggfly
	H. misippus	Danaid Eggfly
	Phalanta phalantha	Common Leopard
	Neptis hylas	Common Sailer
	Parantica aglea	Glassy Tiger
Lycaenidae	*Jamides celeno*	Common Cerulean
	Arhopala amantes	Large Oak blue
	Lampides boeticus	Pea Blue
	Spindasis vulcanus	Common Silver line
	Everes lacturnus	Indian Cupid
Hesperiidae	*Borbo cinnara*	Rice Swift
Sphingidae	*Cephonodes hylas*	Coffee Hawk moth
Apidae	*Apis dorsata*	Rock honey bee
	Apis cerana	Indian honey bee
	A. florea	Dwarf honey bee
	Trigona iridipennis	Stingless honey bee
	Ceratina sp.	Small carpenter bee
Crabronidae	*Stizus* sp.	Digger wasp
Eumenidae	*Eumenes petiolata*	Potter wasp
	Eumenes conica	Mason wasp
Scoliidae	*Scolia* sp.	Blue-winged wasp
Scoliidae	*Campsomeris annulata*	Flower wasp
	Vespa cincta	Yellow wasp
Syrphidae	*Helophilus* sp.	Hover fly

Figure 1. *Wendlandia tinctoria*: a. Habit, b. Inflorescence, c. Bud, d. & e. Flower, f. Pollen grain, g. Ovules, h. *Pachliopta hector*, i. *Papilio clytia*, j. *Catopsilia pyranthe*, k. *Danaus genutia*,

