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Sexual system, pollination mechanism, pollinators and seed dispersal in some species of the sub-families, Asclepiadoideae and Rauvolfioideae of the family Apocynaceae

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ABSTRACT

In *Asclepias curassavica*, *Dregea volubilis*, *Oxystelma esculentum*, *Brachystelma maculatum*, *Pergularia daemia*, *Tylophora indica*, *Catharanthus roseus* and *Rauvolfia serpentina*, the flowers are hermaphroditic, nectariferous, self-compatible, self- and cross-pollinating. Of these, the last two species produce monad pollen grains while all other species produce pollinia. *A. curassavica* is principally pollinated by bees, *D. volubilis* by the diurnal hawk-moth, *Macroglossum gyrans*, *O. esculentum* by juvenile *Xylocopa* bees, *B. maculatum* by flies, *P. daemia* by *M. gyrans* and also by bees, *T. indica* by spontaneous selfing, *C. roseus* by butterflies and *R. serpentina* by papilionid butterflies and honey bees. Fruits are 1- or 2-follicled fruits with comose seeds in *A. curassavica*, *D. volubilis*, *O. esculentum*, *B. maculatum*, *P. daemia* and *T. indica*; these species are autochorous and anemochorous. In *C. roseus*, fruit is follicled with non-comose seeds; it is autochorous, anemochorous and myrmecochorous. In *R. serpentina*, fruit is a single fleshy and shiny purple-black to bluish drupe mostly with 1 seed or a pair of connate drupe mostly with 2-seeds; ornithochory is possible.

Keywords: Asclepiadoideae, Rauvolfioideae, hermaphroditism, pollinia, monads, insect pollination, autochory, anemochory, myrmecochory.

1. INTRODUCTION

The Asclepiadaceae family has been included in Apocynaceae family but the latter is classified into five sub-families, Apocynoideae, Rauvolfioideae, Asclepiadoideae, Periplocoideae and Secamonoideae (APG IV 2016). Of these

subfamilies, Asclepiadoideae is the largest and distinguished by the presence of milky latex, corona, gynostegium and pollinaria (Shah and Ahmad 2014). Most of the species are included in IUCN list (Shah and Wani 2016). In the sub-family Asclepiadoideae, the flowers are morphologically complex due to formation of a gynostegium by the fusion of expanded stylar head with the androecium and the narrow gap between the sclerified wings of adjacent anthers form five grooves. In the anther locule, the pollen is aggregated into a pollinium encased by a waxy wall and linked to another pollinium in an adjacent anther by a pair of translator arms and a single corpusculum forming a pollinarium which acts as a single unit. The corpusculum is sits at the top of the groove between adjacent anthers (Goyder 2009). In Apocynaceae, the corona is ancestrally corolline and develops on the corolla between petals (Fishbein, 2001; Kunze, 2005). In Asclepiadoideae, a staminal corona develops between petals and is morphologically and functionally associated with the androecium; the elements of this corolla also develop between stamens and collectively form a complex nectar holder for nectar-collecting pollinators (Rudjiman 1982; Kunze 2005; Liede and Kunze 1993). In this sub-family, *Asclepias curassavica*, *Dregea volubilis*, *Oxystelma esculentum*, *Brachystelma maculatum*, *Pergularia daemia* and *Tylophora indica* have been investigated for their pollination ecology aspects.

Asclepias curassavica is believed to have originated in South America, Central America or the Antilles. It is very widespread in subtropical and tropical regions of the Americas and has been widely introduced in the tropics of the Old world (Woodson 1954). But, Elizabeth et al. (2010) reported that this species is native to the American tropics and has a pantropical distribution as an introduced species. Holm et al (1997) reported that this species is weedy and invasive in occurrence in many tropical and subtropical regions of the Americas, Australia and Asia. Wyatt and Broyles (1997) reported that *A. curassavica* is self-compatible, self- and cross-pollinated in Australia and Costa Rica. Liza et al. (2010) reported that *A. curassavica* is cross-pollinated and pollinated by butterflies, bees and ants in Bangladesh. Ward et al. (2012) reported that *A. curassavica* is pollinator-dependent for reproductive output; it is pollinated by butterflies in Costa Rica (Wyatt 1980; Bierzychudek 1981), Brazil (Fuhro et al. 2010), butterflies and wasps in Australia (Ward and Johnson 2013), bees, beetles, moths, wasps and hummingbirds in the urban botanical gardens of California (Warren et al. 2020). In view of conflicting reports regarding mating system and pollinator guilds of *A. curassavica*, the present study was contemplated.

The genus *Dregea* has approximately 12 accepted species distributed mainly in southern Asia and tropical Africa (Li et al. 1995). The genus is named after a German Collector, J.F. Drege. In this genus, the species are woody vines have watery or milky sap. They produce pseudumbelliform pendulous inflorescences in the axils of leaves. The flowers are broadly campanulate to rotate with deeply lobed corolla, a fleshy staminal corona obtuse or rectangular outer lobe processes and acute inner lobe processes (Van et al. 2018). Among 12 accepted species in this genus, only *Dregea volubilis* is widely described repeatedly for its taxonomic characters and there is a great dearth of taxonomic information on other species of *Dregea* to validate their species identity. Further, there is absolutely no information on any aspect of sexual reproduction in any of the species of this genus. In India, *D. volubilis* is widely reported by different authors regarding its use in traditional and other systems of medicine. It is used in Ayurveda, Siddha and Unani systems of medicine and also in unorganized folk-medicine. Different parts of this plant are used to treat diabetes, boils, inflammations, eye ailments, stomach ache, tumors, asthma, paralysis, rheumatism, neck pain and general debility (Kirtikar and Basu 1935; Chatterjee and Pakrashi 1995; Hossain et al. 2012; Madhava Chetty et al. 2012; Sreeramulu et al. 2013; Vishnusithan et al. 2014). The flowers are consumed as a seasonal vegetable in summer (Hossain et al. 2013). Further, this species is the larval host plant for the nymphalid butterflies, *Tirumala limniace* and *T. septentrionis* (Churi et al. 2021).

The genus *Oxystelma* belongs to the tribe Asclepiadeae of the subfamily Asclepiadoideae. In this genus, 3 species, *O. bornouense* R.Br., *O. esculentum* (L.f.) Sm. and *O. esculentum* var. *alpini* (Decne.) N.E. Br. have been accepted as valid (The Plant List 2013) but the last two species have been treated as only one species and hence, this genus has only 2 species. In India, only *O. esculentum* has been reported so far (Panda 2019). It is widely distributed from northeastern Africa to southwestern Asia; it grows throughout the plain areas and lower elevation areas, especially near water sources as a wetland species (Lansdown 2011; Pandya and Anand 2011) and as a mangrove associate (Panda 2019). This plant has been reported to have potential therapeutic uses to cure cancer, hepatitis, kidney and stress-related disorders and microbial infections (Pandya and Anand 2011). *Oxystelma esculentum* has been reported to be xenogamous and foraged by *Apis dorsata*, *Vespa* sp., *Borbo cinnara* and thrips of which the first one is the most important pollinator while the last two species are mere nectar robbers without any pollination role (Soumitra Pal and Subrata Mondal 2019).

The genus *Brachystelma* belongs to the tribe Ceropogieae of subfamily Asclepiadoideae of family Apocynaceae. Its name is derived from two Greek words "*brachys*" for short and "*stelma*" for garland or crown which refers to the morphology of corona of the flowers (Masinde 2007). It has 100-200 species distributed mainly in southern Africa with a few species in Southeast Asia and Australia (Forster 1996; Mabberley 2008; Bruyns 2009). Later, Prasad et al. (2016) noted that this genus has about 160 species distributed chiefly in the Old World tropics, especially in sub-Saharan Africa, India, Sri Lanka, South East Asia and Northern Australia. These authors and also Venu and Prasad (2015) documented that in India this genus has 23 species and almost all of them

endemic. Peninsular India has been reported to be the centre of diversity for *Brachystelma* where 80% of the species occur; the remaining 20% of species occur in north and northwest India (Rao et al. 2011). In the Eastern Ghats belt, this genus has only 8 species out of 23 species distributed in India (Rao et al. 2011; Prasad and Rao 2013; Rasingam et al. 2013; Swamy et al. 2013). In Andhra Pradesh State, *Brachystelma* is represented by only 3 species, *B. glabrum*, *B. volubile* and *B. pullaiahii* (Rao et al. 2011). Later, new species in this genus have been reported but their authenticity is debated. In this genus, the species are caudiciform with geophytic habit with root system representing a single globose/ depressed globose tuber or a cluster of spindle-shaped roots (Walker 1982; Meve 2002). *Brachystelma* species have been believed to be exclusively fly-pollinated (Vogel 1990). Later, Ollerton and Liede (1997) reported that many species of *Brachystelma* display the traits of decay-attraction fly pollination syndrome. *B. maculatum* has been given Data Deficient status by IUCN (2017). It occurs in restricted areas of Eastern and Western Ghats where it is prone to forest fires and subject to grazing by wild boars; its tubers serve as a good source of food. In Andhra Pradesh, about 100 individuals of *B. maculatum* were reported as occurring in Sikharam area of Kurnool District (Prasad et al. 2016). A few individuals of *B. maculatum* found in the dry deciduous forest near Chinarutla Gudem in the Nallamalai forest in Markapuram Division of Prakasam District have been chosen to describe its floral aspects with reference to its pollination.

