Collectanea Botanica **42: e012**
enero-diciembre 2023
ISSN-L: 0010-0730
https://doi.org/10.3989/collectbot.2023.v42.012

Reproductive ecology of *Cipadessa baccifera* (Meliaceae)

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Editor: J. López-Pujol

Received 28 August 2023; accepted 20 October 2023; published on line 26 December 2023

Abstract

Reproductive ecology of *Cipadessa baccifera* (meliaceae).— *Cipadessa baccifera* is a woody shrub that propagates through seed and underground root stock. The flowers display urceolate androecium, strong protandry, stigma receptivity displayed by turbinate style-head and secondary pollination mechanism. They are self-compatible, nectariferous and produce all three common sugars and certain amino acids in the nectar, and also certain amino acids in the pollen. Further, the flowers present generalist pollination syndrome adapted for pollination by different classes of insects. Bees, wasps and butterflies act as pollinators with the first group effecting mostly geitonogamy while the other two, mostly xenogamy. In this species, spontaneous autogamy is not functional because protandry prevents it. However, flower-visitors could effect autogamy after the stigma attains receptivity but most of the pollen of the flower has been removed by insects by that time. Hand-pollination tests indicated that manipulated autogamy, geitonogamy and xenogamy are functional with highest fruit set in the last mode. Such breeding system indicates the function of facultative xenogamy which delays self-pollination by strong protandry and promotes cross-pollination. The fruit is a fleshy globular drupe that produces 5–10 seeds united by a common fleshy arillod. Seed dispersal modes include ornithochory, barochory and hydrochory. Therefore, the dual mode of propagation, facultative xenogamy, secondary pollination mechanism, generalist pollination syndrome, entomophily and polychory functional in *C. baccifera* enable it to grow prolifically and expand its distribution in areas where there is no tree cover.

Key words: entomophily; facultative xenogamy; generalist pollination syndrome; polychory; woody shrub.

Resumen

Ecología reproductiva de *Cipadessa baccifera* (*Meliaceae*).— *Cipadessa baccifera* es un arbusto leñoso que se propaga a través de semillas y raíces subterráneas. Las flores muestran androceo urceolado, protandria fuerte y receptividad del estigma mostrada por la cabeza del estilo turbinada que permite un mecanismo de polinización secundaria. Son autocompatibles, nectaríferas y producen los tres azúcares comunes y ciertos aminoácidos en el néctar, y también ciertos aminoácidos en el polen. Además, las flores presentan un síndrome de polinización generalista adaptado a la polinización por diferentes clases de insectos. Las abejas, avispas y mariposas actúan como polinizadores; el primer grupo efectúa principalmente geitonogamia, mientras que los otros dos, principalmente xenogamia. En esta especie, la autogamia espontánea no es funcional porque la protandria la impide. Sin embargo, los visitantes de las flores podrían efectuar la autogamia después de que el estigma alcance la receptividad, pero en ese momento los insectos han dispersado la mayor parte del polen de la flor. Las pruebas de polinización manual indicaron que la autogamia, la geitonogamia y la xenogamia manipuladas son funcionales con la mayor producción de frutos en el último modo. Tal sistema de reproducción indica la función de xenogamia facultativa que retrasa la autopolinización por protandria fuerte y promueve la polinización cruzada. El fruto es una drupa globular carnosa que produce de 5 a 10 semillas unidas por un arillo carnoso común. Los modos de dispersión de semillas son por ornitocoria, barocoria e hidrocoria. Por lo tanto, el modo dual de propagación, la xenogamia facultativa, el mecanismo de polinización secundaria, el síndrome de polinización generalista, la entomofilia y la policoria funcional de permite a *C. baccifera* crecer prolíficamente y ampliar su distribución en áreas donde no hay cobertura arbórea.

Palabras clave: arbusto leñoso; entomofilia; policoria; síndrome de polinización generalista; xenogamia facultativa.

Cómo citar este artículo / Citation
Kala Grace, L., Suvarna Raju, P. & Solomon Raju, A. J. 2023. Reproductive ecology of *Cipadessa baccifera* (Meliaceae). *Collectanea Botanica* 42: e012. https://doi.org/10.3989/collectbot.2023.v42.012

INTRODUCTION

In Meliaceae family, the majority of the species are dioecious, monoecious or polygamous. Confirmed cases of hermaphroditic flowers are reported to be very few (Styles, 1972; Pennington *et al.*, 1981). Most species in this family appear to be insect-pollinated (Mabberley & Pannell, 1989). *Trichilia havanensis* Jacq. and *T. lepidota* Mart. are pollinated by hymenopterans (Pennington & Styles, 1975; Leonhard, 2008), *Guarea rhopalocarpa* Radlk. probably by moths (Bullock *et al.*, 1983), *Guarea* and *Cedrela* by moths (Bawa *et al.*, 1985), *Swietenia mahagoni* (L.) Jacq. by thrips (Howard *et al.*, 1995; Basu *et al.*, 2013), *Cabralea canjerana* (Vell.) Mart. subsp. *canjerana* by nocturnal moths (Franceschinelli *et al.* 2015), *Toona ciliata* M. Roem. by insects (Zhou *et al.*, 2020), *Melia azedarach* L. by moths and bees (Zomlefer, 1994; Miller, 2003), and *M. composita* Willd. and *M. toosendan* Siebold & Zucc. by insects (Johar *et al.*, 2015; Baysunov *et al.*, 2021). In India, Meliaceae is represented by 20 genera and 70 species. A few studies have been made on the reproductive ecology of this family in that area. *Azadirachta indica* A. Juss. is hermaphroditic and pollinated by bees (Solomon Raju, 1998) and by wind and insects (Vikas & Tandon, 2011). *Dysoxylum malabaricum* Bedd. ex Hiern is a hermaphroditic and pollinated by insects (Ismail *et al.*, 2014). *Toona ciliata* is morphologically bisexual but functionally unisexual and pollinated by thrips and bees (Singh & Gupta, 2017). The oviparous mangrove tree species, *Xylocarpus granatum* J. Koenig and *X. mekongensis* Pierre, are pollinated by hawkmoths, bees and butterflies (Solomon Raju, 2020).

