

Reproductive ecology of *Terminalia pallida* Brandis (Combretaceae), an endemic and medicinal tree species of India

A. J. Solomon Raju*, P. Vara Lakshmi and K. Venkata Ramana

Department of Environmental Sciences, Andhra University, Visakhapatnam 530 003, India

Terminalia pallida is a semi-evergreen tree species. Leaf fall and flushing events occur during pre-monsoon season; leaf flushing extends into the monsoon season. Flowering occurs during late dry season and early monsoon season. The flowers are bisexual and obligately outcrossed and this is enforced by self-incompatibility. Protogyny is a device to promote outcrossing, but it is weak. However, it is partly substantiated by gradual anther dehiscence over a period of six hours. Individual trees flower for a brief period of three weeks with massive floral display. The flowers offer both nectar and pollen for the foragers; the nectar provides five essential amino acids – threonine, arginine, histidine, lysine and methionine, and also some non-essential amino acids. The plant is entomophilous, and cross-pollination is effected mainly by large bees, wasps and butterflies. The natural fruit set is around 6% as against the 62% realized in manual xenogamous pollinations. Fruits fall to the ground when mature and dry, but wind is also instrumental in shedding fruits. The fallen fruits are dispersed by rain water and the seeds germinate and establish seedlings depending on the soil status. The study suggests that *T. pallida* does not suffer from pollinator limitation to maximize fruit set but from the limitation of compatible pollen, flower and fruit predation by a beetle, fruit predation by a rodent and fruit fungal infestation. Nutrient-poor rocky habitat appears to be an important limiting factor for the recruitment and population expansion.

Keywords: Entomophily, obligate outcrossing, self-incompatibility, *Terminalia pallida*.

THE genus *Terminalia* includes about 200 species of trees and shrubs distributed in the tropical and subtropical regions of the world. In India, 20 species belonging to four sections, namely *Catappa*, *Myrobalanus*, *Chuncea* and *Pentaptera* have been reported to be distributed in the tropical and subtropical states. They include *T. alata*, *T. arjuna*, *T. bellerica*, *T. berryi*, *T. bialata*, *T. catappa*, *T. chebula*, *T. citrina*, *T. coriacea*, *T. crenulata*, *T. gella*, *T. manii*, *T. moluccana*, *T. myriocarpa*, *T. pallida*, *T. paniculata*, *T. parviflora*, *T. procera*, *T. tomentosa* and *T. travancorensis*^{1,2}. Almost all these species are valued as

sources of an array of non-wood forest products such as tannins, gums, oils, wood, fodder and certain organic compounds from their leaves, trunk, bark and fruits in certain indigenous drug preparations throughout the Indian sub-continent. They are used by industries such as pharmaceutical, animal husbandry, leather, dyeing, soap, chemical, resin and gum, paper, railways, match sticks, oil and cosmetics¹⁻³. Despite these various economic values, *Terminalia* species have been poorly studied for their reproductive ecology to understand the sexual and breeding systems, and pollinators in the context of their effective conservation and management in their natural areas. Srivastava¹ reported that *Terminalia* species are predominantly outcrossing. *T. catappa* is monoecious, whereas *T. superba* is hermaphroditic; both are self-incompatible and pollinated by Coleoptera, Diptera, Hemiptera, Hymenoptera and Lepidoptera^{4,5}. *T. amazonia* is protogynous with self-incompatibility functional during the post-zygotic stage^{6,7}. *T. bellerica* is pollinated by insects, especially by flies due to unpleasant odour of the flowers⁸. *T. paniculata* is dichogamous, self-incompatible and speculated that it is fly-pollinated^{9,10}. *T. tomentosa* is hermaphroditic, protandrous, self-incompatible and pollinated primarily by bees and flies¹¹. *T. pallida* is an endemic medicinal plant species of India. It has been given an endangered status at the global level based on IUCN criteria by the Conservation Assessment and Management Planning Workshop held at Hyderabad in 2001. It is now included in the First Red List of Medicinal Plants of Andhra Pradesh¹². It occurs in the rocky hilly areas of dry deciduous forests of Chittoor, Cuddapah and Kurnool Districts in Andhra Pradesh, at 700–800 m elevation in the Eastern Ghats, but it is mainly centred at Tirumala Hills, Chittoor. The leaf is used for treating skin blisters and skin diseases, whereas the stem bark is used as a diuretic and for swellings. The fruit is used as an anti-pyretic, purgative, for diarrhoea, peptic ulcers, diabetes, venereal diseases, cough, cold, dysentery, fissures, cracks and in tanning and dyeing. It is also used as a substitute for the fruit of *T. chebula*^{13,14}. Despite its multiple medicinal values and also being an endemic and red-listed species, *T. pallida* has not been studied for its reproductive biology to understand the causes for its limited distribution in the Eastern Ghats. It is in this context that the present study was undertaken to study the reproductive biology of this tree species and the same is also discussed in the light of relevant published literature.