In *Pergularia* genus, only 12 species have been accepted as valid. They include *P. brunoniana*, *P. calesiana*, *P. clausa*, *P. daemia*, *P. exilis*, *P. flavescens*, *P. glabra*, *P. hamiltonii*, *P. rostrata*, *P. roylei*, *P. suaveolens* and *P. viridiflora* (The Plant List 2013). Of these, only *P. daemia* is widespread across tropical and subtropical regions of subsaharan Africa, the Arabian Peninsula and the Indian subcontinent (Goyder 2006). The genus *Pergularia* is characterized by the presence of narrow corolla tube, ciliate corolla lobes, a translucent germination pore in exodistolateral position on the pollinia (Rao and Kumari 1979) and production of 2-follicled fruits covered with soft spines (Kuriachen and Dave 1989). This genus easily recognizable by its twining habit, heart-shaped leaves and characteristic flower buds in which a large ovoid cone formed by the corolla lobes is seated on much narrower corolla tube (Goyder 2006). *P. daemia* is used to treat different diseases such as gastric ulcers, uterine and menstrual complaints, leprosy, haemorrhoids, body pains, asthma, bronchitis, whooping cough, boils, sores and gonorrhoea (Karthishwaran and Mirunalini 2010). It is the larval host plant for *Danaus chrysippus* (Churi et al. 2021). It has been reported to be pollinated by *Apis dorsata* (Vijayaraghavan and Shukla 1980), and by bees of *Tetragonula* sp., *Apis dorsata*, *A. cerana* and *A. florea* (Ramakrishna et al. 2016).

The genus *Tylophora* comprises of 60 species distributed chiefly in the tropical and subtropical Asia, Africa and Australia, Oceanic Islands, Ceylon, Malay Island and Borneo (Tseng and Chao 2011; Murugan and Kamble 2012; Nazar et al. 2020). In India, 22 species and 2 varieties of this genus have been reported (Jagtap and Singh 1999; Karthikeyan et al. 2009; Murugan and Kamble 2012). In *Tylophora* species, the flowers have patent corolla lobes with nectar easily accessible to insect foragers (Ollerton and Liede 1997). Pollination biology information is almost not available for *Tylophora* genus as a whole. However, little information is available on this aspect for certain species such as *T. hirsuta*, *T. matsumurae*, *T. aristolochioides*, *T. floribunda*, *T. japonica* and *T. tanakae*; in the first species, natural self-pollination effected by spontaneous pollinia germination on the stylar head within the flower has been reported by Chaturvedi (1988), dipteran and lepidopteran pollination in the second species and dipteran pollination in all other species by Yamashiro et al. (2008). In India, *T. indica* is a widespread species but its pollination ecology has not been studied so far despite its value in treating dysentery, diarrhea, humoral, bronchial asthma, allergic rhinitis, cold and cough (Masur et al. 2016).

In the sub-family, Rauvolfioideae, the flowers are simple with constant morphology (Endress 1994; Endress and Bruyns 2000). Fruits and seeds are vary in dehiscence, nutritious portion, size and pericarp consistency. In this sub-family, *Catharanthus roseus* and *Rauvolfia serpentina* have been investigated for their pollination ecology aspects.

The genus *Catharanthus* is derived from two Greek words "*cathar*" meaning "pure" and "*anthus*" meaning "flower". It has 8 species of which 7 are endemic to Madagascar while one species, *C. pusillus* is endemic to India and Sri Lanka. The Madagascan species, *C. roseus* is widely cultivated and naturalized all over the tropics, and occasionally in the subtropics of both hemispheres (Plazier 1981; Nejat et al. 2015). It is a fast-growing species and grown in gardens and parks globally (Sutarno and Rudjiman 1999). But, other workers reported that autogamy does not normally occur in *C. roseus* due to physical separation between the anthers and stigma as a result of the position of stigma below the level of anthers; this situation is referred to as reverse herkogamy by these authors (Kulkarni et al. 2001; 2005; and Kulkarni and Bhaskaran 2013). Further, Albers and van der Maesen (1994) reported that some strains of *C. roseus* produce flowers with elongated ovaries or styles that facilitate intra-flower selfing. It is in fact cross-pollinating, the rate of which varies with ambient environmental conditions and the availability of seasonal pollinating butterflies and moths; the floral structure in this species is adapted for pollination by long-tongued insects. Sevestre-Rigouzzo et al. (1992) and Prota (2011) reported that self-incompatible strains of *C. roseus* display natural inter-specific hybridization and this form of hybridization is common in Madagascar. But, Nejat (2015) documented that both intra-flower pollination and cross-pollination occur in *C. roseus*. Miyajima (2004) reported that *C. roseus* flowers are functionally almost cleistogamous due to pollination

limitation by insects which principally consist of butterflies and hawk moths. These studies indicate that there are conflicting reports on the pollination modes in *C. roseus* and hence warrant for further studies to conform the pollination modes in this species as it is commercially and ornamentally important.

Rauwolfia spelled also as *Rauwolfia* is a genus named in honour of Leonhard *Rauwolf*. Its distribution has been reported variously by different workers - native to tropical and subtropical parts of Europe, Africa, Asia, Australia, and the Central and South Americas (Vakil 1955), in South America, mainly centered in Brazil (Koch 2002), throughout the tropical regions of the world (Koch et al. 2007) and in tropical climatic conditions (Nair et al. 2012). The species accepted under this genus have also been variously reported - about 70 species by Koch (2002), 80 by Nair et al. (2012), more than 100 by Vakil (1955) and 110 by Mabberley (1987). In this genus, the species represent only evergreen trees and shrubs which are characterized mainly by the presence of indole alkaloids (Mandinaveitia et al. 1995). Among species of this genus, only *Rauwolfia serpentina* is widely documented due to its high medicinal value. Tyler et al. (1981) noted that *R. serpentina* grows well under varying edapho-climatic conditions in the humid tropics of South and South East Asian countries. Akbar (2020) reported that it is native to India, Bangladesh, Sri Lanka, Burma, Thailand, Malaya, the Andaman Islands, the Philippines, and Indonesia. Jain et al. (2003) documented that it is commonly found in shady, moist or swampy areas in India. Further, these authors also noted that IUCN has listed this species as "endangered". Nair et al. (2012) reported that *R. serpentina* is the best source of indole alkaloids of which reserpine is the most prominent which is used in the treatment of hypertension, cardiovascular problems, nervous disorders and as a tranquilizing agent. Spinella (2001) reported that *R. serpentina* is used in Asian medicine and in particular in the Ayurveda system which is native to India. Akbar (2020) reported that the root has been used to treat snake and scorpion bites, insect stings, nervous disorders and epilepsy for thousands of years.

Little information is available on the sexual system and pollination aspects of *Rauwolfia* genus. Ingrid et al. (2002) reported that *R. sellowii* with hermaphroditic flowers is functionally dioecious while *R. vomitoria* is gynodioecious. Lopes and Machado (2008) documented that *R. grandiflora* with hermaphroditic flowers exhibits secondary pollen presentation, herkogamy, self-compatibility, and is pollinated by exclusively by a long-tongued bee, *Exaerete smaragdina*. Kulloli and Sreekala (2009) reported that *R. micrantha* is hermaphroditic, protogynous, self-incompatible, and pollinated by honey bees, ants and butterflies. Usmani et al. (2016) reported that *R. serpentina* is hermaphroditic, protogynous by the commencement of stigma receptivity a day before anthesis. Anoosha et al. (2020) reported that *R. serpentina* attract a wide variety of insects such as lepidopterans, coleopterans, dipterans and hymenopterans. Of these, the butterfly *Papilio demoleus* and the bee, *Amegilla zonata* are very important pollinators. Keeping in view, the availability of limited information on the pollination ecology of *Asclepias curassavica*, *Dregea volubilis*, *Oxystelma esculentum*, *Brachystelma maculatum*, *Pergularia daemia*, *Tylophora indica*, *Catharanthus roseus* and *Rauwolfia serpentina*, the present study was contemplated to provide details of these species with reference to their sexual system, pollination mechanism, pollinators and seed dispersal.