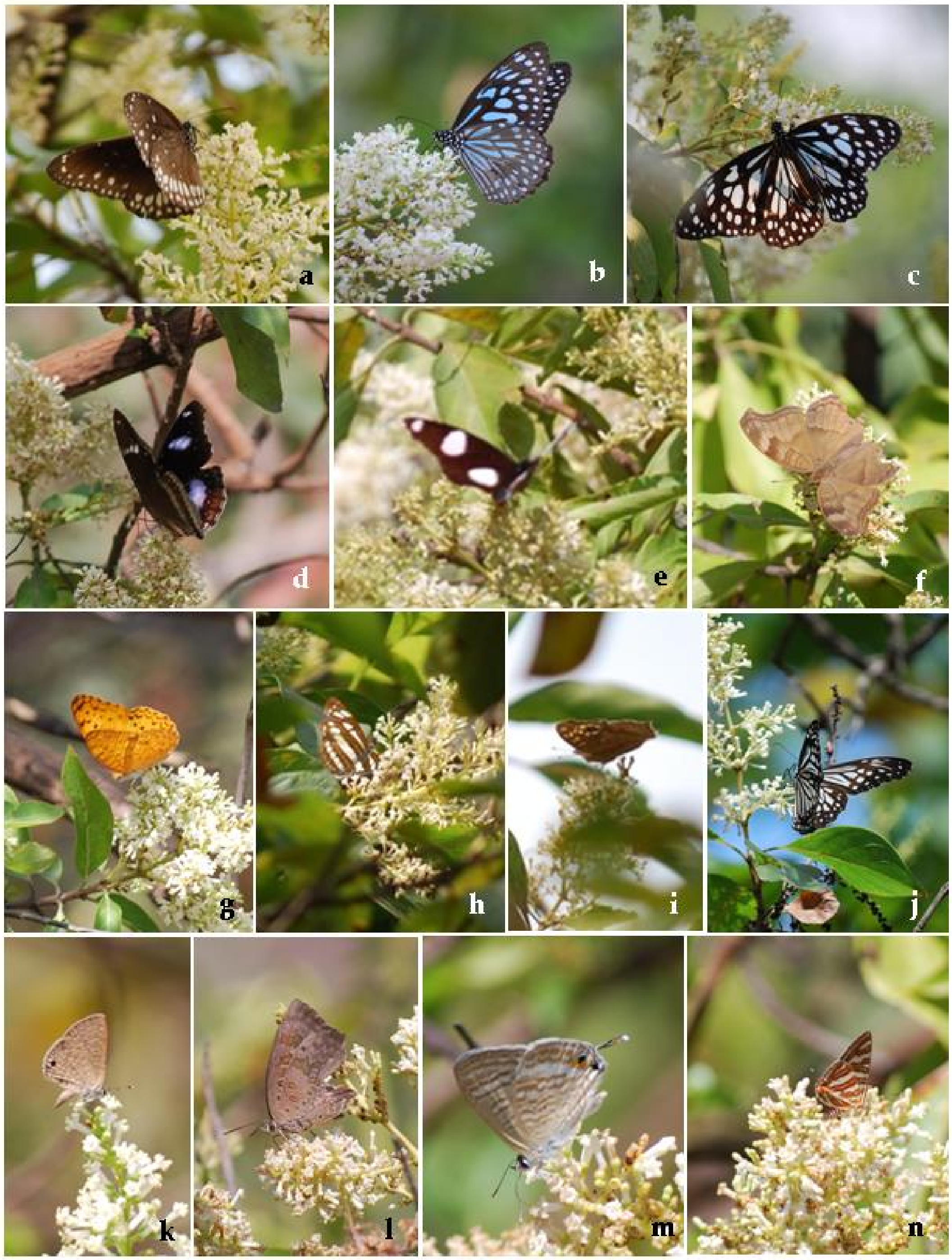

Figure 2. *Wendlandia tinctoria*: a. *Euploea core*, b. *Tirumala septentrionis*, c. *Tirumala limniace*, d. *Hypolimnas bolina*, e. *Hypolimnas misippus*, f. *Precis iphita*, g. *Phalanta phalantha*, h. *Neptis hylas*, i. *Junonia lemonias*, j. *Parantica aglea*, k. *Jamides celeno*, l. *Arhopala amantes*, m. *Lampides boeticus*, n. *Spindasis vulcanus*.

Figure 3. *Wendlandia tinctoria*: a. *Borbo cinnara*, b. *Cephonodes hylas*, c. *Apis dorsata*, d. *Apis cerana*, e. *A. florea*, f. *Trigona iridipennis*, g. *Ceratina* sp., h. *Helophilus* sp., i. *Stizus* sp., j. *Eumenes petiolata*, k. *Eumenes conica*, l. *Scolia* sp., m. *Campsomeris annulata*, n. *Vespa cincta*.

Figure 4. *Wendlandia tinctoria*: a-c. Fruiting, d-f. Healthy seeds, g. Ill-formed seeds.

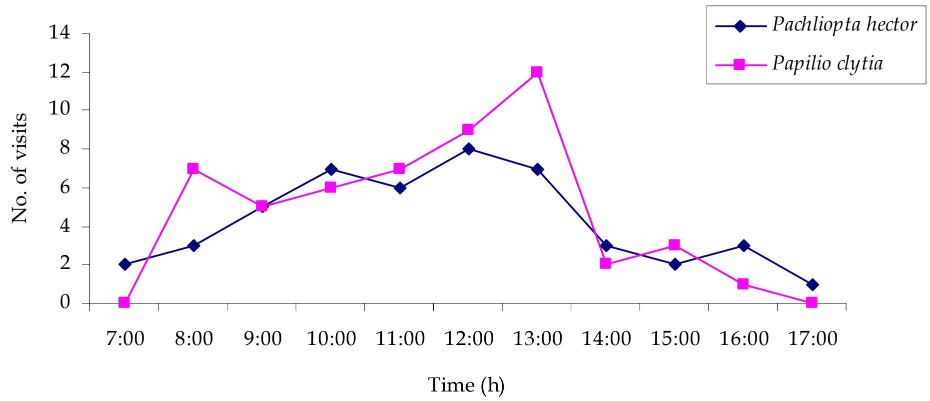

Figure 5 : Hourly nectar foraging activity of Papilionid butterflies on *W. tinctoria*

