# Pollination ecology of *Sida acuta*, *S. cordata* and *S. cordifolia* (*Malvaceae*)

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**Abstract.** *Sida acuta, S. cordata* and *S. cordifolia (Malvaceae)* exhibit almost the same flowering phenology, floral morphology, floral biology, sexual, breeding and pollination systems, fruiting behavior, and seed dispersal. They complete vegetative and reproductive events in quick succession during rainy season and disperse seeds at the onset of dry season. Their simultaneous flowering, anthesis schedules, anther dehiscence schedules, and similar floral structural and functional characteristics attract the same bees, wasps and butterflies to their flowers. Bees use these plants as principal pollen source, while wasps and butterflies use them as a nectar source and thus contact the anthers and stigmas and pollinate the flowers. The plants display functional autogamy and allogamy, and produce the highest natural fruit set and seed set. Fruits mature quickly, split apart and disperse seeds into the air early in the dry season. The seeds are dispersed by wind, humans, animals, and rain water. *Sida* species are suitable for initial restoration of degraded, disturbed and mined habitats. As annual weeds, they have a unique role to play in plant community restoration, bloom quickly and sustain diverse insect pollinators, as well as herbivore communities.

Key words: Sida, hymenopterophily, mixed breeding system, psychophily

## Introduction

Malvaceae is a worldwide family of herbs, shrubs and small trees with major concentration of genera in the tropical regions (La Duke & Dobley 1995). This family has clearly derived as a group from the woody members of Malvales. It exhibits diversified flower ecological and reproductive differentiation pattern (Gottsberger 1972). The most primitive tree or shrub habit with allogamous reproductive system is associated with ornithophily (Gottsberger 1967, 1972; Sazima 1981). Hummingbirds probably have influenced the origin of ornithophilous flowers in this family in the neotropics (Gottsberger 1986). Parallel with this bird pollination, the staminal column might have formed by the fusion of the filaments, in order to protect the ovary (Grant 1950). This adaptive character is manifest in flowers of all recent members of this family. The position of flowers is specially designed for exploration by hummingbirds. Chiropterophily is of a more recent origin from ornithophilous ancestors within the neotropical forest regions. The woody, forest-inhabiting, probably also chiropterophilous and allogamous species, show a tendency towards an increase in height and more robust flowers with a more accentuated nectar secretion for foraging by bats (Vogel 1969). Together with the species diversification and their migration into the more open regions, pollination by bees apparently has become prominent. When compared with the ornithophilous members within a genus, the entomophilous species are often lower woody plants, occasionally still shrubby, but usually perennial or annual, and with a strong tendency towards a herbaceous habit. As another derived character, autogamy increasingly prevails, being one of the reasons for the success of many herbaceous *Malvaceae* as pantropical weeds (Gottsberger 1986).

Wroblewska (2009) reported that Alcea rosea, Malope trifida, Malva mauritiana, and M. moschata (Malvaceae) produce the biggest seed set (70–90%) in insect-pollinated flowers and the smallest seed set (3-10%) in flowers insulated from insect visitation. Kozuharova (2008) reported that honey bees do not use Astragalus dasyanthus (Fabaceae) and Haberlea rhodopensis (Gesneriaceae) as foraging sources, because they visit other plants in their vicinity due to missmatch between the flower morphology of plants and tongue lengths of the honeybees. These two species have been shown to be bumblebee flowers and, accordingly, bumblebees pollinate them. Bogacheva-Milkoteva & al. (2013) reported that H. rhodopensis is self-compatible, but not autogamous. Phenology, herkogamy and weak protandry favour outcrossing in natural populations. Successful pollination is characterized by high seed production.