2. MATERIALS AND METHODS

Wild populations of *Asclepias curassavica*, *Dregea volubilis*, *Oxystelma esculentum*, *Brachystelma maculatum*, *Pergularia daemia*, *Tylophora indica*, *Catharanthus roseus* and *Rauwolfia serpentina* growing in different locations of Andhra Pradesh were selected for study during May 2019 to February 2020. *A. curassavica* growing in two varieties, red-orange and golden yellow at Dumuku area near Borra Caves, *C. roseus* in two varieties, pink and white and *R. serpentina* at Anantagiri area in Visakhapatnam District, *D. volubilis*, *P. daemia* and *T. indica* at Adivivaram in Visakhapatnam city area, *O. esculentum* in the outskirts of Ananthapur in Ananthapur District, and *B. maculatum* at Chinarutla Gudem in the Nallamalai forest in Markapuram Division of Prakasam District were used for the study. The plant growing period, flowering period, flower morphology, anthesis, nectar production, pollination mechanism, foraging activity of insect foragers effecting pollination, fruit and seed ecology and dispersal aspects were observed. The protocols described by Dafni et al. (2005) were followed for the examination of stigma receptivity, and nectar volume and sugar concentration. Flower visitors were observed during day time from morning to evening to record the role individual species in pollination. A set of mature buds were tagged and followed daily for 5-6 weeks to record fruit and seed set rates. Fruit maturation, dehiscence and seed dispersal aspects were also recorded.

3. OBSERVATIONS

***Asclepias curassavica* L.:** It is a tender erect annual sub-shrub that grows in damp sites and cultivated fields. But, it grows as a perennial in areas where soil is wet throughout the year. It produces multiple stems from the base of the plant. Two varieties, red-orange and golden yellow, grow side by side or intermingled with each other in the same site in the wild (Figure 1a,b, 2a). Both varieties display same morphological and functional characteristics except in size and color characters. The description provide

relates to both varieties unless and other-wise specified. Leaves are borne opposite to each other, petiolate and elliptic-lanceolate. The flowering occurs throughout the year in permanent damp sites while it is seasonal bloomer in rain-fed sites. Inflorescences are umbellate, pedunculate and born in axillary and terminal positions (Figure 1c,2b,c, 3a-d)); they produce 5-14 pedicellate, actinomorphic and bisexual (Figure 2j). The sepals are 5, green, free, lanceolate and reflexed. The petals are 5, free but fused basally, reflexed and shaped with inwardly curved horns in both varieties, but they are red in red-orange variety and yellow in golden yellow variety. In both varieties, the corona composed of five yellow-colored hoods and horns arises at the top of the gynostegial stipe, and is fleshy and semi-cylindrical (Figure 2d-l, 4e,f). The stamens are 5, ditheous and the pollen is aggregated into pollinia which are connected to the corpusculum through the translator (Figure 4g-i). Two pollinia connected to the corpusculum constitute a pollinarium (Figure 2k).



Figure 1. *Asclepias curassavica* – Red-orange variety: a. & b. Habitat of the plant, c. Individual plant with terminal inflorescence in flowering phase.

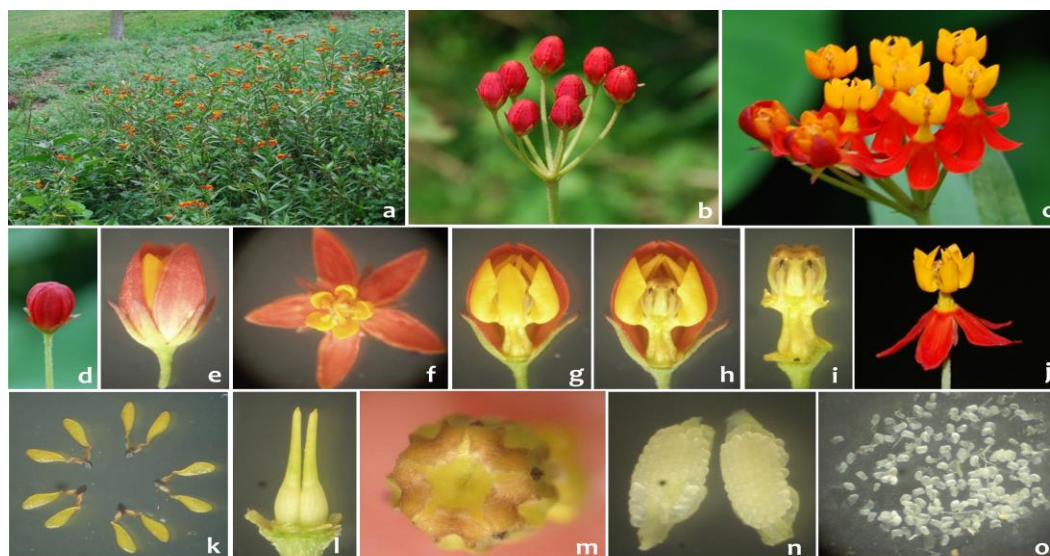


Figure 2. *Asclepias curassavica* – Red-orange variety: a. Habitat, b. Inflorescence in bud phase, c. Anthesed inflorescence, d-g. Bud phase – corollary corona showing position of pollinia, h. & i. Position of pollinia and stigma, j. Flower, k. Pollinia, l. Bicarpellary ovary, m. Stigmatic surface, n. & o. Ovules.



Figure 3. *Asclepias curassavica* – Golden yellow variety: a. & b. Individual plant with terminal inflorescence in flower phase, c. Inflorescence in anthesing phase, d. Inflorescence with just open flowers.



Figure 4. *Asclepias curassavica* – Golden yellow variety: a. Mature bud, b. Anthesing bud, c. & d. Flower, e. & f. Corollary corona showing position of pollinia and stigma, g. Close-up view of placement of pollinia, h. & i. Pollinia, j. Bicarpellary ovary, k. Stigmatic surface.



Figure 5. *Asclepias curassavica* – Red-orange variety: a. *Ceratina* sp., b. *Anthophora cingulata*, c. *Camponotus* sp.

The ovary is bicarpellary, syncarpous with many ovules arranged on marginal placentation (Figure 2l,n,0, 4j). The style is cylindrical with 5-angled depressed stigma (Figure 2m, 4k). In both varieties, mature buds open early in the morning (Figure 4a-d). Individual flowers produce nectar continuously in minute amount for two consecutive days but the amount of nectar secreted varies between inflorescences of the same and different individuals. Individual flowers secrete $1.32 \pm 0.79 \mu\text{l}$ of nectar with sugar concentration varying from 41 to 46%. The flowers last more than a week. The flowers of both varieties attracted only certain bees such as *Ceratina* sp. (Figure 5a), *Anthophora cingulata* (Figure 5b) and the ant *Camponotus* sp. (Figure 5c) although other wild bees, wasps, flies, butterflies and moths were present in the biotope of the study site. All the three insect species were able to extract and insert the pollinia effecting pollination while collecting nectar and departing from the flowers; however, the ant was involved in this process only occasionally.



Figure 6. *Asclepias curassavica* – Golden yellow variety: a. & b. Fruit development phases, c-f. Follicle dehiscence and seed dispersal by wind, g. & h. Empty follicles.



Figure 7. *Brachystelma maculatum*: a. Flowering branch, b. Maturing buds and anthesing buds, c. Mature bud, d. Flower, e. Close-up view of corona, f. Pollinia, g. & h. Pistil, i. Ovules, j. Fruit.

Fruit set in open-pollinations stood at 27% in red-orange variety and 29% in golden yellow variety. In both varieties, fruit is an erect many-seeded fusiform spindle-shaped follicle (Figure 6a,b). It is ovate-lanceolate, small, glabrous and tapering towards the base and apex. It is dehiscent type and splits lengthwise on one side at maturity to release seeds, which characterizes autochory (Figure 6c,d). The seeds are reddish-brown, broadly ovate, flattened, sparsely verrucose, very light in weight and tipped with a tuft of fine silky hairs that acts as a parachute. They drift away on silky parachutes by wind (Figure 6e,f). Empty follicles remain

attached to the plant (Figure 6g,h). Summer season is ideal for anemophily. Autochory enables the production of new plants at parental site while anemophily ensures long distance dispersal and invasion of new sites.

***Brachystelma maculatum* Hook. f.:** It is a tuberous herb with un-branched glabrous stem with watery sap growing in grassy bushes where soil is damp. Leaves are sessile, filiform, hanging and borne opposite to each other. The flowering occurs during wet season from July to October but it extends further if the moisture is damp. Inflorescence is borne in leaf axils, sessile with 2-3 flowered cymes (Figure 7a). The flowers are pedicellate, glabrous, lemon yellow coloured, actinomorphic and bisexual. The calyx has five free green sepals but fused basally; the sepals are linear with acute apex. The corolla is 2 cm long, spreading with broad ovate base which is orderly black mottled, narrowed towards apex where it is tapered and all along the margins are equipped with white hairs. The corona is formed continuously around pentangular gynostegium. It is biseriate, black, glabrous, inter-staminal and pentangular. The staminal part of the corona is 5-lobed and the lobes are triangular, hooded and adpressed to the backside of the anthers (Figure 7e). The pollen grains are aggregated into pollinia which light brown, ellipsoid and attached to corpusculum by light brown caudicles (Figure 7f). The ovary has 2 separate carpels with styles partially joined at the style head which is tipped with pentangular depressed globose stigma (Figure 7g,h); each carpel has many ovules arranged on axile placentation (Figure 7i). Buds are oriented in hanging position and upon anthesis, the corolla becomes reflexed and attains star-shape. Mature buds are open almost immediately after sunrise (Figure 7b-d) and the nectar is secreted in minute quantity continuously for two consecutive days after which the flower begin to show signs of withering. The flowers emit mild putrid odor which attracts flies such as syrphid fly, *Eristalinus* sp. and sarcophagid fly *Sarcophaga* sp. These flies searched for nectar and were able to collect nectar during which they extracted and transferred pollinia from flower to flower effecting pollination. The flowers were never foraged by any other insects. Fruit is 2- or 1-follicled, cylindrical, 8-10 cm long and tapering towards apex; each follicle has many narrowly elliptic comose seeds (Figure 7j). Follicles are dehiscent and release seeds indicating the function of autochory. The seeds thus released dispersed away from the parental plants by wind. But both autochory and anemochory modes are effective mainly during dry season.