Cipadessa (subfamily Melioideae) is a monotypic genus with a single species, *C. baccifera* Miq., which is endemic to Western Ghats of India and Sri Lanka (Lersten & Pohl, 1985; Mabberley *et al.*, 1995). Different parts of this species are widely used in folklore medicine for treating diabetes, dysentery, malaria, rheumatism, piles, head ache and psoriasis. Oil extracted from the seeds is used for soap-making (Kavitha *et al.*, 2016). Bees use *C. baccifera* as a forage source (Laha *et al.* 2020). With this backdrop, the present study was contemplated to provide details of reproductive ecology of *C. baccifera* growing wild in the Eastern Ghats forests of Alluri Sitharama Raju District in the State of Andhra Pradesh. The intent 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 *C. baccifera* to understand how all these aspects enable this woody shrub to propagate prolifically in open areas/slopes of forests of Eastern Ghats.

MATERIALS AND METHODS

Flowering season and floral biology

Cipadessa baccifera populations growing at Sunkarametta (18.2783° N, 82.9670° E) and Kasipatnam (18.1732° N, 83.0771° E) near Ananthagiri Reserve Forest in Alluri Sitharama Raju District, Andhra Pradesh, India, were used for the present study during

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 20 plants 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 10 plants 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.* (2005).

Nectar analysis

Twenty-five mature buds which were about to open were bagged before sunrise and removed at noon time to measure total nectar produced by each flower by inserting a micropipette into the flower base. Since nectar was not secreted after noon time, 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. A hand sugar refractometer (Erma, Japan) was used for measuring nectar sugar concentration. Nectar analysis was carried out for sugar types and amino acid types using the paper chromatography method described in Dafni *et al.* (2005).

Pollen output

Twenty mature but undehisced anthers were collected from different plants and placed in a Petri dish. Later, each time a single anther was taken out and placed on a clean microscope slide and dabbed with a needle in a drop of lactophenol-aniline blue. The anther tissue was then observed under the microscope for pollen. The pollen mass was drawn into a band and the total number of pollen grains was counted under a compound microscope (400X). This procedure was followed for counting the number of pollen grains in each anther collected. Based on these counts, the mean number of pollen grains produced per anther was determined. The mean pollen output per anther was multiplied by the number of anthers in the flower for obtaining the mean number of pollen grains per flower. Another set of 10 dehisced anthers was collected in a Petri dish and the pollen removed from these anthers was examined under microscope for recording the pollen grain features.

Pollen analysis

The protocols described by Mondal *et al.* (2009) 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.* (2009). 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 behavior of each insect species was recorded. The number of foraging visits made by each insect species was recorded for 15 min 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 twenty flowers without hand-pollination. Twenty 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. Twenty 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. Twenty 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 10 plants 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 5–10 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 and perennial old root stock to record vegetative growth and development.

RESULTS

Phenology

Cipadessa baccifera is a seasonal woody shrub which grows on hill slopes and hill sides with rocky bed (Fig. 1A). With the onset of wet season in June, the underground stout root stock sprouts to produce new growth and begin sexual reproduction first (Fig. 1B). Seeds from the soil bank also germinate at the same time to produce new plants and add new individuals. These new individuals show sexual reproduction about two months later to the plants that emerged from the old root stock. The dual mode of propagation functional in this plant contributes to the extension of the period of sexual reproduction. The flowering occurs early in plants that originated from the previous root stock and late in plants that emerged from seeds. The flowering season begins from July and ends in November but it extends into January provided the soil is sufficiently wet. The aerial parts gradually wither away by the end of March. The inflorescence is an axillary cymose inflorescence consisting of few-clustered flowers (Fig. 1C).

Floral morphology

The flowers are pedicellate, creamy-white, 2 mm long, 3–4 mm diameter, actinomorphic and bisexual (Fig. 1E). The calyx is 5-lobed, each lobe 2 mm long, pubescent, triangular and spreading. The corolla has five free creamy white petals, and each petal is ovate and 3–4 mm long. The stamens are 10 with filaments connate to the extent of ¾ of their length forming an urceolate staminal tube with hairy middle portion (Fig. 1F, G); the filaments are terminated by a pair of lanceolate erose appendages. The anthers are yellow, acute, pubescent and inserted just below the appendages. The ovary has patelliform disk with 5–6 locules and each locule has two collateral ovules. The style is short, stout and columnar with swollen capitate to turbinate stigma consisting of 5–6 stigmatic lobes without any hairs.

Floral biology

Mature buds are open during 07:30–09:30 h (Fig. 1C). The process of bud opening involves only the unfolding of petals exposing the staminal tube with anthers inside, which lie on the rim of capitate portion of the style-head throughout flower life (Fig. 1D, E). The anthers dehisce by longitudinal slits shortly before the petals unfold and the pollen from anthers is attached to the rim of capitate style-head which is unreceptive to pollen during the entire period of flower life (Fig. 1F, G). The turbinate portion of the style-head protrudes out from the style at 15:00 h, is receptive to pollen almost instantaneously and its receptivity continues until the evening of the following day. The pollen