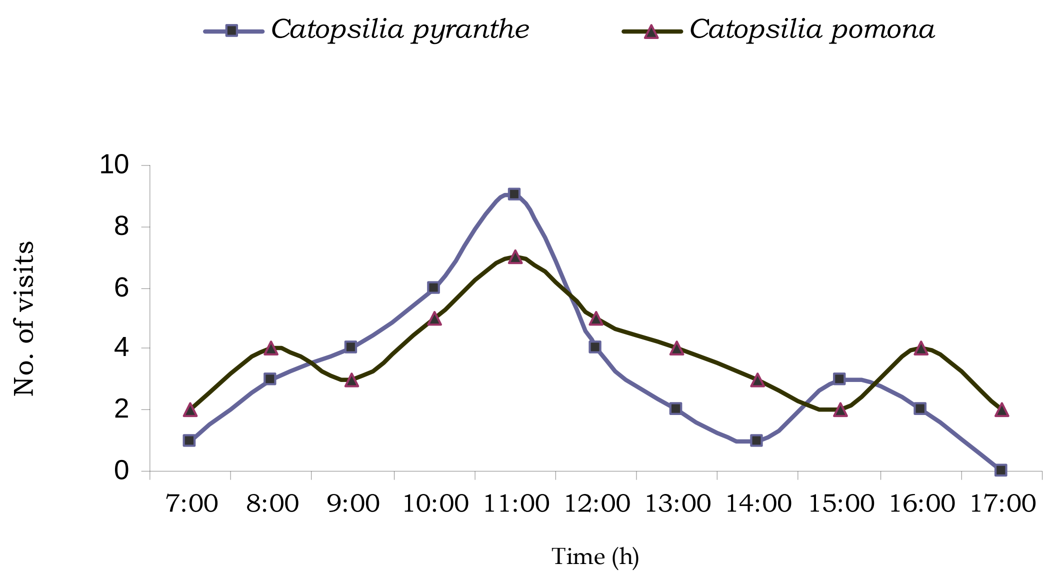

Figure 6: Hourly nectar feeding activity of Pierid butterflies on *Wendlandia tinctoria*

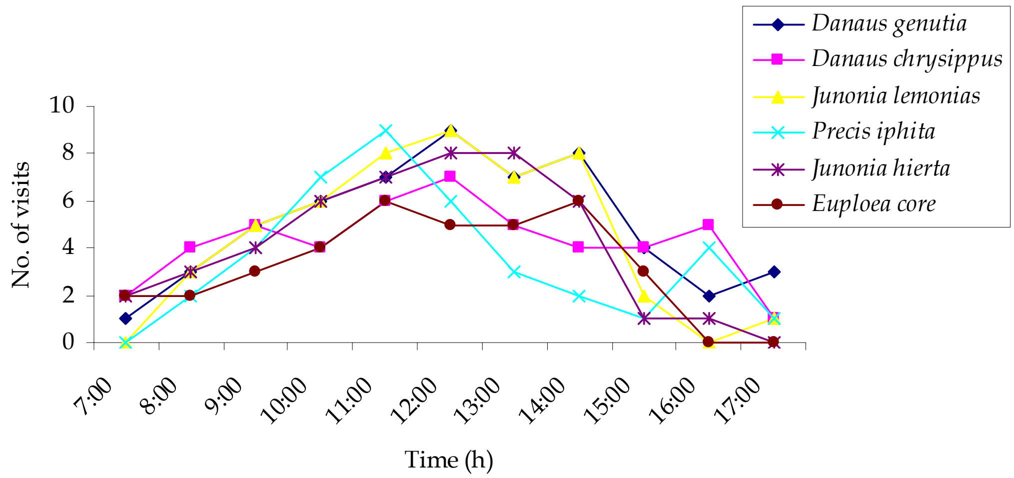

Figure 7: Hourly nectar foraging eactivity of Nymphalid butterflies on *W. tinctoria*