***Dregea volubilis* (L.f.) Benth. Ex Hook. f.:** It is a large twining smooth shrub with woody stems (Figure 8a). It grows in moist and well-drained soil which is open to full sunlight. Leaves are glabrous, ovate with cordate base and acuminate apex. The plant is almost leafless while in flowering which occurs during April-May. Flowers are borne in axillary drooping pedunculate and umbellate cymes (Figure 8b). They are pedicellate, light yellowish-green, 10 across, sweet scented, actinomorphic and bisexual. Mature buds are open during early morning after sunrise (Figure 8c,d). Calyx consists of 5 ovate to elliptic, pubescent, lanceolate sepals with glands at the base. Corolla has 5 yellowish green orbicular rotate petals but tubular at base. Corona is single with 5 fleshy lobes and attached to the base of staminal column which arises from the corolla base (Figure 8f). Anthers are 5, erect, ovate, obtuse and appendiculate; each anther has a pair of pollinia (Figure 8g-i). Ovary is globose, pubescent with two carpels and each carpel has many ovules (Figure 8e,j,k). The style is short with dome-shaped apex with pentangular flat stigma. Nectar is secreted in minute quantity continuously for two consecutive days after which the flower begin to show signs of wilting. Insect foragers included one ant, *Camponotus* sp. (Figure 8l), two beetles, *Brachinus* sp. (Figure 8n) and another unidentified one (Figure 8m), and the diurnal hawkmoth, *Macroglossum gyrans* (Figure 8q); these insects foraged throughout the day from sunrise to sunset. All the three species were nectar feeders and removed pollinia while probing for nectar and then transferred to other flowers in their successive flower visits effecting either self- or cross-pollination. The pollinia were attached to these insects by the short caudicles. Further, ground mealy bug, *Lygaeus* sp. (Figure 8o,p) was also recorded feeding on the sap of leaves, buds and flowers and hence it was treated as a pest.

Fruit initiation occurs after fertilization but it is a slow process. Fruits mature and become dry by the time of onset of dry season which begins from March onwards. Fruit is either 1- or 2-follicled indicating the fertilization of ovules of one or both free carpels (Figure 9b,c). Fruit set rate is 12% only out of which 34% are 1-follicled while the remaining percentage is represented by 2-follicled fruits (Figure 9a). Follicles are broadly lanceolate but blunt at apex, woody, green initially, light brown when mature, 7-8 cm long, longitudinally ribbed, velvety inside and many-seeded (Figure 9d,f). Individual seeds are yellowish-brown, broadly ovate, concave, flattened, shiny, sharp-edged, 10 x 6 mm, and crowned with very fine copious white silky hairs (Figure 9g-i). Follicles dehisce to disperse comose seeds which either spontaneously or subsequently disperse by wind (Figure 9j,k). The crown of silky hairs at one end of the seeds enable the latter to fly away by wind very easily. Empty follicles remain attached to the plant (Figure 9e). Follicle dehiscence and seed dispersal principally occurs during dry season when the ambient temperature is very high and air humidity is very low. During follicle dehiscence and seed dispersal, the floor around the plant area appears decorated with the fallen seeds with plentiful silky hairs that emerge from the follicles. Seeds germinate and produce new plants during wet season (Figure 9l).

***Oxystelma esculentum* (L.f.) Sm.:** It is a slender lactescent twining perennial shrub that grows profusely in wet soils. The leaves are petiolate, simple, arranged opposite to each other at nodes and oblong to linear. The flowering occurs during July-February with profuse blooming during September-October (Figure 10a). The flowers are pedicellate and borne in 2-4 flowered pedunculate

cymes which are in extra-axillary position (Figure 10b). They are large, campanulate, actinomorphic, nectariferous and bisexual. Mature buds open at sunrise by gradually unfolding the corolla and exposing the gynostegium (Figure 10c-e). The calyx is 5-lobed but connate at base, lanceolate, glabrous and light reddish on the outside. The corolla is white to pink with maroon stripes inside the corolla, 5-lobed to about half-way with saucer-shaped tube. The stamens are 5, epipetalous, anthers bilocular, pollinia in horizontal orientation, pollinial sacs oval, oblong and tipped with whitish outgrowth that covers the stigmatic surface. The corona is staminal, bi-seriate, swollen, outer one is corolline, annular, pubescent at the base inside the corolla while the inner one is staminal, inflated basally. The corona lobes are positioned adnate to the gynostegium. The ovary is bicarpellary, bilocular syncarpous with short style and convex stigma which shows receptivity from anthesis onwards and until the noon of next day; the ovary collectively contains numerous ovules. The nectar is secreted in minute volume continually for two days from the time of anthesis.



Figure 8. *Dregea volubilis*: a. Straggling woody shrub, b. Flowering, c. Mature bud, d. Flower, e. Ovary position in relation to stamens, f. Gynostegium, g. Translator -1. Pollinia, 2. Corpusculum, 3. Retinaculum, h. Pollinial mass, i. Adherence of stamens to gynoecium, j. Bicarpellary ovary with two styles, k. Ovules, l. *Camponotus* sp. collecting nectar, m. Beetle collecting nectar, n. *Brachinus* sp. collecting nectar, o. & p. *Lygaeus* sp. , q. Diurnal hawkmoth, *Macroglossum gyrans* collecting nectar.



Figure 9. *Dregea volubilis*: a. Fruit set, b. & c. 2-follicled fruit, d. Follicle with numerous seeds, e. Empty follicle, f. Seed arrangement on the placenta, g. & h. Seed crowned with a tuft of silky hairs, i. Seeds free from silky hairs, j. Follicle dehiscence, k. Seeds ready for dispersal, l. New growth from seeds.

Mature buds were used by thrips for breeding. They were found at different stages of their life cycle just after anthesis. They were resident foragers feeding on nectar throughout the day until flower fall. They were not involved in the removal of pollinaria due to their minute body size and hence they were treated as mere nectar robbers. Field observations indicated that the flowers were foraged and pollinated during day time by juvenile carpenter bees representing *Xylocopa latipes* and *X. pubescens* but these bees were not very consistent in their visits during the entire phase of flowering of this plant. They landed on the campanulate corolla and probed the flower base for nectar. While inserting their tongue, they had contact with the pollinaria and in consequence the latter were transferred to their body parts. Further, after nectar collection, they moved either forward or backward along the rail gap between pollinia during which they either removed pollinaria or transferred pollinaria to the stigma point effecting pollination. The flowers were never foraged by any other insect visitors. The fruit is either 1- or 2-follicled, 4.5-5 cm long, lanceolate, sickle-shaped, base rounded and apex pointed (Figure 10f-h). Each follicle produces several small, smooth, ovate, flattened seed tipped with a tuft of white hairs, which is collectively referred to as "coma". In open-pollinations, fruit set stood at 6% and fruited flowers mostly 1-follicled indicating the fertilization of ovules of only one carpel. A few fruited flowers were 2-follicled indicating the fertilization of ovules of both carpels of the flowers. Follicles dehisce longitudinally to disperse seeds and the latter either spontaneously or subsequently disperse by wind.



Figure 10. *Oxystelma esculentum*: a. Flowering patch, b. Twig with flowers, c-e. Anthesis stages, f-h. Fruiting stages.

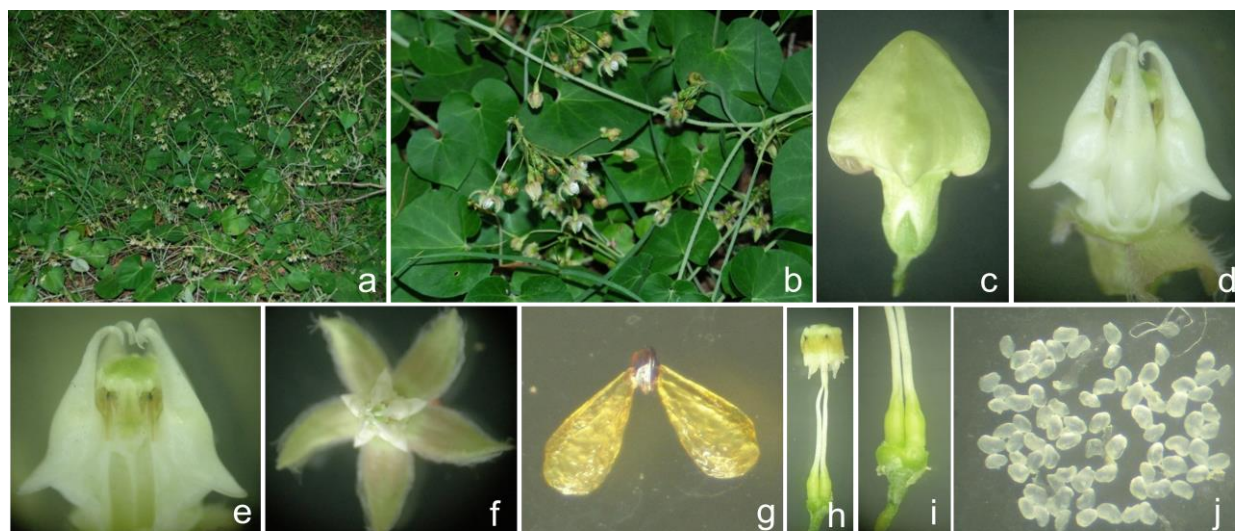


Figure 11. *Pergularia daemia*: a. Habit, b. Flowering phase, c-f. Bud to flower stages, g. Pollinia, h. Pistil crowned by corollary corona, i. Bicarpellary ovary, j. Ovules.