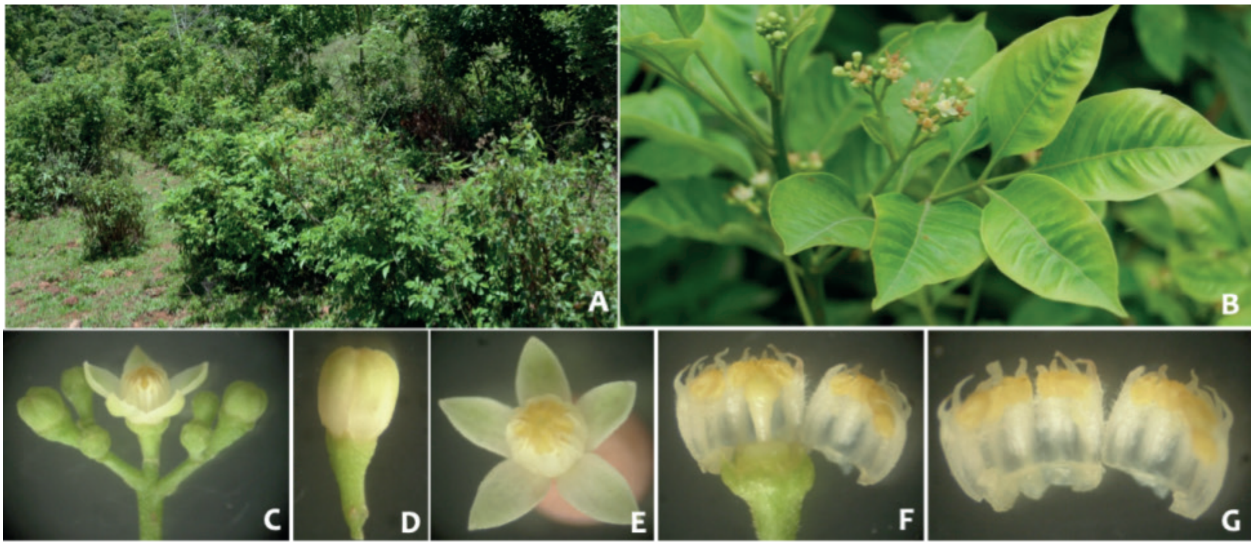

Figure 1. Floral biology details of *Cipadessa baccifera*: (A), population; (B), flowering twig; (C), anthesis of central flower in a cyme; (D), mature bud; (E), flower; (F), position of stigma in relation to anthers; (G), staminal tube with dehisced anthers.

grains are 375 ± 36 per anther and 3,750 per flower. The pollen grains are prolate-spheroidal, 35–40 µm, tetra-colporate with smooth exine and thickened apertures. The pollen contains four essential amino acids which include threonine, methionine, lysine and arginine, and five non-essential amino acids such as alanine, amino-butyric acid, cystine, glycine and hydroxy proline (Table 1). Nectar is secreted in minute volume at the base of ovary and concealed by the staminal tube; its secretion ceased about 2 h after anthesis. It is accessible to nectar foragers only when they probe through the narrow gaps between staminal sheath and the columnar style. Individual flowers produce 1.2 ± 0.45 µl of nectar with sucrose, glucose and fructose sugars; the sugar concentration was 25 ± 2.5%. The nectar contains six essential amino acids such as threonine, valine, leucine, isoleucine, histidine and arginine, and nine non-essential amino acids such as alanine, amino-butyric acid, cysteine, cystine, glutamic acid, glycine, hydroxy proline, proline and serine (Table 1). The petals together with the staminal tube wither away and fall off on 4th day while the columnar style and its head falls off on 9th or 10th day, and the sepals gradually dry up. The ovary portion gradually grows and bulges out to produce fruit.

Table 1. Essential and non-essential amino acids present in the pollen and nectar of *Cipadessa baccifera*.

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

+ = Present; - = Absent

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. But, turbinate head with stigmatic lobes springs out from the centre of capitate style-head from 15:00 h onwards on the day of anthesis. The stigmatic lobes commence receptivity to pollen almost spontaneously and continue to be receptive until the evening of the next day. The anthers lie on the capitate style-head throughout the flower lifespan. Since the anthers dehisce during bud stage, the pollen grains attach automatically to the the rim of capitate style-head which is non-receptive to pollen and hence, it merely acts as pollen presenter and facilitates only the occurrence of cross-pollination until the time of emergence of turbinate style head with its stigmatic lobes by which time most of the self-pollen is picked up by the pollen vectors. However, the temporal separation of male and female phases displayed by protandry and secondary pollen presentation do not totally prevent the occurrence of vector-mediated autogamy and geitonogamy.

Foraging activity and pollination

The flowers were visited by insects during day time from 09:00 to 16:00 h with a peak of foraging activity during 10:00–12:00 h (Fig. 2). The insects visiting the flowers were one honey bee species, *Apis cerana* F. (Apidae) (Fig. 3A), one halictid bee species, *Nomia* sp. (Halictidae) (Fig. 3B), four wasp species, *Polistes* sp. (Fig. 3C), *Rhynchium* sp. (Fig. 3D) (Vespidae), *Sphex* sp. (Fig. 3E), *Eremnophila* sp. (Fig. 3F) (Sphecidae), and three lycaenid butterflies, *Chilades pandava* Horsfield (Fig. 3G), *Spindasis vulcanus* F. (Fig. 3H) and *Zizeeria karsandra* Moore (Fig. 3I) (Table 2). All these insects collected nectar while the bees also collected pollen. They approached the flowers in 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 style-head. These insects approached the flowers in 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