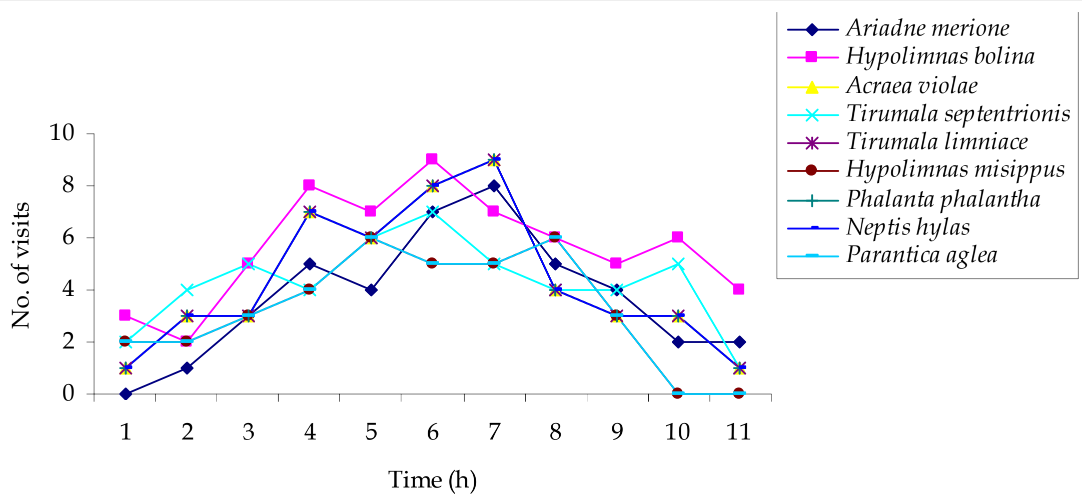

Figure 8: Hourly nectar foraging activity of Nymphalid butterflies on *W. tinctoria*

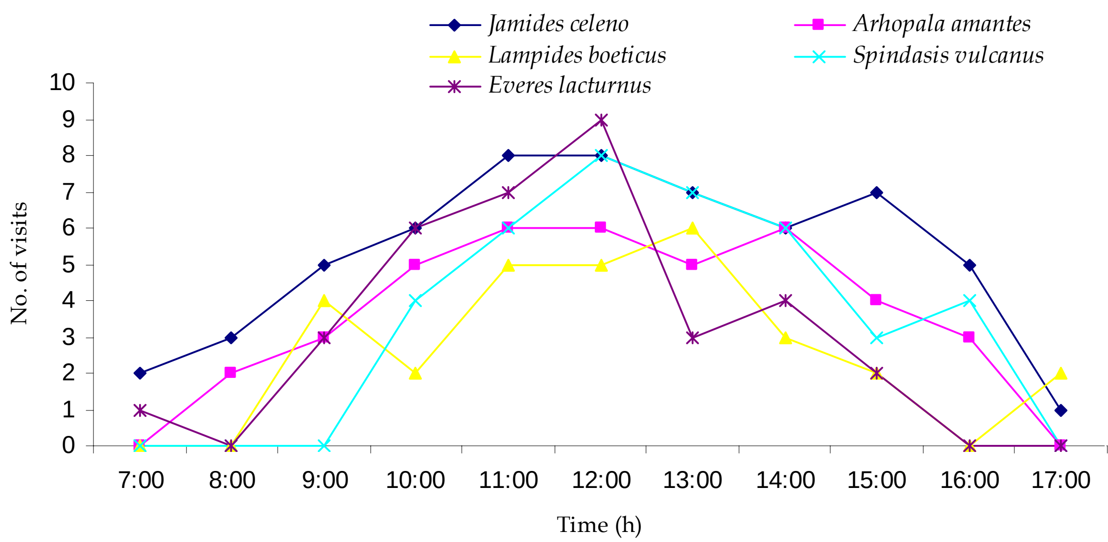

Figure 9: Hourly nectar feeding activity of Lycaenid butterflies on *Wendlandia tinctoria*