***Pergularia daemia* (Forssk.) Chiov.:** It is a hispid perennial twining herb (Figure 11a). It scrambles over the ground or twines into co-occurring plants for support. It grows widely along roadsides, in dry bush lands and in open lands. The stem is woody at base, bears milky juice, covered with stiff erect hairs and emits foul smell when bruised. Leaves are petiolate, borne opposite to each other, thin, broadly ovate and covered with soft hairs. Flowering occurs during July-February (Figure 11b). Flowers are pedicellate, greenish yellow or dull white, sweet-scented, 1.5-2 cm across and borne on lateral long-pedunculate, umbellate clusters. The flowers open in the evening (Figure 11c-f). The calyx has 5 short hispid sepals. Corolla is short-tubed with 5 ovate acute petals bearded margins, creamy white or greenish. Gynostegial corona is white, 2-whorled, outer whorl truncate, membranous, shallowly lobed and inner whorl very conspicuous with fleshy lobes and acute spur, arising from the back of anthers, incurved high over the head of the gynostegium (Figure 11h). Pollinaria are pendulous and consist of laterally compressed corpusculum with a minute keel and extremely short translator arms and pollinial sacs are directly attached to corpusculum due to absence of caudicle (Figure 11g). Ovary is bicarpellary with many ovules (Figure 11i,j). Nectar is secreted in minute quantity continually for two consecutive days and the flowers begin to show signs of wilting from day 3 onwards. The flowers were visited by nectar-seeking diurnal hawk moth, *Macroglossum gyrans* as soon as the flowers were open during dusk hours and again during dawn hours on the following day and by bees consisting of *Apis dorsata*, *A. cerana* and *Anthophora* sp. from 0800 to 1400 h. The hawk moth was able to remove and transfer pollinaria effecting pollination but its activity is confined to dusk hours only. On the contrary, bees while visiting the flowers for a long period during daytime effected pollination. When the bees landed on the flower, the bristles on the legs of bees hooked to corpusculum of the translator, they probed and collected nectar, and when they finally departing from the flower mined out the pollinaria. The bees in their next flower visits for nectar inserted the pollinarium into the receptive stigmatic chamber effecting pollination.

Fruits mature in about 9 months. Fruit is 1- or 2- follicled, lanceolate, long pointed and covered with soft spiny outgrowth all over and a long curved beak, 6-8 cm long, reflexed on the pedicel. It splits open to release seeds but the dehisced follicles contain the seeds still attached to the placenta at the tip through hair. However, the seeds after follicle dehiscence are also dispersed by wind to long distances. Seeds are broadly ovate, flattened, wings fringed densely covered on both sides with white hairs. Field observations indicated that dry season was ideal for fruit dehiscence and seed dispersal.

***Tylophora indica* (Burm.f.) Merrill:** It is a perennial twining herb with hairy branches and short knotty root system. It grows in open sunlight areas with sufficient soil moisture. Leaves are petiolate with opposite leaf arrangement, ovate-oblong blade, cordate base and acute apex. Inflorescence is a few to many-flowered umbellate cyme and axillary in position. The flowering occurs throughout the year with concentrated flowering during July-October (Figure 12a). Mature buds open soon after sunrise exposing the corona combined with gynostegium (Figure 12b,d). The flowers are pedicellate, small, greenish yellow on the outside and purplish on the inside, mildly fragrant, actinomorphic and bisexual. The calyx has 5 narrowly lanceolate sepals with acute apex and hairy all over. The corolla has 5 petals with rotate arrangement but fused at the base; the petals are glabrous outside and sparsely pubescent inside. The corona consists of 5 thickened erect and turgid obovate lobes tipped with narrow fleshy points, fused partly to the base of the staminal column. Pollinarium consists of 2 yellow-green erect globular pollinia with apically attached translators, ascending cylindrical caudicle and small retinaculum (Figure 12e). The ovary has 2 free carpels with many ovules (Figure 12g), columnar style with 5-sided depressed and flattened stigmatic head (Figure 12f). Nectar is secreted in minute quantity continually for two successive days and the flower then begin to show signs of wilting. Flower visitors were not recorded during the observation period.

Fruits grow slowly and mature within 5-6 months (Figure 12h). Since profuse flowering occurs during rainy season, maturation of fruits from the fertilized flowers occurs mainly during dry season. The fruits that mature outside the dry season are small in number. Fruit set in open-pollinations was 4% of which 1% are 1-follicled while 3% are 2-follicled. Fruit is either 1- or 2-follicled, divaricated and each follicle is ellipsoid, 7-8 cm long, tapering at the apex and many-seeded. The seeds are small, brown, ovate, flat and crowned with a tuft of white silky hair. The follicles are autochorous, split open to disseminate seeds (Figure 12i) and most seeds remain attached to the placenta but they disperse effectively by wind during dry season than in other seasons.

***Catharanthus roseus* (L.) G. Don:** It is a long-lived profusely branched perennial evergreen erect sub-shrub. It grows well on sandy soils in coastal areas and on dry, waste places. The stem is cylindrical and longitudinally ridged. Leaves are simple, opposite, decussate, petiolate, elliptic ovate to oblong with acute base and apiculate apex. The flowering occurs throughout the year in damp sites while it is seasonal in semi-dry and dry sites. Inflorescence is a terminal cyme with one or two pedicellate nectariferous actinomorphic and bisexual flowers which open during early morning soon after sunrise. At the study site, two varieties of *C. roseus* occur, pink (Figure 13a) and white (Figure 13b). The flowers of the two varieties are morphologically similar except in size measurements. The calyx is tubular, fused to the ovary base and topped with 5 flexible tines. The corolla is pink in pink variety and white in white variety; it is tubular, pilose inside with villous throat which is extended into five broadly obovate spreading lobes

forming star-shape. The throat portion is hairy and swollen due to the placement of anthers. The stamens are 5, inserted near the throat with short filaments and sagittate ditheous, dorsifixed and introrse anthers which form a cone-like structure above the stigma. The anthers produce monad pollen grains which are tricolporate, prolate and spheroidal. The ovary has two long narrow free carpels, each with numerous ovules arranged on marginal placentation; the carpels are united apically into a long style which in turn is tipped with a glabrous capitate stigma. The flowers were foraged for nectar by butterflies only. The butterflies visited pink variety flowers in preference to white variety flowers. They were *Papilio demoleus* (Figure 12c), *P. polytes* (Figure 12d) (Papilionidae), *Catopsilia pyranthe* (Figure 12e) (Pieridae), *Junonia lemonias* (Figure 13f), *Tirumala limniace* (Figure 13g) (Nymphalidae), *Spindasis vulcanus* (Figure 13h) (Lycaenidae) and *Borbo cinnara* (Figure 13i) (Hesperiidae). They probed the flowers through the throat of the corolla to access nectar during which their proboscis invariably passed through the stamens and stigma facilitating the occurrence of either self- or cross-pollination depending on the source of pollen transferred onto the stigmatic head.