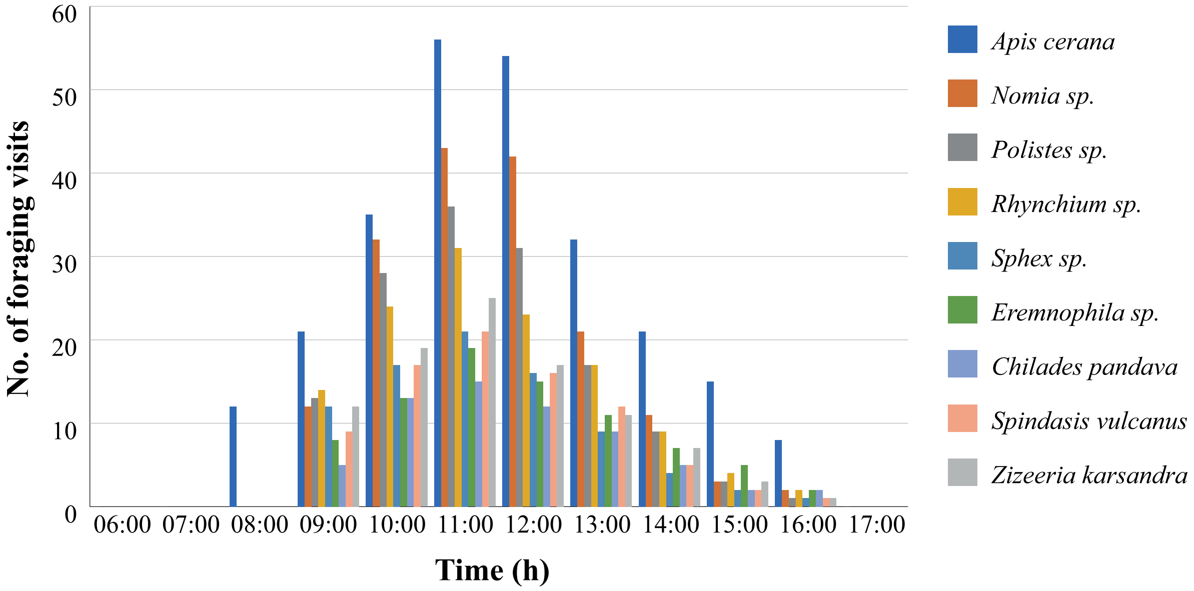

Figure 2. Hourly foraging activity of insects on *Cipadessa baccifera*.

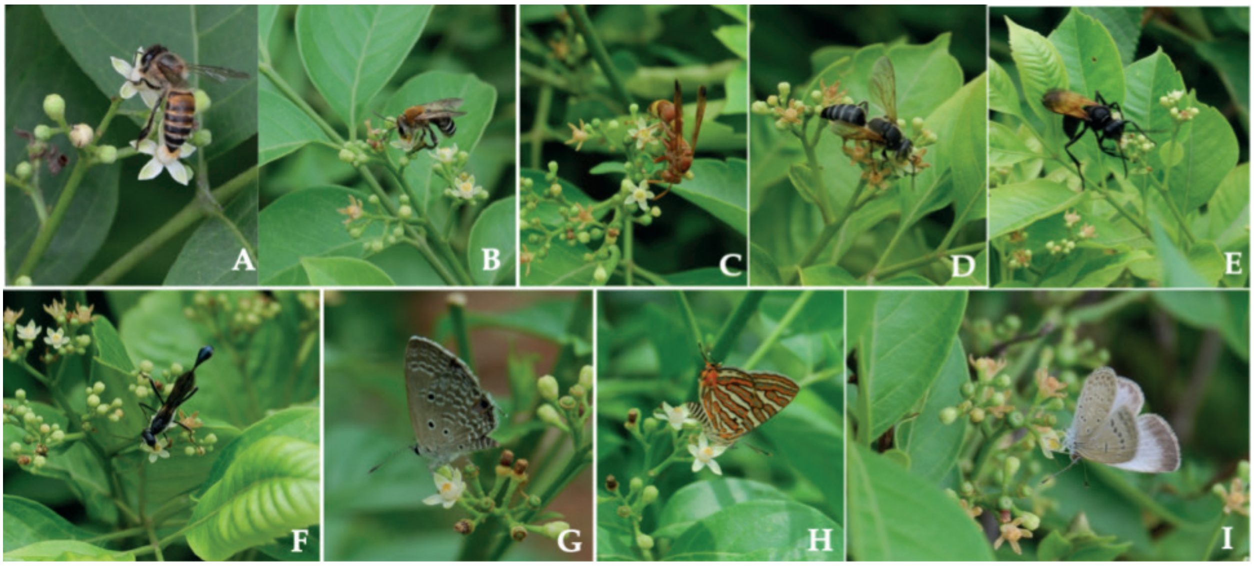

Figure 3. Insects visiting the flowers of *Cipadessa baccifera*: (A), honey bee, *Apis cerana*; (B), halictid bee, *Nomia* sp.; (C–D), vespid wasps – *Polistes* sp. (C), *Rhynchium* sp. (D); (E–F), sphecid wasps – *Sphex* sp. (E), *Eremnophila* sp. (F); (G–I), lycaenid butterflies – *Chilades pandava* (G), *Spindasis vulcanus* (H), *Zizeeria karsandra* (I).

Table 2. List of insect foragers on *Cipadessa baccifera*.

Order/family	Insect species	Common name	Forage sought
Hymenoptera			
Apidae	*Apis cerana* F.	Asiatic hive bee	Pollen + Nectar
Halictidae	*Nomia* sp.	Alkali bee	Pollen + Nectar
Vespidae	*Polistes* sp.	Paper wasp	Nectar
	Rhynchium sp.	Potter wasp	Nectar
Sphecidae	*Sphex* sp.	Digger wasp	Nectar
	Eremnophila sp.	Thread-waisted wasp	Nectar
Lepidoptera			
Lycaenidae	*Chilades pandava* Horsfield	Plains Cupid	Nectar
	Spindasis vulcanus F.	Common silverline	Nectar
	Zizeeria karsandra Moore	Dark grass blue	Nectar

tongue/proboscis/ventral side of abdomen of insects invariably contacted 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 is transferred to other conspecific flowers in their successive foraging visits for nectar and/or pollen collection. Pollination occurs only when they visit the flowers with receptive style-head. In flowers with receptive style-head, these insects first contacted the turbinate portion of the style-head with their forehead and the ventral side of their body; then pollen transfer to the receptive portion of the turbinate 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. The honey bee, *Apis cerana*, loaded the collected pollen into its pollen baskets. The alkali bee (*Nomia* sp.) is known to nest in salt-saturated soils. In flowers with unreceptive style-head, the bees gathered pollen from the rim of the capitate style-head and in this act, the bees moistened the pollen with the saliva using its tongue, transferred it to its hind legs and packed it 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. When the bees with pollen load made successive visits to the flowers with receptive style-head, its pollen basket brushed