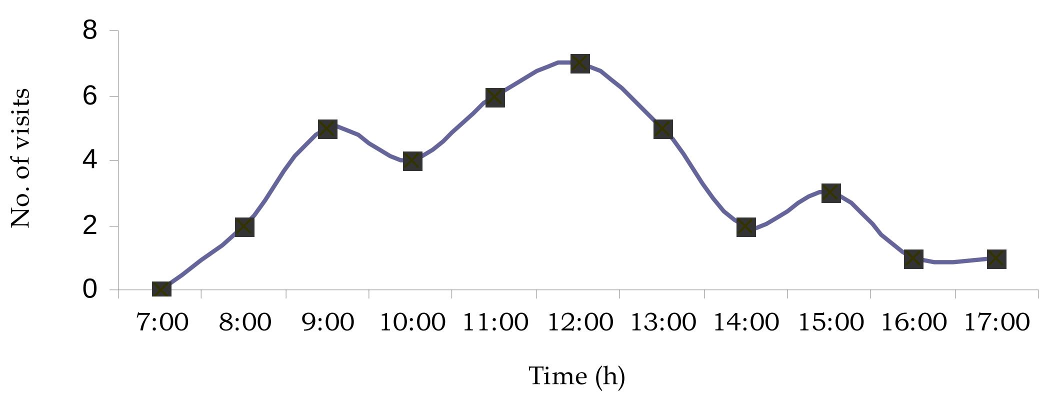

Figure 10: Hourly nectar feeding activity of Hesperiid butterfly, *Borbo cinnara* on *Wendlandia tinctoria*

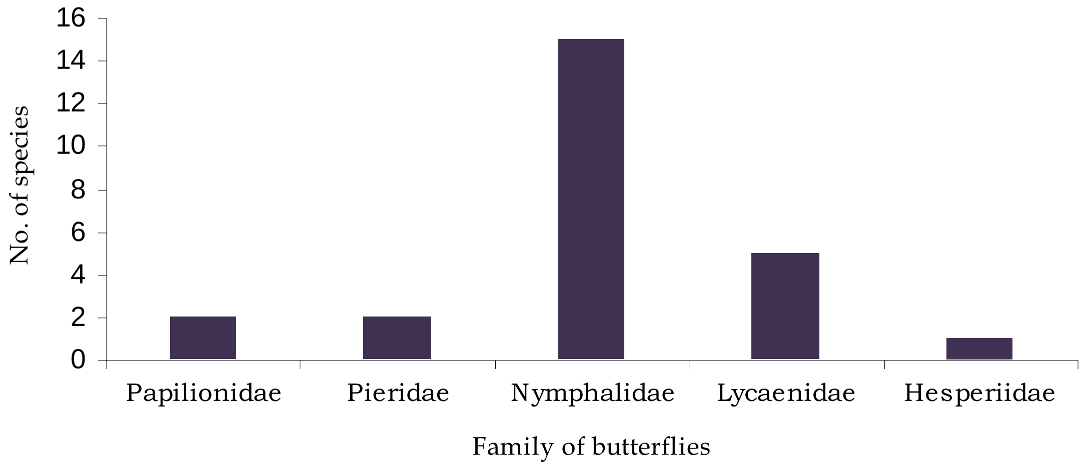

Figure 11: Family-wise number of butterfly species foraging for nectar on *Wendlandia tinctoria*

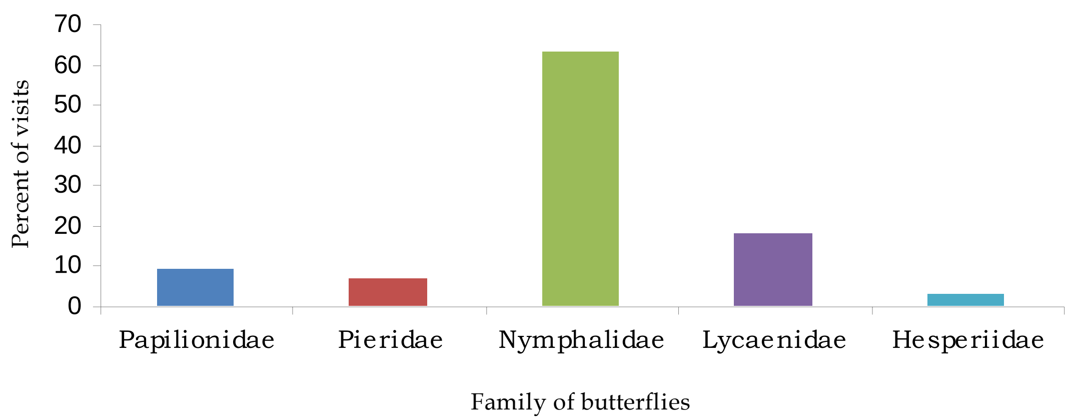

Figure 12: Family-wise percentage of foraging visits of butterflies on *Wendlandia tinctoria*