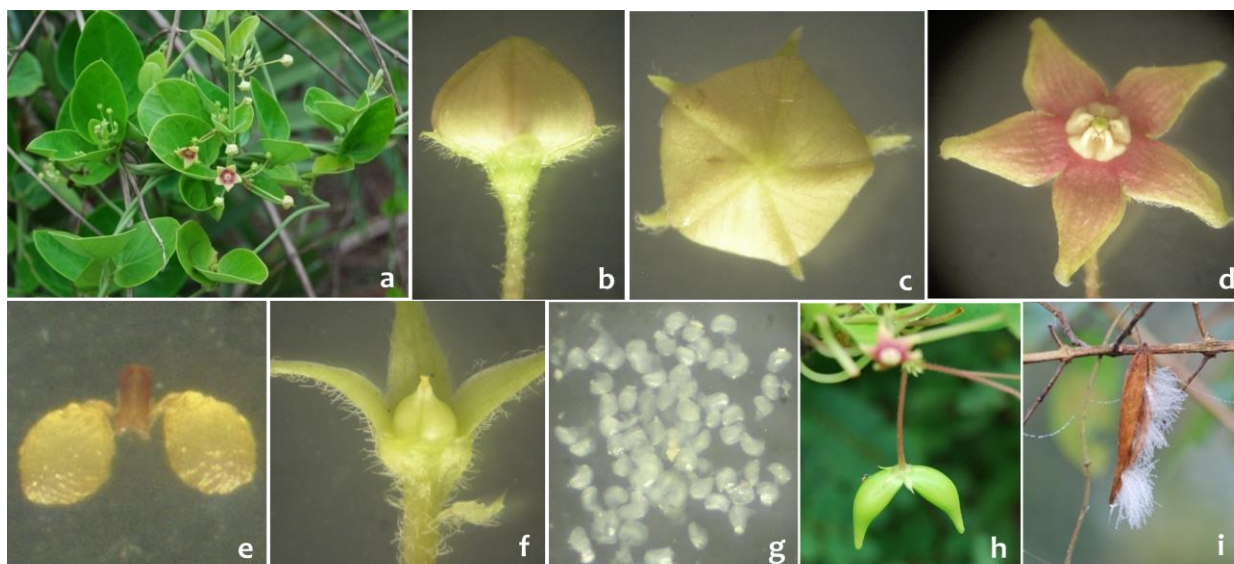


Figure 12. *Tylophora indica*: a. Flowering phase, b-d. Anthesis stages, e. Pollinium, f. Pistil, g. Ovules, h. Fruit development, i. Fruit dehiscence and seed dispersal.

The fruit is either 1- or 2-follicled. It is 3-4 cm long, erect, curved and slightly divergent with many very small black oblong rough seeds. Follicles split open longitudinally to release seeds, which characterized the function of autochory. Since the seeds are very small, wind also disperses them especially during dry season. Seeds fallen to the ground are dispersed by ants during dry season and by water during rainy season.

***Rauwolfia serpentina* (L.) Benth. ex Kurz:** It is an evergreen shrub with prominent tuberous taproots. Leaves are pale green, elliptical and 3-4 whorled. The flowering occurs during May-July with profuse flowering during May (Figure 14b,c). Inflorescence is terminal, pedunculate and consists of small pedicellate hermaphroditic and actinomorphic flowers in compact cymes (Figure 14a). The entire terminal inflorescence consists of a mean of 36.5 flowers (Range 27-47). Mature buds open during 0500-0630 h. The calyx is basally greenish, fused and apically with five deep red glabrous sepals. The corolla is narrow tubular, and swollen in the middle portion; the tubular portion is pink while the throat part with five free lobes is white. The stamens are 5, epipetalous and enclosed within the dilated part of the tubular portion of the corolla. The anthers are introrse and form a cone above the stigmatic head. They dehisce on the second day of anthesis during 0800-0900 h. The pollen grains are monads, The ovary has two connate carpels, each with a single locule consisting of two ovules. The style is filiform with a wet bifid stigma which is receptive from anthesis onwards and until the end of the day of anthesis. Nectar is secreted by the time of the occurrence of anthesis and its secretion is continued until late evening; the sugar concentration varied from 28 to 34%. The flowers were foraged during day time by papilionid butterflies (*Papilio demoleus*, *P. polytes*, *Graphium agamemnon* and *G. doson*) and honey bees (*Apis dorsata*, *Apis cerana* and *A. florea*), the former were found to be best pollinators as they inserted their proboscis through corolla tube contacting the stamens and stigma in the act of accessing nectar located at corolla base while the latter were found to be additional pollinators as they tended to collect only pollen during which they could effect pollination and the extent of acting as pollinators depended on the depth at which they attempted to collect pollen by contacting the stigmatic portions.

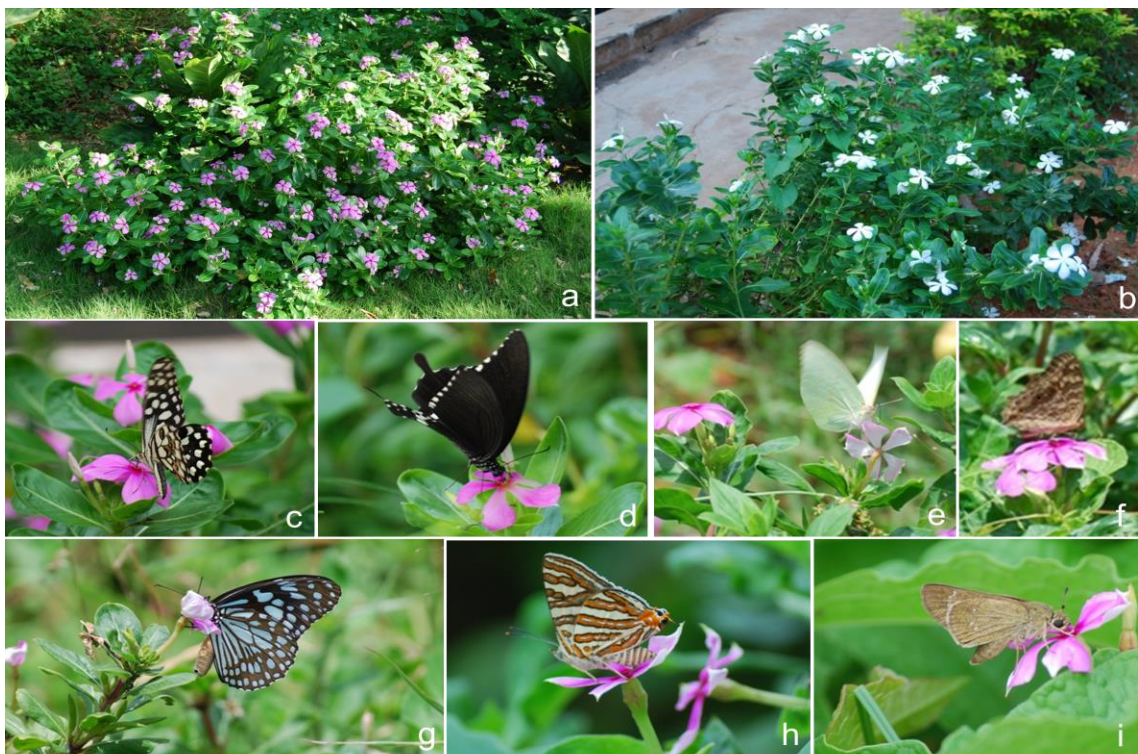


Figure 13. *Catharanthus roseus*: a. Pink variety, b. White variety, c. & d. Papilionid butterflies – c. *Papilio demoleus*, d. *Papilio polytes*, e. Pierid butterfly, *Catopsilia pyranthe*, f. & g. Nymphalid butterflies – f. *Junonia lemonias*, g. *Tirumala limniace*, h. Lycaenid butterfly, *Spindasis vulcanus*, i. Hesperiid, *Borbo cinnara*.



Figure 14. *Rauwolfia serpentina*: - a. Twig with buds, b. Flowering phase, c. Flowering and fruiting phase.

Fruits mature in about 2 months (Figure 14c). Fruit set in open-pollination is only 5%. Fruit is a single or a pair of connate shiny purple-black to bluish ovate drupe. Single drupe fruits are mostly 1-seeded while a few are 2-seeded. Connate drupes are most 2-seeded while a few are 3 or 4-seeded. Seeds are light brown and stone hard.

4. DISCUSSION

Asclepias curassavica: *Asclepias curassavica* is a small shrub that grows as an annual in wet season damp sites and as a perennial in wetland sites. At the study site, two varieties, red-orange and golden yellow grow together and display their flowers attractive to foragers or to human eye from a long distance. The two varieties exhibit similar morphological and functional characters although they show variation in size and color characters. The flowers are characteristically hermaphroditic and offer nectar with high sugar concentration as a reward to flower foragers since pollen in the form of pollinia or pollinaria is not useful as forage source to them.

Anthesis in both varieties is diurnal as mature buds are open early in the morning. As nectar is continuously produced in minute volume for two consecutive days, individual flowers provide nectar for the foragers accordingly.

Wyatt and Broyles (1997) reported that *A. curassavica* is self-compatible, self- and cross-pollinated in Australia and Costa Rica. The percentage of fruit set is almost the same in both self- and cross-pollinated flowers. Further, seed viability is also uniformly high in both types of pollination. Liza et al. (2010) reported that *A. curassavica* is an out-crosser because the bagged flowers failed to form fruits. In this study, hand-pollination tests were not conducted but fruit set rate evidenced in open-pollinations suggest that it is both self- and cross-pollinating.