Ashman & Stanton (1991) reported that Sidalcea oregano ssp. spicata is a gynodioecious species pollinated by oligolectic bees, bumblebees, bee-flies, and skippers. Klips (1999) reported that *Hibiscus moscheu*tos and Hibiscus laevis are self-compatible perennial shrubs and are incompatible with each other in mating due to the pollen competition barrier. Machado & Sazima (2008) reported that in Melochia tomentosa the flowers are bimorphic, distylous, self-incompatible and principally pollinated by bees, followed by butterflies and hummingbirds. Li & al. (2012) documented that Alcea rosea is self-compatible, exhibits delayed selfing and produces seed in the absence of pollinators. Pechon & al. (2013) mentioned that Trochetia granulata, an endemic to the Mascarenes Island in Indian Ocean, is self-compatible and obligately dependent on pollen vectors for fruit set. The pollinators include honey bees, white eyes and geckos. Its allied species, T. blackburniana, is mainly pollinated by the Mauritian day gecko in Mauritius. Suvarna Raju & Solomon Raju (2013) stated that Malachra capitata is self-compatible and pollinated by bees and butterflies. Dawar & al. (1996) reported that natural hybridization takes place between S. ovata and S. tiagii. These authors showed supporting evidence for the data on morphology, phenolic chemistry, cytology, and pollen and seed fertility. Dawar & al. (1994) mentioned that S. ovata, S. tiagii and their hybrids are facultative autogamous and hybridization between the two species takes place in natural populations through the Cuckoo Wasp, Chrysis species. However, hybridization is limited due to

the scarcity and limitation of the pollinators and also due to some genetic barriers in both species. Furthermore, low pollen fertility and meiotic irregularities have been attributed to the reduction in fruit and seed set in hybrids. Harms (1965) reported that the annual and ruderal species S. spinosa is self-compatible, autogamous and also outcrossing; these modes of breeding allow efficient to rapid colonization of newly-opened and disturbed habitats. Yorkston and Daehler (2006) reported that S. fallax occurs as two genetically distinct forms, a beach ecotype which grows as a prostrate shrub with small, pubescent leaves, and a mountain ecotype, which grows as an erect shrub with larger, nearly glabrous leaves. The experimental crosses between these two ecotypes carried out by these authors produced fertile hybrids. The beach ecotype had a higher flowering frequency under drought conditions in comparison with the hybrids and the mountain ecotype. In the field, lower water availability in the beach environment appears to be against hybrids, reinforcing differentiation between beach and mountain ecosystems. Furthermore, human land use has reduced intermediate habitats, decreasing opportunities for natural hybridization. Arora (2014) noted that Sida acuta is a weedy species with pantropical distribution. It is a small herbaceous plant with yellow flowers and five sepals, five petals, numerous stamens, and branched stigma. The pollen grains are colporate and almost half the size of pollen of Hibiscus rosa-sinensis. McMullen (1985) stated that Xylocopa darwini is the major pollinator of Sida acuta, S. spinosa and S. rhombifolia. Sivaram (2001) noted that S. acuta, S. cordata and S. cordifolia are simultaneously pollen and nectar sources for honey bees. The present study is aimed at providing information on plant phenology, floral biology, pollination, pollinators, and fruiting phenology of three Sida species: S. acuta, S. cordata and S. cordifolia. The information will help understand their sexual reproduction and the reasons for their invasiveness.

## Material and methods

Sida acuta, S. cordata and S. cordifolia (Malvaceae), which grow seasonally in Visakhapatnam (17°42'N longitude and 82°18'E latitude), Andhra Pradesh, India, were selected for study during 2012–2014. S. acuta is an erect annual weedy herb which grows up to 60 cm in different soils of open habitats. The stem is upright, hairy and strong. The leaves are borne on short, hairy stalks, they are ovate and dentate. The flowers are solitary, borne in axillary or terminal position, small (9 mm long and 10 mm wide), cup-like, yellow, bisexual, and actinomorphic. The sepals and petals are five each; the latter fuse with the staminal tube at the base. The staminal column is tomentose and contains 30 stamens at the top and each bears a reniform, monothecous extrorse anther. The ovary is commonly 5-locular, occasionally 6-locular, each locule with a single ovule arranged on axile placentation; the styles are five or six, each terminated with a capitate stigma. S. cordata is a semi-erect annual weedy herb which grows up to 80 cm on different soils of open habitats. The leaves are cordate, with long petioles attached to slender trailing branches. The flowers are solitary, borne in axillary or terminal position, small (7-8 mm long and 10 mm wide), cup-like, dark-yellow, bisexual and actinomorphic. The sepals (hairy) and petals are five each; the latter fuse with the staminal tube at the base. The staminal column is tomentose and contains 24 stamens at the top and each bears a reniform, monothecous extrorse anther. The ovary is commonly 5-locular, each locule with a single ovule arranged on axile placentation; the styles are five, each terminated with a capitate stigma. S. cordifolia is an erect annual weedy herb or under-shrub which grows up to 1.5 meters high in open, dry, gravelly, and sandy soils. The stem is stout, hairy and strong. The leaves are heart-shaped, serrated and truncate. The flowers are solitary, borne in axillary position, small (10 mm long), cup-like, yellow, bisexual and actinomorphic. The sepals and petals are five each; the latter fuse with the staminal tube at the base. The staminal column is tomentose and contains 32 stamens at the top, and each bears a reniform, monothecous extrorse anther. The ovary is 10-locular, each locule with a single ovule arranged on axile placentation; the styles are ten, each terminated with a capitate stigma.