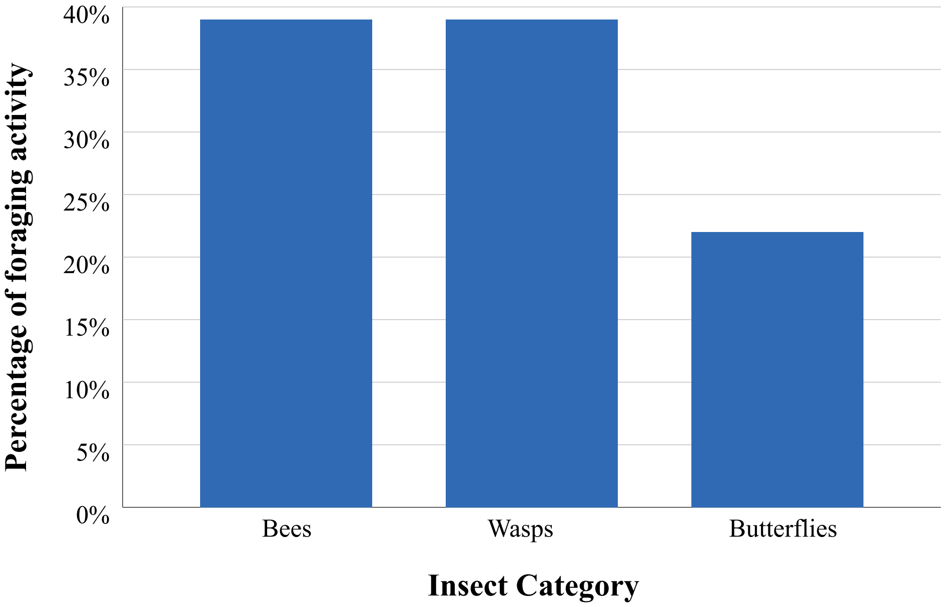

Figure 4. Percentage of foraging activity of insects on *Cipadessa baccifera.*

against the turbinate portion of the style-head which ended up in pollen transfer and pollination.

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 turbinate style-head but provides opportunity for both self- and cross-pollination after turbinate style-head commences receptivity to pollen in the evening hours of day 1 flowers and day-long in day 2 flowers. But, insects did not visit the flowers during the receptivity period of style-head in day 1 flowers indicating that the day 1 flowers 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 allow geitonogamy and xenogamy. Among the insects recorded at the flowers, wasps and lycaenid butterflies were found to be visiting the flowers across conspecific plants within the population and also between nearby populations in quest of more nectar collection and such inter-plant 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 plant, and such a foraging behavior was treated to be promoting geitonogamous pollination rather than cross-pollination. Of the total foraging visits made by all insect species, bees and wasps groups made 39% each and butterflies 22% (Fig. 4). Body washings of insects which were collected at 11:00 h for assessing pollen carry-over efficiency showed that the mean number of pollen grains carried by individual species ranged from 13.3 to 97.3. The bees carried a mean number of 83.8 to 97.3 pollen grains, wasps from 26.8 to 45.8 and butterflies from 13.3 to 34.3 (Table 3). These values indicated that the bee species had high pollen carrying capacity when compared to wasps and butterflies but bees are important for effecting mostly geitonogamous pollination. Wasps had moderate pollen carrying capacity but their frequent inter-plant foraging activity is important for effecting mostly xenogamous pollination. Butterflies are also important for promoting xenogamous pollination but they had low pollen carrying capacity. Therefore, wasps were found to be the principal pollinators in promoting cross-pollination while the bee and butterflies are supplementary pollinators.

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 5% only. Fruit set is 40% in geitonogamy, 80% in xenogamy and 82%

Table 3. Pollen recorded in the body washings of insects foraging on *Cipadessa baccifera.*

Insect species	Sample size (N)	Number of pollen grains recorded		
		Mean	SD	Range
Apis cerana F.	10	97.3	24.3	78–245
Nomia sp.	10	83.8	15.0	62–116
Polistes sp.	10	45.8	15.76	24–81
Rhynchium sp.	10	31.9	9.12	19–52
Sphex sp.	10	26.8	9.55	17–48
Eremnophila sp.	10	35.1	11.55	18–57
Chilades pandava Horsfield	10	34.3	11.98	20–62
Spindasis vulcanus F.	10	13.3	3.74	9–23
Zizeeria karsandra Moore	10	16.4	6.10	8–25

Pollen loads from corbiculae of the bees were excluded. SD: standard deviation.

Table 4. Results of breeding systems in *Cipadessa baccifera.*

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	1	5
Geitonogamy (flowers hand-pollinated and bagged)	20	8	40
Xenogamy (flowers hand-pollinated and bagged)	20	16	80
Open pollination (flowers tagged)	50	41	82

in open-pollination mode (Table 4). The results of hand-pollination tests showed that the plant has facultative xenogamous breeding system which is completely vector-dependent.