Liza et al. (2010) reported that *A. curassavica* is cross-pollinated and pollinated by butterflies, bees and ants in Bangladesh. Ward et al. (2012) reported that *A. curassavica* is pollinator-dependent for reproductive output. It is pollinated by butterflies in Costa Rica (Wyatt 1980; Bierzychudek 1981), Brazil (Fuhro et al. 2010), butterflies and wasps in Australia (Ward and Johnson 2013), bees, beetles, moths, wasps and hummingbirds in the urban botanical gardens of California (Warren et al. 2020). Fuhro et al. (2010) reported that *Danaus erippus* and *Heliconius erato* remove pollinia and carry them on their tarsi and proboscis. Ramos et al. (2017) reported that *Danaus erippus* and *Heliconius erato* have the ability to manipulate and learn how to extract reward from the flowers of complex morphology produced by *A. curassavica*. But pollinia insertion rate into stigmatic part is far less than pollinia removal rate indicating that the learning ability of these butterflies do not benefit the plant in pollination. Rabelo and Francini (2014) reported that *A. curassavica* flowers were foraged by different species of ants for nectar collection. The ants act as nectar thieves by diminishing the nectar availability to potential pollinators and subsequently the ability of the plant to produce more fruits. In the present study, the flowers of both varieties being very attractive and lasting more than a week have been able to attract only certain bees such as *Ceratina* sp., *Anthophora cingulata* and the ant *Camponotus* sp. although a variety of other insect foragers are present in the habitat. All the three insect species extract and transfer pollinia between flowers of the same or different plants effecting both self- and cross-pollination; but the ant is not efficient in carrying out pollinations *on par* with bees. Therefore, bees are the appropriate and efficient pollinators and hence *A. curassavica* varieties are principally melittophilous.

In both varieties of *A. curassavica*, fruit is an erect many-seeded fusiform spindle-shaped follicle and is dehiscent indicating autochory. A tuft of fine silky hairs possessed by seeds acts as a parachute and enable seeds to drift away by wind, especially during dry season. The functionality of autochory ensures new recruitment at parental sites while the functionality of anemophily ensures new recruitment at sites far away from parental sites.

Elizabeth et al. (2010) reported that *A. curassavica* is grown as an ornamental garden plant and as a food source for some butterflies in North America. It is the primary larval host plant for the migratory butterfly, *Danaus plexippus*. Pegram and Melkonoff (2020) reported that since *A. curassavica* is cultivated due to its ornamental value and also it does not go dormant in the winter season, the migration pattern of *D. plexippus* is affected as the latter forms non-migratory groups and remain in the same place during its migratory period. Churi et al. (2021) documented that *A. curassavica* is the larval host plant for *Parantica sita*, *Tirumala limniace*, *Danaus genutia* and *D. chrysippus* in India. At the study site, butterfly larvae have not been observed on both varieties of *A. curassavica*.

***Brachystelma maculatum*:** *B. maculatum* has been reported to be restricted to certain habitats of Eastern and Western Ghats. This species is stated to be prone to forest fires and subjected to grazing by wild boars (Prasad et al. 2016). Since this plant has tuberous roots, wild boars appear to be digging for its tuberous roots as food source and hence their feeding activity on tubers is a great threat for the buildup of populations of this species. In this context, it is important to mention that IUCN (2017) also documented that *B. maculatum* is under Data Deficient status. Prasad et al. (2016) reported that *B. maculatum* is represented by about 100 individuals at Sikharam area in Kurnool District of Andhra Pradesh. In this study, it is found that a few individuals of *B. maculatum* grow naturally in the dry deciduous forest at Chinarutla Gudem in the Nallamalai forest in Markapuram Division of Prakasam District of Andhra Pradesh. The flowering occurs during rainy season but this event extends further in damp soils. The inflorescences display hermaphroditic flowers very distinctly to attract pollinating insects. Further, the floral characters such as mottled corolla base, mild putrid odor and production of minute amount of nectar indicate that *B. maculatum* is adapted for fly-pollination. Accordingly, only flies visit and pollinate this plant by extracting pollinia during nectar collection and transferring them to other flowers in successive visits. However, they are not as effective pollinators as bees. This study substantiates the speculation by Vogel (1990) that *Brachystelma* species are exclusively fly-pollinated and also by Ollerton and Liede (1997) who reported that many species of *Brachystelma* display the traits of decay-attraction fly pollination syndrome. Field observations indicated that fruit set in open pollination is very low as individual plants produce a few follicles. Follicles disperse seeds by autochory and anemochory, the former mode is effective for recruitment at parental sites while the latter mode is effective for recruitment at sites far away from parental sites. Since follicle production rate is very low, *B. maculatum* is not unable to populate either *in-situ* or *ex-situ* habitats.

***Dregea volubilis*:** *Dregea volubilis* is a woody twining shrub that grows well in moist and well-drained soils exposed to full sunlight. As soon as the follicles of the previous flowering season dehisce and disperse their seeds, the plant begins its flowering. The leafless state of the plant enables yellowish-green sweet scented flowers to attract the intended pollinating insects for effecting pollination. As the flowers offer only nectar, the pollinating insects collect only this reward and while doing so the pollinia get attached to their body parts and transferred subsequently in their visits to other flowers which eventually results in pollination and fertilization. The long period of nectar production indicates that the plant prefers cross-pollination over selfing and the flowers by being in place for more than two days enhance attraction to the intended foraging insects in order to enable the latter to carry out more foraging visits and effect more pollinations. Among the flower visitors recorded, the hawkmoth, *M. gyrans* appears to be principal pollinator, especially in effecting cross-pollinations due to its ability to visit as many flowers as available in the habitat. The ant and beetles act as supplementary pollinators only as the former as a resident forager while the latter with the tendency to visit mostly the flowers of the same plant mostly effect self-pollinations. *Lygaeus* mealy bugs by feeding on leaves, buds and flowers act as a pest affecting the reproductive success of the plant. The production of 1- and 2-follicled fruits from open-pollinations is an indication of either pollination or pollinator limitation and lack of sufficient nutrients in the soil environment. The 1- or 2-follicled fruits are autochorous as well as anemochorous. The function of these two modes enable the plant to recruit new individuals at parental and non-parental sites.

In India, *D. volubilis* is widely reported by different authors regarding its use in traditional and other systems of medicine. It is used in Ayurveda, Siddha and Unani systems of medicine and also in unorganized folk-medicine to treat various human diseases and ailments (Kirtikar and Basu 1935; Chatterjee and Pakrashi 1995; Hossain et al. 2012; Madhava Chetty et al. 2012; Sreeramulu et al. 2013; Vishnusithan et al. 2014). In view of its medicinal value, the chemical analysis of all parts of the plant is recommended for using it scientifically in the modern medicine. Churi et al. (2021) reported that *D. volubilis* is the larval host plant for the nymphalid butterflies, *Tirumala limniace* and *T. septentrionis*. In the habitat of the plant, these two butterfly species occur and may be utilizing *D. volubilis* as their larval host plant.

***Oxystelma esculentum*:** *Oxystelma esculentum* blooms during wet and winter season but flowering occurs profusely only during wet season. The flowers are quite distinct against the foliage enabling the foragers to identify the forage source. But, only juvenile *Xylocopa* bees visit and pollinate the flowers despite the presence of other wild bees in the habitat. These bees are large-bodied, efficient in probing the flowers for nectar collection, removing and transferring pollinia between flowers of the same or of different plants effecting both self- and cross pollinations. On the contrary, Soumitra Pal and Subrata Mondal (2019) reported that this species is foraged by *Apis dorsata*, *Vespa* sp., *Borbo cinnara* and thrips. These authors also noted that only *A. dorsata* is the most important forager while *B. cinnara* and thrips are mere nectar robber. In this study also, thrips have been observed to use the flower buds as breeding site and flowers as nectar source. Since the pollen grains are not monads and aggregated as pollinia/pollinaria, thrips are unable to feed on pollen and also they are not able to remove pollinia due to their tiny size. Their feeding activity as resident nectar foragers could only deplete nectar that is intended for actual pollinators and hence qualify as nectar robbers. However, the nectar robbery employed by thrips could promote foraging activity by *Xylocopa* bees to enhance pollination rate.

Soumitra Pal and Subrata Mondal (2019) reported that *O. esculentum* is xenogamous with partial self-compatibility because it fruits through geitonogamy. Further, these authors mentioned that fruit set rate is below 10% in open-pollinations. In this study, fruit set rate in *O. esculentum* is only 6% and also many fruits are 1-follicled instead of 2-follicled. This situation could be attributed to pollination or pollinator limitation, self-incompatibility, insufficient cross-pollinations and soil nutrient environment. Follicles are self-dehiscent to disperse seeds which either spontaneously or subsequently disperse by wind and hence *O. esculentum* is both autochorous and anemochorous, the former mode enables to form new plants at parental sites while the latter mode ensures long distance dispersal and form new plants in sites other than parental sites.

***Pergularia daemia*:** It is a common perennial twining herb which flowers during wet and winter seasons. The pedunculate umbellate clusters consisting of greenish yellow to dull white flowers are prominent and attractive to foragers. The flowers are hermaphroditic with a distinct corolla and an elaborate gynostegial corona that crown the stigma head and pollinaria. The floral traits such as evening anthesis, floral color, sweet fragrance and nectar production indicate that the plant is mainly adapted for pollination by hawk moths. Accordingly, the diurnal hawk moth, *M. gyrans* visits the flowers as soon as the flowers are open, continue until sunset, and revisit the flowers at dawn hours on the next day. But, bees also visit these flowers after dawn hours and until the onset of dusk time. All foragers while collecting nectar effect self- and/or cross-pollination by extracting pollinaria and inserting them into the receptive stigmatic chamber in successive flower visits. The study indicates that *P. daemia* is actually adapted for pollination by hawk moths but the visits of the latter are confined to dawn and dusk hours only. In effect, the foraging visits by bees assume importance in enhancing the pollination rate and subsequent fruit set rate. Previous workers noted that *P. daemia* is

pollinated by *Apis dorsata* (Vijayaraghavan and Shukla 1980), and by bees of *Tetragonula* sp., *Apis dorsata*, *A. cerana* and *A. florea* (Ramakrishna et al. 2016).