Twenty-five marked mature buds on five plants were used to record the anthesis schedule and anther dehiscence. Twenty undehisced anthers from ten plants were used to determine the pollen output. Each time a single anther was taken and placed on a clean microscope slide ( $75 \times 25$  mm) and dabbed with a needle in a drop of lactophenol-aniline blue. The pollen mass was drawn into a band and the total number of pollen grains was counted under a compound microscope ( $40 \times$  objective,  $10 \times$  eye piece). On the basis of these counts, the mean number of pollen produced per anther was determined. The mean pollen output per anther was multiplied by the number of anthers in the flower for obtaining the mean number of pollen grains per flower. Twenty-five dehisced anthers were examined under microscope to record the pollen grain features. The protocols described in Mondal & al. (2009) were used to identify amino acid types present in the pollen. The protocol described in Sadasivam & Manickam (1997) was followed for the extraction of protein from the pollen samples and Lowry & al. (1951) method was followed for estimating the protein content in the sample. The pollen-ovule ratio was determined by dividing the average of the number of pollen grains per flower by the exact number or average number of ovules per flower. The value thus obtained was taken as pollen-ovule ratio (Cruden 1977). Ten flowers each from five plants were used to test stigma receptivity. It was tested with hydrogen peroxide as described in Dafni & al. (2005). Furthermore, receptivity was also observed visually, whether the stigma is shiny, wet or changing colors and withering.

The insect species were observed visually and by using binoculars. The hourly foraging visits of each insect species on each plant species were recorded on four occasions and the data was tabulated for further analysis. For each species, approximately a patch of five hundred flowers was selected to record the foraging visits of insects. The data obtained was used to calculate the percentage of foraging visits of each category of insects per day, in order to understand the relative importance of each category of insects. The insects were observed on a number of occasions on each plant species for their foraging behavior, such as mode of approach, landing, probing behavior, the type of forage collected, contact with essential organs, and inter-plant foraging activity. The hourly forage collection activity of each forager species was also recorded to understand whether any relationship exists between standing crop of nectar or pollen and flower visiting activity. A beetle, Mylabris phalerata, was the flower feeder on Sida acuta and S. cordifolia. Two hundred and thirty-five flowers of S. acuta and one hundred and twenty-five flowers of S. cordifolia collected at random were used to calculate the percentage of flower predation.

Sixty flowers on fifteen plants of each species were bagged without manual pollination to record fruit and seed set rates in autonomous selfing. Two hundred flowers on twenty plants of each species were tagged prior to anthesis and followed for two weeks to record fruit and seed set rates. The resulting fruit and seed output were pooled up for calculating fruit and seed set rates for each species. Fruit maturation period and fruit and seed characteristics were recorded. The role of wind, rain water and humans in fruit and seed dispersal was examined for the studied plant species. The fallen seeds in the vicinity and away from the mother plants were followed for seed germination and establishment. The seeds of all three Sida species began to germinate after monsoon showers in June. Fifty seedlings were followed for each species to observe their growth, development and establishment. Quantitative study was not made to note seed germination and seed establishment rate.

## Results

### Sida acuta Burm.f.

**Plant phenology and flower morphology**: The plant appears following first rains in June, forms a thick blanket with numerous individuals richly covering the ground and disappears in January/February. The concurrently growing plants include *Sida cordata*, *S. cordifolia (Malvaceae), Triumfetta rhomboidea (Tiliaceae), Merremia tridentata (Convolvulaceae), Tribulus terrestris (Zygophyllaceae), Justicia procumbens (Acanthaceae), Borreria hispida (Rubiaceae), Antigonon leptopus (Polygonaceae), Pedalium murex (Pedaliaceae), Tridax procumbens*, and Vernonia cinerea (Asteraceae). The flowering is during August-December.