Fruiting dispersal

Fruits mature within 6–7 weeks and display color shifts from green to light red to dark and finally to reddish brown (Fig. 5A–F). Fruit is a fleshy globular drupe with five pyrenes each with one or two seeds, 5–8 mm across and all seeds are united by a common translucent fleshy arillode. The seeds are orange-segment-shaped with thin and membranous testa (Fig. 5G, H). The fruits are edible and eaten occasionally by 20 species of frugivorous birds belonging to 10 families of the order Passeriformes during day time from 08:00 to 16:00 h. They were *Artamus fuscus* Vieillot (Artamidae), *Pericrocotus cinnamomeus* Linnaeus, *P. flammeus* J. R. Forster (Campephagidae), *Dendrocitta vagabunda* Latham (Corvidae), *Dicaeum erythrorhynchos* Latham (Dicaeidae), *Dicrurus adsimilis* Bechstein, *D. caerulescens* Linnaeus (Dicruridae), *Turdoides caudatus* Dumont (Leiothrichidae), *Oriolus kundoo* Sykes, *O. xanthornus* Linnaeus (Oriolidae), *Pycnonotus cafer* Linnaeus, *P. jocosus* Linnaeus, *P. luteolus* Lesson (Pycnonotidae), *Gracula religiosa* Linnaeus, *Sturnus roseus* Linnaeus, *S. malabaricus* Gmelin, *S. pagodarum* Gmelin, *Acridotheres ginginianus* Latham, *A. tristis* Linnaeus (Sturnidae) and *Tephrodornis pondicerianus* Gmelin (Vangidae) (Table 5). These birds possess a short, curved or uncurved beak with a specialized tip for feeding on edible part of the fruits. They were found to open the fruits to feed on the fleshy arillode in which seeds are enclosed; the seeds were left out by many of these birds. They usually plucked the fruits, held them with their beak and carried them to new locations where they broke open the fruits to feed on the arillode and dropped the seeds. The seeds germinate during rainy season if the soil has sufficient

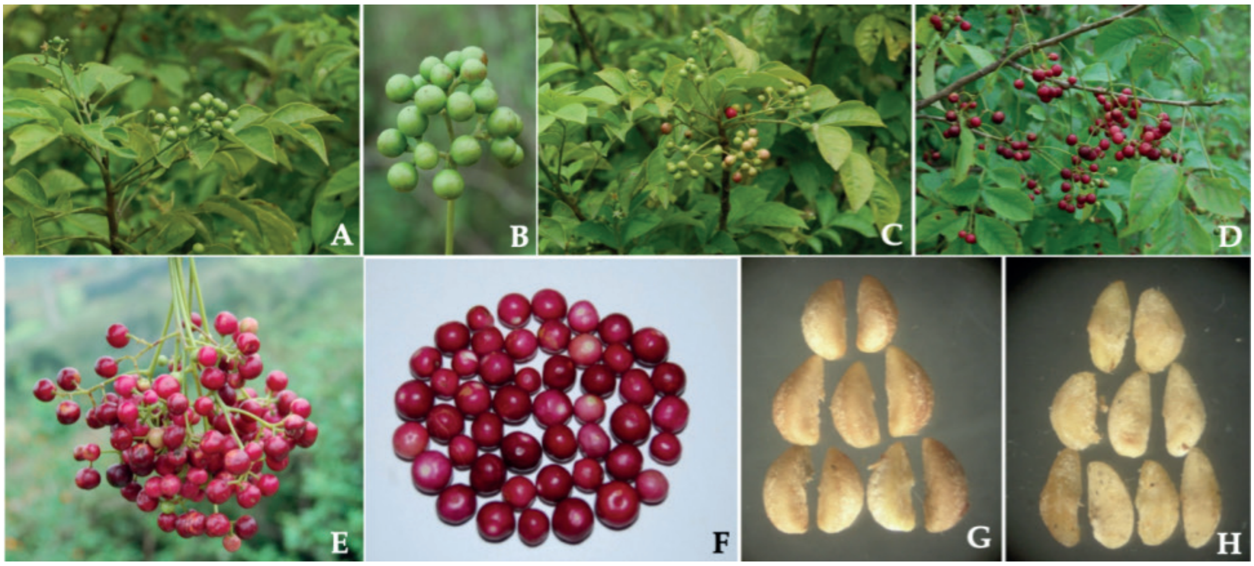

Figure 5. Fruits and seeds of *Cipadessa baccifera*: (A–E), fruit development stages; (F), ripen fruits; (G), healthy (filled) seeds; (H), unhealthy (unfilled) seeds.

Table 5. List of bird species involved in seed dispersal of *Cipadessa baccifera.*

Family	**Species**	**Common name**
Artamidae	*Artamus fuscus* Vieillot	Ashy woodswallow
Campephagidae	*Pericrocotus cinnamomeus* Linnaeus	Small minivet
	Pericrocotus flammeus J. R. Forster	Orange minivet
Corvidae	*Dendrocitta vagabunda* Latham	Indian tree pie
Dicaeidae	*Dicaeum erythrorhynchos* Latham	Tickell’s flowerpecker
Dicruridae	*Dicrurus adsimilis* Bechstein	Black drongo
	Dicrurus caerulescens Linnaeus	White-bellied drongo
Leiothrichidae	*Turdoides caudatus* Dumont	Common babbler
Oriolidae	*Oriolus kundoo* Sykes	Indian Golden oriole
	Oriolus xanthornus Linnaeus	Black-hooded oriole
Pycnonotidae	*Pycnonotus cafer* Linnaeus	Red-vented bulbul
	Pycnonotus jocosus Linnaeus	Red-whiskered bulbul
	Pycnonotus luteolus Lesson	White-browed bulbul
Sturnidae	*Gracula religiosa* Linnaeus	Hill myna
	Sturnus roseus Linnaeus	Rosy starling
	Sturnus malabaricus Gmelin	Chestnut-tailed starling
	Sturnus pagodarum Gmelin	Brahminy starling
	Acridotheres ginginianus Latham	Bank myna
	Acridotheres tristis Linnaeus	Indian myna
Vangidae	*Tephrodornis pondicerianus* Gmelin	Common woodshrike

moisture and nutrients. Since the birds carry them to new locations to feed, they are treated as effective seed dispersal agents. Further, when the birds fed on the arillode without plucking the fruits from the plant, the seeds fallen at the parental habitats germinate during rainy season adding new individuals to the existing population. The unutilized fruits fall to the ground and disperse by gravity and rain water easily because the habitats of the parental population are slopy and facilitate easy dispersal of fruits/seeds. The seeds become exposed after the decomposition of the composite transculent arillode and germinate during rainy season to produce new plants.