T. pallida populations growing on rocky areas at Akasaganga, Papanasanam, Japalitheertham, Srivari mettu and Talakona in Tirumala Hills of the Eastern Ghats (lat. 13°40'N, long. 79°19'E and altitude 2443 ft) were selected for study during 2009–10. The study aspects included flowering, fruiting, seed dispersal and seedling ecology. Twenty inflorescences, four each from five trees were tagged and followed for their flowering duration. Thirty flowers collected from six trees were used to record floral

*For correspondence. (e-mail: ajsraju@yahoo.com)

details. Mature flower buds on 20 inflorescences were tagged and followed for recording the time of flower opening. The same flowers were followed for recording the time of anther dehiscence. The pollen-grain characteristics were recorded by consulting the literature¹⁵. Pollen production per flower and pollen-ovule ratio were calculated following the method described by Cruden¹⁶. Stigma receptivity and nectar volume, sugar concentration and sugar types were recorded by following the protocols given in Dafni *et al.*¹⁷. For nectar volume and sugar concentration, a total of 20 flowers were bagged each day. The nectar was also analysed for amino acid types by following the paper chromatography method of Baker and Baker¹⁸. Fifty mature buds, five each from ten inflorescences on five trees were bagged a day before anthesis without manual self-pollination, to know whether fruit set occurs through autogamy. Another set of 50 mature buds was selected in the same way, then emasculated and bagged a day prior to anthesis. The next day, the bags were removed and the stigmas were brushed with the freshly dehisced anthers from the flowers of the same tree and re-bagged to know whether fruit set occurs through geitonogamy. Five trees each at Akasaganga, Papanasanam and Talakona were selected for manual cross-pollination and open-pollination. Fifty flowers were used per tree for manual cross-pollination. For this, mature buds were emasculated and bagged a day prior to anthesis. The next day the bags were removed; freshly dehisced anthers from the flowers of another tree were brushed on the stigma and re-bagged. Ten inflorescences with a total of 567 flowers on each tree were tagged for fruit set in open-pollination. The bagged flowers and tagged inflorescences were followed for 4 weeks to record the results. Further, 10 inflorescences from each of the three places were tagged and followed for calculating the percentage of fruit set at the inflorescence level. The total flowers used were 578 at Akasaganga, 623 at Papanasanam and 592 at Talakona. Observations were made on flower visitors and their foraging activity period with reference to pollination using binoculars. The foraging visits made by each forager species to a selected patch of about 500 flowers were counted for 15 min at each hour during daytime to record foraging activity pattern. The data of foraging visits for each forager species are the average of five replicates on five different days. The insect species visiting the flowers and the forage sought by them were recorded. Five hundred fruits collected at random from 15 trees, five each from the above-mentioned three places were examined to record the percentage of fruit infestation by the beetle. One hundred fallen fruits were collected and examined for fungus infestation rate. Fruit maturation and fruit-fall timing and dispersal aspects were observed in the field. Fruit and seed characteristics were recorded. Fruit feeding activity of Three-Striped Palm Squirrel, *Funambulus palmarum* was observed at maturing and mature dry-fruit stage. Field observations

were also made on the natural seed germination and establishment rate.

T. pallida is a semi-evergreen tree species. Leaf shedding, flushing and flowering are annual events. Leaf shedding and flushing processes are slightly asynchronous; the former begins in the 3rd week of March, and the latter in the 1st week of April. Leaf flushing extends until the end of June (Figure 1a). Flowering occurs during the 2nd week of April and 3rd week of June at the population level. It ceases during late May in most of the trees. An individual tree flowers for about 3 weeks only. The flowers are borne in simple terminal and axillary spikes (Figure 1b and c). Each spike is 9.94 ± 2.19 cm and produces 81 ± 14 flowers acropetally over a period of 5–6 days. Flowers are stalked, pale yellow, bisexual, slightly foetid, 10 mm long, 5 mm in diameter and slightly zygomorphic. Calyx tube is ovoid and divided into five triangular valvate lobes. Petals are absent. Stamens are ten, arranged in two whorls of five each and inserted inside the distal part of the calyx tube; filaments are 4 mm long and incurved in bud and anthers exerted from calyx tube after anthesis. The anthers are versatile, dithecous, fertile and cream-coloured. A nectariferous disc is present on the summit of the ovary and it is enveloped by massive silky hair (Figure 1d). The ovary is inferior, unilocular with two pendulous anatropous ovules. The style is simple, 4 mm long. The stigma is simple, cream white, 2 mm long, wet and shiny.

The flowers remain open the whole day (Figure 1d). The stigma protrudes out of the calyx during the mature bud stage. It is receptive since then and continues until the evening of the 3rd day. The anthers dehisce during the post-anthesis period in a gradual manner. In a flower, the stamens dehisce at 2-h intervals and the dehiscence process is complete within 6 h. First, two stamens dehisce, then six stamens and finally two stamens. All anthers dehisce by longitudinal slits only. A mature anther produces 1511 ± 85 pollen grains. The mean pollen output per flower is 15,110. The pollen grains are spherical, tricolpate, $24.9 \mu\text{m}$ in diameter, exine smooth and yellow (Figure 1h). The pollen-ovule ratio is 7555:1. Nectar secretion occurs continuously for three days. A flower produces $4.2 \pm 0.99 \mu\text{l}$ of nectar consisting of glucose, fructose and sucrose with the first two types being dominant. The nectar sugar concentration increases from day 1 to day 3; it is 8–9% on day 1, 10–12% on day 2, 12–15% on day 3 and 16–18% on day 4. The nectar also contains both essential and non-essential amino acids. The essential amino acids are threonine, arginine, histidine, lysine and methionine. The non-essential amino acids include glutamic acid, glycine, hydroxyproline, serine, alanine, aspartic acid, cystine, proline and butyric acid. The flowers fall off on the 5th day.