**Floral biology**: The flowers open during the period 08:00–09:00 h. The cup-like corolla exposes the stigma and stamens following anthesis. The stamens are protandrous and anther dehiscence occurs during mature bud stage by transverse slits at the top. The pollen output per anther is  $255 \pm 16$  and per flower is 7650. The pollen-ovule ratio is 1530:1. This indicates facultative autogamy and obligate autogamy (Cruden 1977 – 168.5 ± 22.1 for facultative autogamy and 27.7 ± 3.1 for obligate autogamy). The pollen grains are monads, yellow, spheroidal, sticky, tricolporate, and 83 µm in diameter, with spiny exine. The stigma attains receptivity after anthesis and remains receptive for two hours only; then onwards it shows signs of withering. Nectar is produced in trac-

es and is collected at the base of corolla tube. The pollen contains six essential amino acids and eight nonessential amino acids. The essential amino acids are threonine, valine, methionine, isoleucine, lysine, and phenylalanine. The non-essential amino acids include alanine, aspartic acid, cysteine, cystine, glutamic acid, hydroxyproline, proline, and serine. The total protein content per 1 mg of pollen is 217.65µg.

The flowers facilitate the occurrence of delayed autonomous selfing by the curling of styles that enables the stigmas touch the anthers, and also by the bending of stamens upward late in flowers causing the anthers to collide with the stigmas. In autonomous pollination, fruit set is 63 % and seed set is 61 % (Table 4). The flowers close back within three hours and the petals and sex organs fall off on the morning of the next day. Furthermore, on rainy days, the rain drops falling on the flowers splash the dehisced anthers and in effect the pollen flies off and deposits on the stigmas, due to which self-pollination occurs.

 Table 4. Fruit and seed set rates in autonomous selfing and open pollinations in Sida species.

Breeding system	No. of	No. of	Fruit	Seed
Plant species	flowers bagged/ tagged	flowers set fruit	set (%)	set (%)
Sida acuta				
Autonomous selfing	60	38	63	61
Open pollination	200	192	96	85
Sida cordata				
Autonomous selfing	60	49	82	73
Open pollination	200	200	100	91
Sida cordifolia				
Autonomous selfing	60	43	72	68
Open pollination	200	195	98	87

Flower visitors and pollination: The flowers were visited regularly during forenoon period from 08:00 to 11:00 h by bees for both pollen and nectar, and by wasps and butterflies for only nectar (Table 1; Figs 1-3). The bees were *Apis dorsata, A. cerana, A. florae,* and *Trigona iridipennis* (Apidae). The wasps were *Scolia quadripustulata* (Scoliidae) and one unidentified species. The butterflies included members of *Pierid, Nymphalid, Lycaenid,* and *Hesperiid* families. The pierids were *Catopsilia pomona, C. pyranthe, Eurema hecabe,* and *Anaphaeis aurota.* The nymphalids were *Acraea violae, Phalanta phalantha, Junonia lemonias,* and *Danaus chrysippus.* The lycaenids were *Pseudozizeeria maha, Zizina otis, Chilades pandava,* and *Jamides celeno.* The hesperiid was *Borbo cinnara.* 

Order	Family	Genus	Species	Common name	Forage sought
Hymenoptera	Apidae	Apis	dorsata F.	Rock Honey Bee	Pollen + Nectar
	-	Apis	cerana F.	Indian Honey Bee	Pollen + Nectar
		<b>Apis</b>	florea F.	Dwarf Honey Bee	Pollen + Nectar
		Trigona	iridipennis Smith	Stingless Honey Bee	Pollen + Nectar
	Scoliidae	Scolia	quadripustulata F.	Blue Winged Wasp	Nectar
	Vespidae	Wasp (unidentified)	_	-	Nectar
Coleoptera	Meloidae	Mylabris	<i>phalerata</i> Pallas	Chinese Blister Beetle	Petals, stigmas & anthers
Lepidoptera	Pieridae	Catopsilia	pomona F.	Common Emigrant	Nectar
		Catopsilia	pyranthe L.	Mottled Emigrant	Nectar
		Eurema	hecabe L.	Common Grass Yellow	Nectar
		Anaphaeis	aurota F.	Pioneer	Nectar
	Nymphalidae	Acraea	violae F.	Tawny Coster	Nectar
		Phalanta	<i>phalantha</i> Drury	Common Leopard	Nectar
		Junonia	lemonias L.	Lemon Pansy	Nectar
		Danaus	chrysippus L.	Plain Tiger	Nectar
	Lycaenidae	Pseudozizeeria	maha Kollar	Pale Grass Yellow	Nectar
	-	Zizina	otis F.	Lesser Grass Blue	Nectar
		Chilades	pandava Horsfield	Plains Cupid	Nectar
		Jamides	celeno Cr.	Common Cerulean	Nectar
	Hesperiidae	Borbo	cinnara Wallace	Rice Swift	Nectar

Table 1. List of insect foragers on Sida acuta.