DISCUSSION

Pullaiah & Sri Ramamurthy (2002) reported that *Cipadessa baccifera* is common in shrub and dry deciduous forests of Eastern Ghats above 600 m. Botanical Survey of India reported that this plant species occurs in dry forests and hilly areas of Peninsular India. This organization also noted that this plant species flowers almost throughout the year with two peaks, one during March–April and the second during July–August. In the study region, this species is found to grow and establish huge populations from 705 m to 1168 m on hill slopes, hill sides and open terrain with low ground grass cover. This species being a perennial woody shrub is highly seasonal in vegetative growth, flowering and fruiting events which occur in gradual succession. Wet season characterized by heavy rain fall facilitates intense leaf production and flowering from perennial root stock and seed produced in the previous year while fruit production reaches its peak during early winter season.

In Meliaceae family, androecial structure is an important diagnostic feature to distinguish it from other families. Pennington & Styles (1975) reported that the partial or complete fusion of the staminal filaments to form a staminal tube is the characteristic feature. The subfamily Swietenioideae in this family appears to be unique in presenting the variable degree of connation of the basal portions of filaments and the variability in the adnation to the petals and to the gynoecium. These authors also stated that the origin of staminal tube might rely on the expansion of the connate zone of the filaments upwards to the whole structure in other species of Meliaceae. Further, these authors also documented that *Pseudocedrela* in the subfamily Cedreloideae has an urceolate staminal tube with anthers inserted in the middle of deltate teeth of the lobes. In the present study, *C. baccifera* belonging to the subfamily Melioideae produces flowers with urceolate staminal tube formed by the connation of filaments to the extent of ¾ of their length. Further, the filaments are terminated by a pair of lanceolate erose appendages with anthers inserted just below them. The urceolate staminal tube present in this plant species is similar to that reported in *Pseudocedrela* but, in *C. baccifera*, the anthers are not fixed in the middle of the lanceolate appendages. The urceolate structure of the staminal tube with anthers fixed below the terminally lobed filaments has been reported in *Xylocarpus mekongensis* and *X. granatum* which belong to the subfamily Cedreloideae (Solomon Raju, 2020). Since there is paucity of information on the floral biology of Meliaceae members, it is not possible to evaluate the evolution of urceolate structure of staminal tube in the members of different subfamilies of Meliaceae.

Different authors (Hooker, 1862; Harms, 1940; Keay, 1958; Smith, 1960; Lamb, 1966) documented that Meliaceae flowers are always hermaphroditic but White & Styles (1963) described that hermaphroditism is not fully functional in most of the species of this family. Individual trees produce bisexual flowers but they are functionally either monoecious or dioecious. However, some species have functionally bisexual flowers but they may also produce male flowers indicating the function of polygamous condition. On the contrary, Styles (1972) and Pennington *et al.* (1981) reported that the majority of the species in Meliaceae family are dioecious, monoecious or polygamous. *Trichilia* and *Guarea* genera are dioecious, *Cedrela* and *Swietenia* monoecious, and *Azadirachta* and *Melia* polygamous. Further, these authors noted that confirmed cases of functionally hermaphroditic species are few. In the present study, *C. baccifera* flowers are morphologically and functionally bisexual and hence they are perfect flowers. Further, there is no change in the sexual expression of hermaphroditic flowers between two consecutive years of the study. But, the flowers are strikingly protandrous due to anther dehiscence before the unfolding of petals and attainment of stigma receptivity which commences in the afternoon of the day of anthesis itself. The style-head is initially capitate and unreceptive but the anthers leaning on the capitate style-head upon dehiscence release pollen which automatically attach to the unreceptive style. At this stage, the capitate style-head acts as pollen presenter and facilitates pollen transfer for the occurrence of only cross-pollination by pollen vectors until the time of commencement of stigma receptivity which is displayed by the protrusion of turbinate mass from center of capitate style-head. Such a manner of pollen presentation by capitate style-head characterizes the secondary pollen presentation mechanism. Since pollen is available right from anthesis which occurs early in the morning, 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 turbinate portion of the style head and effect cross-pollination in their foraging visits between flowers of different conspecific plants. Further, the self-pollen transferred within and between flowers of the same plant during the gap period during male and female phase of the flowers is ineffective to effect self-pollination due to non-receptivity of the stigma but there is a possibility for self-pollination after the stigma attains receptivity. The protandrous condition and secondary pollen presentation mechanism in *C. baccifera* appear to have an important role in promoting cross-pollination while minimizing self-pollination. The function of secondary pollen presentation mechanism through style-head has been reported in most species of *Turraea* genus (Yeo, 2012).

In *C. baccifera*, 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 mode of pollination functional in this plant species ensures 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* King in Hook. (Larekeng *et al.*, 2020).