Flower buds and the just open flowers contained thrips. Thrips were found to use the flower buds for breeding and the open flowers for food. They were the first foragers of

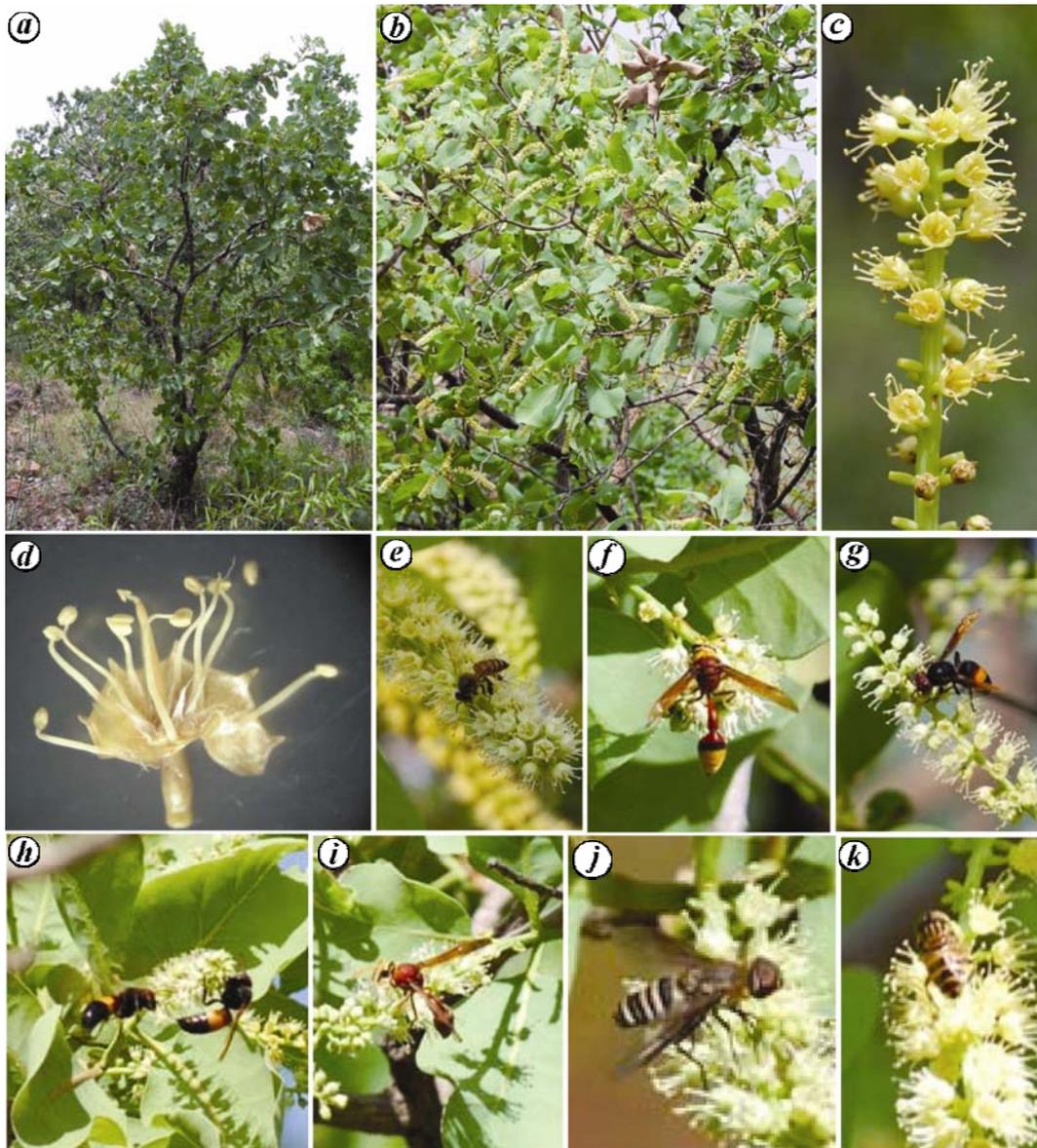


Figure 1. *Terminalia pallida*: **a**, Tree with new leaf flushing; **b**, Flowering branches; **c**, Flowering inflorescence; **d**, Flower; **e–k**, Foragers: **e**, *Apis cerana*; **f**, *Eumenes petiolata*; **g**, *Vespa cincta*; **h**, *Vespa orientalis*; **i**, *Eumenes conica*; **j**, *Hyperalonia* sp. and **k**, *Helophilus* sp.