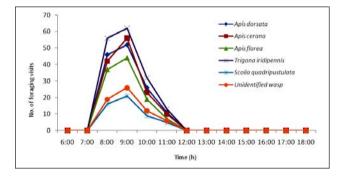
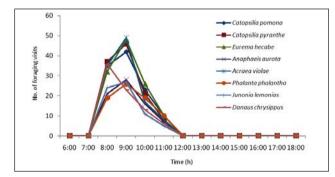
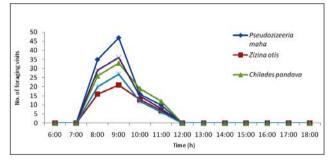


Fig. 1. Hourly foraging activity of bees on *Sida acuta* (average of foraging visits on four different days during wet season in 2012 and 2013).



**Fig. 2.** Hourly foraging activity of Pierid and Nymphalid butterflies on *Sida acuta* (average of foraging visits on four different days during wet season in 2012 and 2013).

Bees accounted for 39%, wasps for 8% and butterflies for 53% of all visits made during the forenoon period. Among the butterflies, pierids accounted for 36%, lycaenids for 30%, nymphalids for 29%, and hesperiids for 5% of all visits. All recorded insect species approached the flowers in upright position, landed on



**Fig. 3.** Hourly foraging activity of Lycaenid and Hesperiid butterflies on *Sida acuta* (average of foraging visits on four different days during wet season in 2012 and 2013).

the corolla and probed for the forage without any difficulty due to the cup-like corolla with exposed stigmas and dehisced anthers. The bees collected both floral rewards during the same visit but they mostly concentrated on pollen collection. The wasps and butterflies probed the corolla base for collecting nectar. At the study area, T. iridipennis had its nest close to Sida species and regularly collected the pollen during the period when flowers were in an open state. The pollen pots of this bee were found mixed with the pollen of Sida species. The solitary state of flowers was found to be driving these insects to hop from plant to plant across population(s) in a quest for more forage and such foraging behavior was considered important for effecting and promoting cross-pollination. The bees and wasp were coated with pollen all over during forage collection, while the proboscis and/or forehead part of the butterflies were sprinkled with pollen too. These insects invariably contacted the stamens and

stigmas, while probing and collecting the forage and this contact was considered to be effecting pollination.

**Flower predation**: The beetle *Mylabris phalerata* fed on the flowers, especially the petals, stigmas and anthers. Flower predation rate was 43%; the flowers were partly or fully consumed by this beetle. Such flowers subsequently withered and fell off without producing fruit.

Fruiting ecology and seed dispersal: The fruit growth and development begins immediately after pollination and fertilization. The calyx turns into persistent fruiting calyx. The fruits mature within 10 days and show colour shifts from green to dark-brown towards maturity. In open pollinations, fruit set is 96 % and seed set is 85% (Table 4). The fruits are small, hard, 4-5 mm long, 5-6 mm wide and normally produce five or six seeds. The mature fruits split apart loculicidally into five or six segments and dehisce dry seeds into the air during January/February. The seeds are wedge-shaped, brown to black, smooth, obovoid with three angles, 2 mm long and topped with two sharp awns. The fallen seeds remain in the soil, germinate and produce new plants during the wet season. Since the seeds are minute, they disperse effectively during the dry season by wind and during the wet season by rain water. Furthermore, they also disseminate by attaching to the fur or wool of animals and to the clothes of human beings. As the plant is a short-lived annual, it reproduces exclusively by seed.

### Sida cordata (Burm.f.) Borss.

Plant phenology and flower morphology: The plant appears following the first rains in June, forms a thick blanket with numerous individuals richly covering the ground and disappears in January/February. In areas where soil is saturated with water, it shows growth, flowering and fruiting throughout the year. The concurrently growing plants along with this weed include: Sida acuta, S. cordifolia (Malvaceae), Triumfetta rhomboidea (Tiliaceae), Merremia tridentata (Convolvulaceae), Tribulus terrestris (Zygophyllaceae), Justicia procumbens (Acanthaceae), Borreria hispida (Rubiaceae), Antigonon leptopus (Polygonaceae), Pedalium murex (Pedaliaceae), Cleome viscosa, C. gynandra (Capparaceae), Tridax procumbens, and Vernonia cinerea (Asteraceae). Seasonally, the plant flowers during August-December.