In *P. daemia*, fertilized flowers produce mature fruits after nine months. The follicled fruits split longitudinally to release seeds indicating the functionality of autochory. But, some seeds remain attached to the placenta of the follicles and such seeds subsequently fly away by wind. The long gestation period of follicle production appears to be advantageous for the plant to time its seed dispersal period during dry season because this season is very ideal and effective for seed dispersal. Therefore, although autochory is functional, anemochory is the principal mode of seed dispersal.

***Tylophora indica*:** It is a perennial twining herb that flowers throughout the year if the soil damp but flowering is profuse only during wet season. The pedicellate flowers borne in umbellate cymes at leaf axils project out of the foliage and prominently visible. Despite their prominence, floral bud opening just after sunrise and profuse flowering during wet season, the flowers were never visited by insects during the observation period. This situation could be due to the availability of other appropriate floral sources simultaneously at the site for insect foragers. In this context, this study suggests to carry out field observations on the foraging activity of insects at other sites where this plant occurs. The flowers being bisexual and nectariferous have a complex pollination mechanism characterized by staminal corona, and pollinaria. Despite the absence of insect foragers at the flowers, the plant is able to fruit to some extent indicating the function of self-compatibility and self-pollination by spontaneous pollinia germination the stylar head as reported in *T. hirsuta* by Chaturvedi (1988). In certain *Tylophora* species, *T. matsumurae*, *T. aristolochioides*, *T. floribunda*, *T. japonica* and *T. tanakae*, dipteran and/or lepidopteran pollination has been reported (Yamashiro et al. 2008). Therefore, *Tylophora* species display spontaneous selfing as well as insect-mediated pollination; for the occurrence of latter mode, nectar is offered as a reward.

In *T. indica*, the growth, development and maturation of fruits take place in about 6 months. The bulk of fruits produced in this species result from the flowering occurred during wet season and these fruits represent 1 or 2-follicles, each follicle producing several seeds. The follicles are autochorous but this mode is not effective to disperse seeds as some seeds remain attached to the placenta. The seeds after follicle dehiscence are either spontaneously or subsequently dispersed by wind which is effective during dry season. Therefore, seed dispersal is both autochorous and anemochorous. Since this plant is twiner and spreads covering the low ground herbaceous plants, it suppresses associated herbaceous flora. However, it can be controlled by harvesting its parts for use in treating certain diseases in traditional medicine (Masur et al. 2016).

***Catharanthus roseus*:** It is a perennial evergreen erect sub-shrub that grows well on sandy soils. As the plant is profusely-branched, the flowers borne in terminal cymes are very distinct against the foliage and attract the attention of butterflies at the study sites. In this species, pink and white varieties with similar flower morphology occur in the same habitat but form distinct populations. Butterflies prefer to visit the flower of pink variety while they make occasional visits to white variety. As mature buds open soon after sunrise, fresh flowers with nectar are available then onwards for visitation by butterflies. As the corolla lobes are star-shaped, they provide sufficient landing place for the butterflies to probe the flower with great ease. Since the corolla is tubular, the butterflies insert their proboscis through the throat where the stigma is over-arched by stamens during which they contact both the sex organs and effect pollination. Therefore, *C. roseus* is typically psychophilous.

Kulkarni et al. (2005) and Sreevalli et al. (2000) reported that *C. roseus* is self-compatible but intra-flower selfing does not occur normally because the stigma is receptive to pollen mainly at its base. Miyajima (2004) noted that nectar-seeking butterflies and hawk moths are required to press pollen from dehisced anthers to the basal receptive portion of the stigma for the occurrence of pollination. Albers and van der Maesen (1994) reported that in some strains of *C. roseus*, the flowers have elongated ovaries or styles that facilitate intra-flower selfing but they are in fact cross-pollinated by butterflies and moths. Nejat (2015) documented that both intra-flower pollination and cross-pollination occur in *C. roseus*. The present study suggests that *C. roseus* is self-compatible but it is both self- and cross-pollinating and pollination is effected exclusively by butterflies. Sawant (2021) noted that *C. roseus* is an important nectar plant for the butterflies *Udaspes folus*, *Papilio demoleus* and *Delias eucharis*.

In the present study, it is found that the follicled fruit of *C. roseus* is autochorous but this mode is effective mainly during dry season. Seed dispersal from dehisced follicles occurs also by wind and ants during dry season, and by water during rainy season. Sutarno and Rudjiman (1999) also reported that *C. roseus* seeds are easily dispersed by ants, wind and water. Prota (2015) reported that *C. roseus* seeds are viable for 3-5 years which enable the plant to produce new plants when soil environment is favorable. This species can also be raised vegetatively by stem cuttings (Sutarno and Rudjiman 1999). Therefore, *C. roseus* has the ability to propagate through sexual and asexual modes which enable to it to become a widespread species.

***Rauwolfia serpentina*:** It is an evergreen seasonal bloomer. The flowers are very prominent due to pedunculate and pedicellate compact cymes. The anthesis schedule indicates that the flowers are destined for pollination by day time foragers. The flowers with pink and white colors and concealed nectar attract certain bees and butterflies only. Since the corolla is tubular, the nectar is

accessible to long-tongued insects; accordingly papilionid butterflies with long proboscis visit and collect nectar successfully in a legitimate manner during which they effect self- and/or cross-pollination. The honey bees with their short tongue could collect only pollen and this pollen collection activity results in pollination accidentally. As the flowers are hermaphroditic with protogyny, spontaneous selfing is ruled out but selfing between flowers of the same plant is possible due to the presence of flowers in female and male phase simultaneously. Usmani et al. (2016) also reported that *R. serpentina* is protogynous. Wadhwa and Sihag (2012) reported that *R. serpentina* is pollinated by lepidopterans and hymenopterans out of which only *Papilio demoleus* is the best pollinator. Anoocha et al. (2020) reported that *R. serpentina* is visited by lepidopterans, coleopterans, dipterans and hymenopterans of which the butterfly *Papilio demoleus* and the bee, *Amegilla zonata* are very important pollinators. Sihag and Wadhwa (2011 and the references therein) reported that *R. serpentina* flowers represent psychophilous pollination syndrome. Therefore, these reports and the present study indicate that *R. serpentina* is typically psychophilous.

In *R. serpentina*, low fruit set is an indication that it is self-incompatible and vector-dependent for pollination. Fruit is a drupe with 1 to 4 seeds but mostly 1- or 2-seeded. The fruits are attractive to birds due to their fleshy and shiny purple-black to bluish nature. The seeds germinate only when the stony fruit part decomposes and exposes them. As the plant is highly valued in traditional as well as in modern medicine, seed propagation is the best method to raise as commercial crop (Bhadwar et al. 1956). Therefore, further studies on seed production and germination rate to raise *R. serpentina* as a cost-effective commercial crop.

5. CONCLUSIONS

Asclepias curassavica has red-orange and golden yellow varieties with similar morphological and functional characters but they show variation in size and color characters. In this species, *Dregea volubilis*, *Oxystelma esculentum*, *Brachystelma maculatum*, *Pergularia daemia*, *Tylophora indica*, *Catharanthus roseus* and *Rauwolfia serpentina*, the flowers are hermaphroditic, actinomorphic, nectariferous, self-compatible, self- and cross-pollinating. *A. curassavica* is principally melittophilous, *D. volubilis* pollinated by the diurnal hawk-moth, *Macroglossum gyrans*, *O. esculentum* by juvenile *Xylocopa* bees, *B. maculatum* by flies, *P. daemia* by *M. gyrans* and also by bees, *T. indica* by spontaneous selfing, *C. roseus* pink and white varieties by butterflies and *R. serpentina* by papilionid butterflies also by honey bees. Fruits are 1- or 2-follicled fruits with comose seeds in *A. curassavica*, *D. volubilis*, *O. esculentum*, *B. maculatum*, *P. daemia* and *T. indica*. In all these species, autochory and anemochory are functional. In *C. roseus*, fruit is follicled with non-comose seeds and autochory, anemochory and myrmecochory are functional in this species. In *R. serpentina*, fruit is a single fleshy and shiny purple-black to bluish drupe mostly with 1 seed or a pair of connate drupe mostly with 2-seeds; ornithochory is possible.

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Authors' contributions

All authors contributed equally.

Conflict of Interest

The authors declare that there are no conflicts of interests.

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Ethical approval

The ethical guidelines for plants & plant materials are followed in the study for species collection & identification.

Data and materials availability

All data associated with this study are present in the paper.

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