pollen and nectar. They tended to fly mostly within and between flowers of the same tree and hence their foraging activity was considered to be important in self-pollination. The flowers were foraged during daytime by 33 species of insects representing bees, wasps, bugs, flies, butterflies and beetles (Table 1). The bees included *Apis dorsata*, *Apis cerana* (Figure 1e), *Apis florea*, *Trigona iridipennis*, *Ceratina* sp., *Xylocopa latipes* and *Halictus* sp. The wasps included *Campsomeris annulata*, *Scolia* sp., *Eumenes petiolata* (Figure 1f), *Vespa cincta* (Figure 1g), *Vespa orientalis* (Figure 1h), *Eumenes conica* (Figure 1i), *Eumenes* sp. and two unidentified wasp species. Flies were *Hyperalonia* sp. (Figure 1j) and *Helophilus* sp. (Figure 1k). The butterflies were *Papilio polytes* (Figure 2a), *Graphium nomius* (Figure 2b), *Ju-*

nonia lemonias (Figure 2c), *Precis iphita* (Figure 2d), *Hypolimnas bolina* (Figure 2e), *Danaus chrysippus* (Figure 2f), *Phalanta phalantha* (Figure 2g), *Tirumala limniace* (Figure 2h), *Euploea core* (Figure 2i), *Neptis hylas* (Figure 2j), *Arhopala amantes* (Figure 2k) and *Pseudocoladenia indrani* (Figure 2l). Further, *Lygaeus* sp. a true bug, and two unidentified beetle species were also recorded.

The bee foragers except *X. latipes* were found to collect both nectar and pollen; they were regular throughout the flowering season. *Xylocopa* bee collected nectar only. They showed maximum foraging visits at 0900–1000 h in the forenoon and at 1700 h in the afternoon. The foraging activity of some common pollinators is presented in Figure 3. The forehead and ventral side of the insects except

butterflies were found to be contacting the anthers and stigma invariably while probing the flower for nectar. The bees while collecting pollen from the anthers normally contacted the stigma on their underside and hence were considered to be transferring pollen and effecting pollination. *Trigona*, *Ceratina* and *Halictus* bees tended to stay mostly on the same tree for forage collection, effecting mostly self-pollination. *Apis* and *Xylocopa* bees made frequent inter-tree flights in search of more pollen and nectar promoting cross-pollination simultaneously. The wasps foraged for nectar only and showed peak activity during 1000–1300 h, but their foraging intensity was less compared to bees activity. The bees were found to be foraging and moving fast from flower to flower and from plant to plant in quest of more nectar effecting both self-and cross-pollinations. *Lygaeus* species visited flowers in groups for only nectar during 0900–1100 h but they remained mostly on the same plants. Flies were very slow in their flower-to-flower movements and collected both pollen and nectar mainly during 0900–1100 h but they were not consistent foragers throughout the flowering season. Butterflies being nectarivorous visited the flowers

regularly and consistently throughout the flowering season. They showed maximum foraging activity during 0900–1200 h, although they continued foraging until late evening. They made frequent inter-tree foraging visits in search of more nectar promoting cross-pollinations. The beetles being day-long foragers collected nectar, pollen and also fed on delicate floral parts causing damage to the stamens and stigma. They were, however, occasional flower feeders and tended to stay on the same plant moving slowly from inflorescence to inflorescence in search of the forage. Data on the foraging visits indicated that the bees made 52%, wasps 29% and butterflies 19% of the total visits (Figure 4).

The manual pollinations performed for autogamy and geitonogamy did not set fruit, whereas those performed for the xenogamous mode set fruit ($61.6 \pm 10.4\%$). The fruit set was $5.5 \pm 0.78\%$ in open-pollinations. Fruit set at inflorescence level varied from 1 to 12 in number. The percentage of 1-fruited inflorescences was 19%, 2- and 3-fruited each 22%, 4-fruited 11%, 5-fruited 10%, 6-fruited 5%, 7-fruited 4%, 8- and 9-fruited each 2% and 10-, 11- and 12-fruited each 1%. The fruits mature in 2 months. They were initially light to dark green and brown when mature (Figure 5 a–c). The fruit was indehiscent drupe, one-seeded, 2.98 ± 0.28 cm in length and 1.6 ± 0.17 cm wide, obovoid and weighs 1.56 ± 0.51 g. Seeds were 1.7 ± 0.24 cm long, 0.9 ± 0.18 cm wide, 0.62 ± 0.36 g in weight, light brown and ridged (Figure 5 i).

In the flower-bud stage, a beetle species was found to be injecting a single egg into the ovary. The egg hatches to produce a larva which feeds and pupates in the developing fruit (Figure 5 e and f). The emerging adult exits from the dry fruit (Figure 5 d). The fruit infestation rate by this beetle was 41%. Further, fruits were also found to be infested with a fungus species after fruit dispersal (Figure 5 g). Fruit fungal infestation rate was 6%. Maturing fruits were found to be eaten voraciously for the internal soft material (Figure 5 h) and mature dry fruits for the embryo and other endogenous material (Figure 5 j) by the rodent, Three-Striped Palm Squirrel, *Funambulus palmarum* (family Sciuridae). High wind speed causes the mature dry fruits to fall to the ground and also disperses the fallen fruit on the ground to some extent. Further, rain water is effective to disperse the fallen fruits up to 1 km distance. The fallen fruits decompose and the seeds then show germination if they are healthy. Seed germination and seedling emergence were found during late August–late September (Figure 5 k). A few seedlings were found in the vicinity; they grow slowly, but their growth and development was found to be related to the water and nutritional status of the soil.