**Floral biology**: The flowers open during 08:00–09:00 h period. The cup-like corolla exposes the stig-

ma and stamens following anthesis. The stamens are protandrous and anther dehiscence occurs during mature bud stage by transverse slits at the top. The pollen output per anther is  $61 \pm 3$  and per flower is 1464. The pollen-ovule ratio is 293:1 indicating facultative autogamy and obligate autogamy (Cruden 1977 – 168.5  $\pm$ 22.1 for facultative autogamy and 27.7  $\pm$  3.1 for obligate autogamy). The pollen grains are monads, yellow, spheroidal, semi-wet, tri-colporate, and 75 µm in diameter, with spiny exine. The stigma attains receptivity after anthesis and remains receptive for two hours only; then onwards it shows signs of withering. Nectar is produced in traces and is collected at the base of corolla tube. The pollen contains six essential amino acids and eight non-essential amino acids. The essential amino acids are threonine, valine, methionine, isoleucine, lysine, and phenylalanine. The non-essential amino acids include alanine, aspartic acid, cysteine, cystine, glutamic acid, hydroxyproline, proline, and serine. The total protein content per 1 mg of pollen is 217.65µg.

The flowers facilitate the occurrence of delayed autonomous selfing by the curling of styles that enables the stigmas touch the anthers and also by the bending of stamens upward late in flowers causing the anthers to collide with the stigmas. In autonomous selfing, fruit set is 82 % and seed set is 73 % (Table 4). The flowers close back within 2–3 hours and the petals and sex organs fall off on the morning of the next day. Furthermore, on rainy days, the rain drops falling on the flowers splash the dehisced anthers and in effect the pollen flies off and deposits on the stigmas, due to which self-pollination occurs.

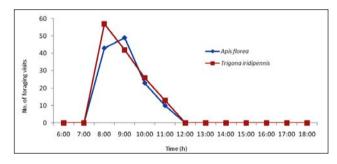
Flower visitors and pollination: The flowers were visited regularly during the forenoon period from 08:00 to 11:00 h by bees for both pollen and nectar, and by butterflies for only nectar (Table 2; Figs 4-6. The bees were Apis florea and Trigona iridipennis (Apidae). The butterflies included members of Pierid, Nymphalid, Lycaenid and Hesperiid families. The pierids were Catopsilia pomona, C. pyranthe and Eurema hecabe. The nymphalids were Acraea violae, Hypolimnas misippus, and Danaus chrysippus. The lycaenids were Leptotes plinius, Zizula hylax, Zizeeria karasandra, Chilades pandava, and Jamides bochus. The hesperiid was Borbo cinnara. Bees accounted for 57% and butterflies for 43% of all visits made during the forenoon period. Among butterflies, lycaenids accounted for 36%, nymphalids for 29%, pierids for

Table 2. List of insect foragers on Sida cordata.

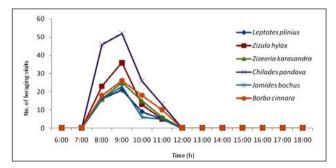
Order	Family	Genus	Species	Common name	Forage sought
Hymenoptera	Apidae	Apis	florea F.	Dwarf Honey Bee	Pollen + Nectar
		Trigona	iridipennis Smith	Stingless Honey Bee	Pollen + Nectar
Lepidoptera	Pieridae	Catopsilia	pomona F.	Common Emigrant	Nectar
		Catopsilia	pyranthe L.	Mottled Emigrant	Nectar
		Eurema	hecabe L.	Common Grass Yellow	Nectar
	Nymphalidae	Acraea	violae F.	Tawny Coster	Nectar
		Hypolimnas	misippus L.	Danaid Egg fly	Nectar
		Danaus	chrysippus L.	Plain Tiger	Nectar
	Lycaenidae	Leptotes	plinius F.	Zebra Blue	Nectar
		Zizula	hylax F.	Tiny Grass Blue	Nectar
		Zizeeria	karasandra Moore	Dark Grass Blue	Nectar
		Chilades	pandava Horsfield	Plains Cupid	Nectar
		Jamides	bochus Cr.	Dark Cerulean	Nectar
	Hesperiidae	Borbo	cinnara Wallace	Rice Swift	Nectar