In Meliaceae, the majority of the species appear to be pollinated by bees and/or flies (Mabberley & Pannell, 1989). Hymenopterans effect pollination in *Trichilia havanensis* (Pennington & Styles, 1975), butterflies, flies, wasps and bees in *T. lepidota* (Leonhard, 2008), ants in *Carapa* species (Kenfack *et al.*, 2014), moths in *Guarea*, *Cedrela* species, *Cabralea canjerana* subsp. *canjerana* (Bullock *et al.*, 1983; Bawa *et al.*, 1985; Franceschinelli *et al.*, 2015), moths and bees in *Melia azedarach* (Zomlefer, 1994; Miller, 2003; Baysunov *et al.*, 2021), hawk moths in *Turraea floribunda* Hochst. (Yeo, 2012), thrips in *Swietenia mahagoni* (Howard *et al.*, 1995), moths and bats in *Chisocheton* and *Dysoxylum* species (Kubitzki, 2010), birds and bees in *Dysoxylum spectabile* Hook. f. (Gardner, 2009), insects in *Toona sinensis* (A. Juss.) M. Roem. (Zhou *et al.*, 2020) and in *Melia composita* (Johar *et al.*, 2015) and insects (mainly bees) in *Melia toosendan* (Baysunov *et al.*, 2021). In the monotypic genus *Cipadessa*, *C. baccifera* is reported to be used as a forage source by bees but their role in pollination has not been documented (Laha *et al.*, 2020). In this study, bees are important for self-pollination (geitonogamy) while wasps and lycaenid butterflies are important for 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 to effect pollination if compared to wasps and butterflies. In *C. baccifera* 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 *C. baccifera* is advantageous for this species to achieve genetic variation which is essential to establish prolific populations on different hill terrains.

In Meliaceae, the fruit types include loculicidal or septicidal capsules and drupes or berries with winged seeds or seeds equipped with a fleshy aril or sarcotesta which are adapted for dispersal by wind, birds and other animals (Pennington *et al.*, 1981; Souza & Pennington, 1999). Different authors reported on fruit nature and dispersal in a few species of Meliaceae. White (1983) reported that *Carapa guianensis* Aubl. fruit is a woody dehiscent capsule with 2–4 seeds. Its seeds are eaten by rodents, monkeys and wild pigs and these animals are speculated to be seed dispersal agents. White (1986) also reported that *Melia azedarach* fruit is a fleshy 1-seeded drupe. Miller (1990) reported that *M. azedarach* fruit is eaten and dispersed by birds and fruit bats while Vines (1960) and Naumann & Young (2007) reported that seed dispersal in this species occurs also by gravity and water. Miller (1990) reported that *Azadirachta indica* fruits are fleshy and likely dispersed by bats. Takhtajan (2009) reported that *Walsura* species are fleshy and the seeds usually have an arillode or sarcotesta but, there is no information on animal agents that are involved in fruit or seed dispersal of these species. Puyravaud *et al.* (2003) reported that

Cipadessa baccifera seeds are dispersed by monkeys in the Western Ghats but these authors have not provided any details of fruit or seed characters. In this study, *C. baccifera* fruit is a fleshy globular drupe with 5–10 seeds united by a common translucent fleshy arillode instead of possessing individual arillodes. The fleshy part of the fruit is a composite arillode which is used as food occasionally by several frugivorous birds and in this process they act as seed dispersal agents. The unutilized fallen fruits also disperse by gravity and rainwater easily due to the sloping habitat. The seeds exposed after the decomposition of fleshy part of the fruit germinate during rainy season to produce new plants. Additionally, the underground root stock also sprouts back to life during rainy season to produce new aerial stalks to repeat their life cycle. Therefore, the dual mode of propagation facilitates *C. baccifera* to grow as a crop naturally in open areas and hill slopes of the Eastern Ghats forest.

Cipadessa baccifera is widely used in folklore medicine for treating different diseases and soap-making (Kavitha *et al.*, 2016). Local people use the leaves of this species as good fodder for goats and in the construction of mud plastered walls. Such traditional uses appear to be contributing to the decline of its populations. Its proliferation on the hill slopes, hill sides and hill tops is ecologically important in binding the soil, increasing organic matter and controlling fertile soil erosion. Its luxuriant populations provide abundant forage for certain local insect species which act as its pollinators. Therefore, appropriate measures are required to protect *C. baccifera* and control its uses by locals in forests.

CONCLUSIONS

Cipadessa baccifera is a woody shrub widely distributed in open sun-lit areas along the hill slopes and hill tops. It exhibits a dual mode of propagation involving seeds and underground root stock which produce new plants/growth during rainy season. The flowers are hermaphroditic and characterized by urceolate androecium, capitate to turbinate style-head and secondary pollen presentation functional through striking protandry. The capitate portion of style-head is unreceptive while turbinate portion of style-head is receptive to pollen. In this plant species, spontaneous autogamy is not functional but vector-mediated autogamy is effective after the stigma becomes receptive but by that time most of the pollen is removed by insects and insect activity is also very low. The flowers display stigma receptivity in the afternoon of the day of anthesis and extend the receptivity until the evening of the next day; this state of stigma receptivity largely facilitates the promotion of cross-pollination while facilitating self-pollination through vector-mediated self-pollination on the 2nd of anthesis only. The flowers are generalists, with urceolate androecium and nectar with certain sugars and amino acids, and pollen with certain amino acids, and provide landing platform for easy landing by insects attracting bees, wasps and lycaenid butterflies; the first group of insects is important for self-pollination mostly through geitonogamy while the other two groups of insects are important for promoting cross-pollination. The mixed mating system functional in this species is an indicative of facultative xenogamy which is advantageous to achieve genetic variation which is essential to establish prolific populations on harsh hill terrains characterized by unstable soil. *Cipadessa baccifera* fruit is a fleshy globular drupe with 5–10 seeds united by a common translucent fleshy arillode instead of possessing individual arillodes. The fleshy part of the fruit is a composite arillode which is used as food occasionally by several frugivorous birds and in this process they act as seed dispersal agents. The unutilized fallen fruits also disperse by gravity and rainwater easily due to the sloping habitat. Therefore, this plant is ornithochorous, barochorous and hydrochorous.

ACKNOWLEDGEMENTS

We thank the Andhra University, Visakhapatnam, for providing physical and laboratory facilities to carry out this research work. We also thank Dr. K. Venkata Ramana, Department of Botany, Andhra University, for providing field assistance.

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