T. pallida is an important constituent of deciduous forest in the Eastern Ghats. Leaf flushing occurring during pre-monsoon period in this species seems to be an inherent mechanism to reduce herbivory, as insect populations emerge to peak level during the monsoon period^{19–21}.

Table 1. Insect foragers on *Terminalia pallida*

Order/Family	Scientific name	Common name
Hymenoptera		
Apidae	<i>Apis dorsata</i>	Rock bee
	<i>Apis cerana</i>	Indian honey bee
	<i>Apis florea</i>	Dwarf honey bee
	<i>Trigona iridipennis</i>	Stingless bee
	<i>Ceratina</i> sp.	Small carpenter bee
	<i>Xylocopa latipes</i>	Large carpenter bee
	Halictidae	<i>Halictus</i>
Scoliidae	<i>Campsomeris annulata</i>	Flower wasp
	<i>Scolia</i> sp.	Digger wasp
Vespidae	<i>Eumenes petiolata</i>	Potter wasp
	<i>Vespa cincta</i>	Yellow-banded wasp
	<i>V. orientalis</i>	Oriental Hornet
Eumenidae	<i>Eumenes conica</i>	Potter wasp
	<i>Eumenes</i> sp.	Potter wasp
Hemiptera		
Lygaeidae	<i>Lygaeus</i> sp.	Black and Red bug
Diptera		
Bombyliidae	<i>Hyperalonia</i> sp.	Pomace fly
Syrphidae	<i>Helophilus</i> sp.	Hoverfly
Lepidoptera		
Papilionidae	<i>Papilio polytes</i>	Common Mormon
	<i>Graphium nomius</i>	Spot Swordtail
Nymphalidae	<i>Junonia lemonias</i>	Lemon Pansy
	<i>Precis iphita</i>	Chocolate Pansy
	<i>Hypolimnas bolina</i>	Great Eggfly
	<i>Danaus chrysippus</i>	Plain Tiger
	<i>Phalanta phalantha</i>	Common Leopard
	<i>Trumala limniace</i>	Blue Tiger
	<i>Euploea core</i>	Common Indian Crow
	<i>Neptis hylas</i>	Common Sailer
Hesperiidae	<i>Arhopala amantes</i>	Large Oakblue
	<i>Pseudocoladenia indrani</i>	Tricolour Pied Flat



Figure 2. *T. pallida*: a, *Papilio polytes*; b, *Graphium nomius*; c, *Junonia lemonias*; d, *Precis iphita*; e, *Hypolimnas bolina*; f, *Danaus chrysippus*; g, *Phalanta phalantha*; h, *Tirumala limniace*; i, *Euploea core*; j, *Neptis hylas*; k, *Arhopala amantes* and l, *Pseudocoladenia indrani*.

This process of refoliation demands the plant to invest in food reserves and stored water²², but ensures the plant with fully developed foliage to take advantage of favourable wet and warm conditions for growth, during the onset of monsoon²³. The slight asynchrony in leaf shedding and flushing events characterizes *T. pallida* as a semi-evergreen tree species. The available information on phenological events in *Terminalia* species is quite fragmentary. *T. alata*, *T. bellerica*, *T. chebula*, *T. gella*, *T. superba* and *T. paniculata* are deciduous trees, whereas *T. paniculata* and *T. catappa* are semi-deciduous trees; and

T. arjuna is an evergreen tree^{4,5,8,13}. The recorded information shows that *T. catappa* changes foliage twice and flowers thrice a year⁴. On the contrary, Subba Reddi *et al.*²⁴ reported that *T. catappa* flowers twice in a year, once during February–March and the second during June–August, each time shedding leaves and putting forth new foliage. *T. bellerica* changes foliage in April, flowers during October–November, fruit set in February and fruit ripening in August–December of the next year⁸. *T. alata* changes foliage during January–February, whereas *T. chebula* changes foliage in April and flowers