28%, and hesperiids for 7% of all visits. All insects approached the flowers in upright position, landed on the corolla and probed for the forage without any difficulty due to the cup-like corolla with exposed stigmas and dehisced anthers. The bees collected both floral rewards during the same visit but mostly concentrated on pollen collection. The butterflies probed the corolla base for collecting nectar. At the study area, T. iridipennis had its nest close to the Sida species and regularly collected pollen during the period when the flowers were in an open state. The pollen pots of this bee were found mixed with the pollen of Sida species. The solitary state of flowers was found to be driving both bees and butterflies to hop from plant to plant across population(s) of S. cordata in a quest for more forage and such foraging behavior was considered important for effecting and promoting cross-pollination. The bees were coated with pollen all over during forage collection, while the proboscis and/or forehead of butterflies were sprinkled with pollen too. These insects invariably contacted the stamens and stigmas, while probing and collecting the forage and this contact was considered to be effecting pollination.

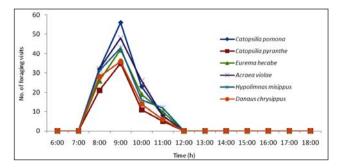
**Fruiting ecology and seed dispersal**: The fruit growth and development begins immediately after pollination and fertilization. The calyx turns into persistent fruiting calyx. The fruits mature within seven days and show colour shifts from green to dark-brown towards maturity. In open pollinations, the fruit set is 100% and the seed set is 91% (Table 4). The fruits are small, hard, 4 mm long, 5 mm wide and produce five seeds. The pericarp of certain fruits was found with the attachment of pupae of an unidentified insect and such fruits subsequently became defective. A sample of 100 fruits showed that 23% were defective due to



**Fig. 4.** Hourly foraging activity of bees on *Sida cordata* (average of foraging visits on four different days during wet season in 2012 and 2013).



**Fig. 5.** Hourly foraging activity of Lycaenid and Hesperiid butterflies on *Sida cordata* (average of foraging visits on four different days during wet season in 2012 and 2013).



**Fig. 6.** Hourly foraging activity of Pierid and Nymphalid butterflies on *Sida cordata* (average of foraging visits on four different days during wet season in 2012 and 2013).

this pupal attachment. The larvae of that insect prior to pupal formation were considered to have fed on the seed content of the fruit. The mature fruits split apart loculicidally into five segments and dehisce dry seeds into the air during January/February. The seeds are wedge-shaped, brown to black, smooth, obovoid with three angles, 2 mm long and topped with two sharp awns. The fallen seeds remain in the soil, germinate and produce new plants during the monsoon or wet season. Since the seeds are minute, they disperse effectively during the dry season by wind and during the wet season by rain water. Furthermore, they also disseminate by attaching to the fur or wool of animals and to the clothes of human beings. As the plant is a short-lived annual, it reproduces exclusively by seed.

### Sida cordifolia L.

**Plant phenology and flower morphology**: The plant appears in June, carpets the soil with numerous individuals and disappears in January/February. The concurrently growing plants include: *Sida acuta*, *S. cordata* (*Malvaceae*), *Triumfetta rhomboidea* (*Tiliaceae*), *Merremia tridentata* (*Convolvulaceae*), *Tribulus terrestris* (*Zygophyllaceae*), *Justica procumbens* (*Acanthaceae*), *Borreria hispida* (*Rubiaceae*), *Tridax procumbens*, and *Vernonia cinerea* (*Asteraceae*). It flowers during August-December.

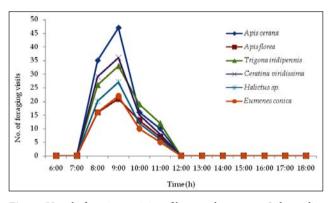
Floral biology: The flowers open during the 08:00-09:00 h period. The cup-like corolla exposes the stigma and stamens following anthesis. The stamens are protandrous and anther dehiscence occurs during mature bud stage by transverse slits at the top. The pollen output per anther is  $83 \pm 9$  and per flower is 2656. The pollen-ovule ratio is 266:1 indicating facultative autogamy and obligate autogamy (Cruden 1977 –  $168.5 \pm 22.1$  for facultative autogamy and  $27.7 \pm 3.1$  for obligate autogamy). The pollen grains are monads, yellow, spheroidal, sticky, tri-colporate, and 83 µm in diameter with spiny exine. The stigma attains receptivity after anthesis and remains receptive for two hours only; then onwards it shows signs of withering. Nectar is produced in traces and is collected at the base of corolla tube. The pollen contains six essential amino acids and eight nonessential amino acids. The essential amino acids are threonine, valine, methionine, isoleucine, lysine, and phenylalanine. The non-essential amino acids include alanine, aspartic acid, cysteine, cystine, glutamic acid, hydroxyproline, proline, and serine. The total protein content per 1 mg of pollen is 210.85µg.