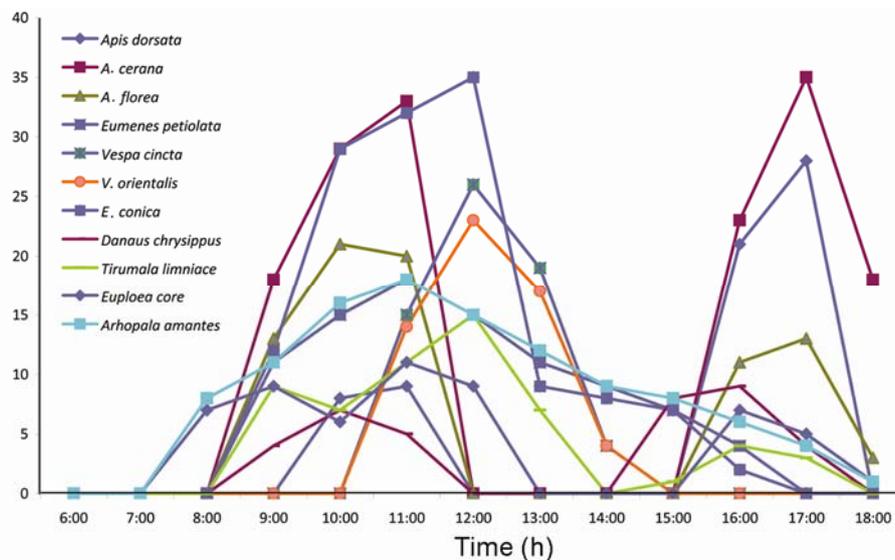


Figure 3. Hourly nectar foraging activity of some common pollinator insects on *T. pallida*.

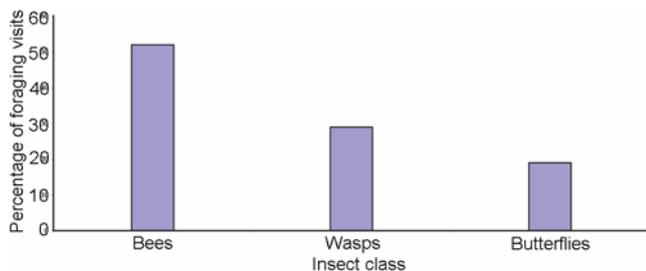


Figure 4. Insect class-wise percentage of foraging visits on *T. pallida*.

immediately after leaf flushing¹³. *T. superba* flowers once in a year for 2–5 weeks; it may show flowering twice if there are two deciduous periods⁵. *T. tomentosa* sheds foliage in May and produces new foliage during June–July; flowering occurs immediately after leaf flushing¹¹. As the information provided on the phenological events in *Terminalia* species is incomplete, systematic field phenological studies are required to confirm the deciduous nature and phenological events occurring in *Terminalia* species in the context of the effects of climate change on phenological events of plant species.

In the genus *Terminalia*, the flowers are commonly bisexual but monoecy and other sexual systems may also exist. *T. catappa* is andromonoecious and its inflorescences bear bisexual flowers at the bottom and staminate ones above. Three types of inflorescence occur and this classification is based on their length. Of all the three types of inflorescence produced, 30% bears only male flowers whereas the rest bears both bisexual and male flowers^{4,24}. *T. arjuna*, *T. bellerica*, *T. gella*, *T. chebula*, *T. paniculata* and *T. amazonia* are hermaphroditic species^{7,13,11}. In the present study, *T. pallida* is a perfect hermaphroditic species. The inflorescences in spike form display the flowers above the foliage and such a display

is advantageous for the plant to attract its pollinating agents even from considerable distances.

Most of the tropical tree species are known to produce a massive bloom in the dry season²⁵. *T. pallida* is also a tropical tree species and exhibits massive bloom by flowering for a brief period. However, flowering at population level is extended and such a flowering pattern may benefit the plant for enhanced fruit set rate and hence for the success of sexual reproduction. The flowering pattern at individual plant level represents the massive flowering pattern described by Gentry²⁶ and Opler *et al.*²⁷. Mass flowering is considered as a property of the individuals of a plant species²⁸ and this pattern of flowering may have evolved in *T. pallida* for effective pollen movement between plants. The new foliage during the flowering phase enables the plant to enhance the photosynthetic efficiency to pump the required photosynthate levels to the growing fruits.

Terminalia species have been reported to be predominantly outcrossing^{1,2}. Self-incompatibility has been reported in *T. paniculata*, *T. tomentosa* and *T. superba*^{5,10,11,23}, whereas self-compatibility in *T. catappa* and *T. amazonia*. *T. catappa* also sets fruit through apomixis, whereas *T. amazonia* exhibits post-zygotic incompatibility^{7,24}. *T. pallida* is an obligate outcrosser by means of self-incompatibility and it is substantiated by fruit formation only in manual xenogamous pollinations. Obligate outcrossers have relatively more paternal reproductive effort and typically have higher pollen–ovule ratios than the related self-incompatible species^{16,29,30}. Pollen–ovule ratio of *T. pallida* is more than 2.5 times larger than that predicted for obligate outcrossers (5859). *T. paniculata* being an obligate outcrosser also has similar pollen–ovule ratio¹¹, suggesting that obligate outcrossers have evolved to invest more in paternal output to qualify the obligate outcrossing mode of pollination.

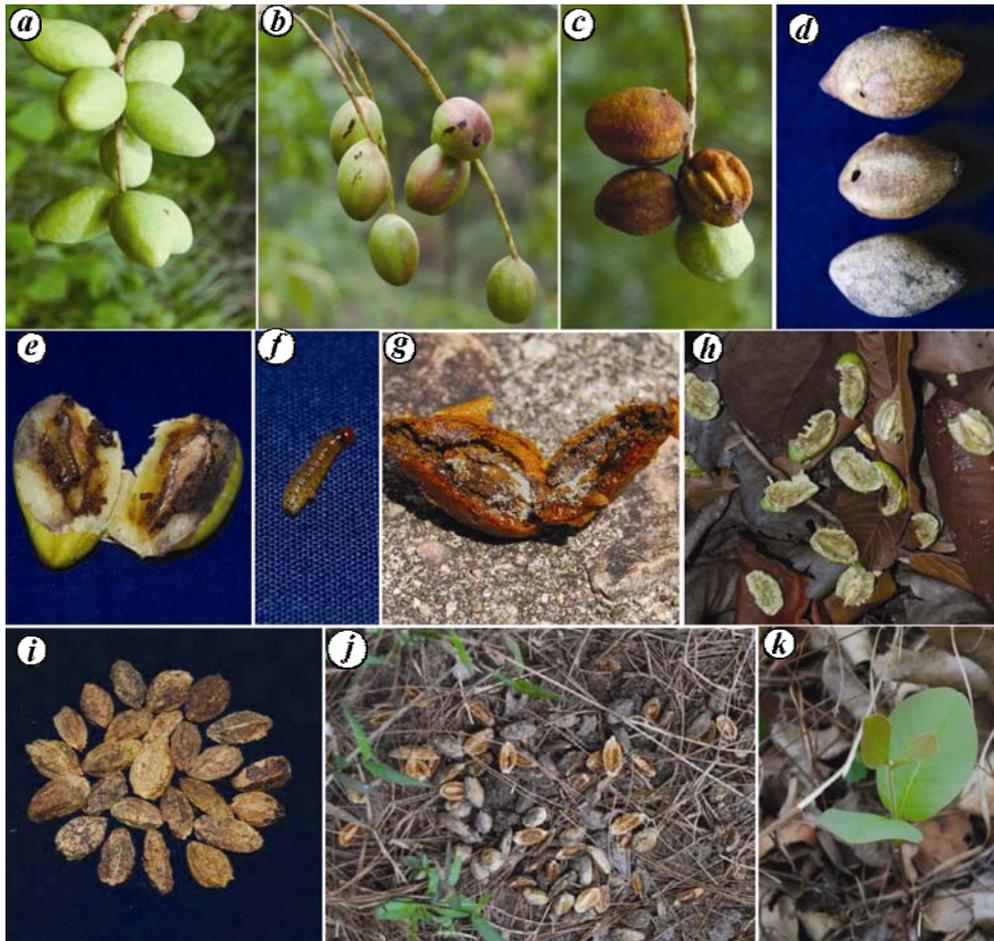


Figure 5. *T. pallida*: **a–c**, Different stages of fruit development; **d**, Fruits with exit hole created by the beetle; **e**, Infested fruit; **f**, Larva; **g**, Fruit fungal infestation; **h**, Growing fruits damaged by rodent; **i**, Healthy seeds; **j**, Mature fruits damaged by rodent and **k**, Seedling.

Dichogamy with protandry or protogyny has been documented in *Terminalia* species. *T. pallida* is dichogamous with weak protogyny. The dehiscence of anthers over a period of 6 h during the post-anthesis phase seems to be an additional mechanism to strengthen protogyny. Weak dichogamy is not effective to prevent self-pollination and selfed flowers do not set fruit. However, this sexual mechanism does not seem to have any role as the species is strongly obligately self-incompatible. Thus, protogyny in this species appears to be a superfluous anti-selfing mechanism, and the occurrence of more than one anti-selfing mechanism is not uncommon^{31–33}.

Mass blooming has a major disadvantage in obligate outcrossers. With intense daily floral forage availability at the plant level, the pollinator insects tend to remain constant to the same plant and move from flower to flower within and between inflorescences, thus causing autogamy or geitonogamy^{34,35}. Different strategies have been suggested through which mass-flowering plant species may achieve inter-plant movements of their pollinators. These include low nectar production forcing pollinators consistently to seek nectar sources, and depletion of nectar supply by robbers in high nectar-producing spe-

cies³⁶, aggressive interactions among flower visitors and the displaced individuals moving to an adjacent conspecific tree³⁵, and the attraction of pollinator predators³⁷. In *T. pallida*, the volume of nectar secreted during the entire flower life is small and the sugar concentration does not exceed 18%. The nectar is an important source for five of the ten essential amino acids required by insects for their growth and development³⁸. They include threonine, arginine, histidine, lysine and methionine. Non-essential amino acids are metabolized by insects from the food they take; however, floral nectar provides some of these amino acids instantaneously. The low-energy-requiring bees such as *Trigona*, *Ceratina* and *Halictus*, flies and beetles seldom move to conspecific plants in search of nectar, whereas the high-energy-requiring bees such as, *Apis* and *Xylocopa*, wasps and butterflies move frequently from plant to plant in search of new forage sources. The simultaneous forage collection activity and the presence of several forage-collecting individuals of each insect species on an individual plant result in aggressive interactions and hence compel the insect foragers to seek new forage sources from conspecific plants. Such a foraging activity of insects enables the plant to counter the disad-

vantage associated with mass blooming and also to enhance the cross-pollination rate in *T. pallida*. In the mass bloomer, *T. tomentosa* also, the nectar volume is small but is resorbed by the plant around noon to enforce the inter-plant movement by low-energy-requiring flies and bees in order to enhance the cross-pollination rate¹¹. *T. pallida* does not resorb nectar and this mechanism is not required for the plant because insect activity is high and such a foraging activity compels the insects to forage on different conspecific plants to satisfy their food requirement. The nectar-feeding activity by thrips during mature bud and flower stages depletes the availability of standing nectar crop, and hence such a state of floral nectar may also serve as a mechanism to promote inter-plant foraging activity by insects.

Flowers pollinated by generalist insects usually have high sugar concentration of nectar³⁹. In contrast, the nectar of *T. pallida* has low sugar concentration. Interestingly, however, the percentage of sugar in the nectar increases with the flower age. Perhaps, this serves to increase its attraction for the insects⁴⁰. Thus, any reduction in the attraction of nectar may reflect in the decline of pollinator visits and the gradual increase of nectar sugar concentration by the flowers keeps the attraction for insects unaffected. Similar increase in nectar sugar concentration and sugar concentration range has been reported in *T. tomentosa*¹¹. The study therefore suggests that *T. pallida* is strictly entomophilous and the plant has all the floral characteristics and mechanisms required for the effective operation of entomophily. Entomophily involving beetles, flies, bugs, bees and butterflies has been reported in *T. superba* and *T. catappa*^{4,5,24}, bees, flies, ants, wasps and butterflies in *T. tomentosa*¹¹, and bees and flies in *T. paniculata*¹⁰. The present study, supported by these previous studies, suggests that the *Terminalia* flower is a generalist and utilizes different categories of insects for pollination and subsequent fruit set irrespective of its sexual and breeding systems.

Lindsey⁴¹ reported that the open flowers are usually indiscriminately visited by diverse insects; but all species may not be effective pollinators. It may be true that all visitors to *T. pallida* have not exhibited the same degree of effectiveness in pollen pick-up and their foraging speed, and they also varied in their visitation frequency; these differences are likely to reflect in their pollination effectiveness. Since most of the foraging insects are compelled to move to other trees due to change in nectar availability and aggressiveness of insects for the available forage, they are to be treated important in the transfer of outcross pollen in *T. pallida*, irrespective of their difference in foraging speed and relative abundance. The body size of certain insects is relatively small. Such small visitors are treated as 'low-energy' pollinators having short foraging ranges⁴², and therefore, the capability of such insects to move outcross pollen can be generally doubted. Analysing the literary data of pollinators of dioecious

taxa in the tropics, Renner and Fiel⁴³ stated that small insects cannot be underestimated to serve as cross-pollinators. Therefore, even the low-energy-requiring insects with their rare inter-plant foraging activity may contribute to cross-pollination in *T. pallida*.

Atluri and Rao¹¹ reported that natural fruit set in *T. tomentosa* is low and does not exceed 2% as against 80% fruit set realized in hand-pollinated flowers. They also mentioned that this lowest fruit set rate is the result of pollinator limitation due to precipitation in the flowering season which adversely affects both foraging and nest sites. In *T. chebula* and *T. bellerica*, the number of fruits per inflorescence does not exceed 10 (ref. 8). In *T. pallida*, the natural fruit set is 6%, and it is 62% in manual xenogamous pollinations. There is no pollinator limitation. The number of fruits per inflorescence does not exceed 12 and most of the fruited inflorescences bear 1–3 fruits. The low natural fruit set and the small number of fruits per inflorescence in *T. pallida* could be attributed to the inherent capacity of the plant, limitation of compatible pollen, flower and fruit predation by a beetle, and nutrient-poor rocky habitat with scanty litter availability. Out of the small percentage of natural fruit set, a major chunk at the maturing stage forms the food for a rodent species, leaving a small quantity of fruits for maturation. Further, the same rodent consumes more fruits on the ground. The rodent fruit-feeding activity at fruit maturation and fallen stage is highly detrimental for the success of sexual reproduction, since such fruits and seeds are destroyed. Morton⁴ reported that fruit bats and birds feed on fruits of *T. catappa* and distribute seeds to other areas. Fundter⁸ reported that rodents and insect pests destroy *T. bellerica* seeds. Therefore, rodents, bats and birds use fruits and seeds of *Terminalia* species as food and in the process regulating their populations in natural areas.

T. catappa seeds float and are carried away considerable distances on the oceans and still remain viable⁴. Seed dispersal in *T. bellerica* is zoochorous and is effected by arboreal and terrestrial animals such as pigs, deer and goats⁸. In *T. pallida*, dry fruits fall to the ground due to abscission at the point of fruit stalk. Wind also causes fruit fall. The fallen fruits serve as food for the rodents and are also susceptible to a fungal species. The fallen fruits are carried away by rain water up to a distance of 1 km, suggesting that rain water is effective in fruit dispersal. The fruits thus dispersed and settled eventually decompose exposing the seed for subsequent germination. However, seed germination and seedling establishment rate appear to be closely related to the nutrient status of the soil. The area being rocky and litter-deficient or free does not seem to favour new recruitment each year for the build-up of *T. pallida* population. Therefore, appropriate measures are required to encourage seed germination and seedling establishment in the natural areas for the effective conservation and management of *T. pallida*.

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