The flowers facilitate the occurrence of delayed autonomous selfing by the curling of styles that enables the stigmas touch the anthers and also by the bending of stamens upward late in flowers causing the anthers to collide with the stigmas. In autonomous selfing, the fruit set is 72% and the seed set is 68% (Table 4). The flowers close back within 2–3 hours and the petals and sex organs fall off on the morning of the next day. Furthermore, on rainy days, the rain drops falling on the flowers splash the dehisced anthers and in effect the pollen flies off and deposits on the stigmas, due to which self-pollination occurs.

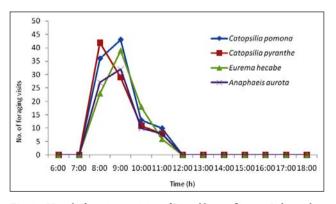
Flower visitors and pollination: The flowers were visited regularly during the forenoon period from 08:00 to 11:00 h by bees for both pollen and nectar, and by wasps and butterflies for only nectar (Table 3; Figs 7-10). The bees were Apis cerana, A. florea, Trigona iridipennis, Ceratina viridissima (Apidae), and Halictus sp. (Halictidae). The wasp was Eumenes conica (Eumenidae). The butterflies included members of Pierid, Nymphalid, Lycaenid and Hesperiid families. The pierids were Catopsilia pomona, C. pyranthe, Eurema hecabe, and Anaphaeis aurota. The nymphalids were Acraea violae, Junonia lemonias, Hypolimnas misippus, Tirumala limniace, Danaus chrysippus, and Euploea core. The lycaenids were Leptotes plinius, Everes lacturnus and Chilades pandava. The hesperiid was Borbo cinnara. Bees accounted for 26%, wasps for 3% and butterflies for 71% of all visits during the forenoon period. Of all bee visits, honey bees of both Apis and Trigona genera made most of the visits, followed by other bees. Of the butterflies, nymphalids accounted for 42%, pierids for 32%, lycaenids for 22%, and hesperiids for 4% of all visits. All insects approached the flowers in upright position, landed on the corolla and probed for the forage without any difficulty due to the cup-like corolla with exposed stigmas and dehisced anthers. The bees collected both floral rewards during the same visit but mostly concentrated on pollen collection. The wasp and butterflies probed the corolla base for collecting nectar. At the study area, T. iridipennis had its nest close to the Sida species and regularly collected pollen during the period when flowers were in an open state. The pollen pots of this bee were found mixed with the pollen of Sida species. The solitary state of flowers was found to be driving these insects to hop from plant to plant across population(s) of S. cordifolia in a quest for more forage and such foraging behavior was considered important

#### Table 3. List of insect foragers on Sida cordifolia.

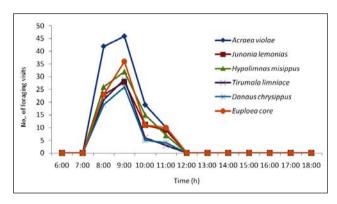
Order	Family	Genus	Species	Common name	Forage sought
Hymenoptera	Apidae	Apis	cerana F.	Indian Honey Bee	Pollen + Nectar
		Apis	florea F.	Dwarf Honey Bee	Pollen + Nectar
		Trigona	iridipennis Smith	Stingless Honey Bee	Pollen + Nectar
		Ceratina	<i>viridissima</i> D.T	Small Blue Carpenter Bee	Pollen + Nectar
	Halictidae	Halictus sp.	_	-	Pollen + Nectar
	Eumenidae	Eumenes	<i>conica</i> F.	Potter Wasp	Nectar
Coleoptera	Meloidae	Mylabris	<i>phalerata</i> Pallas	Chinese Blister Beetle	Petals, stigmas & anthers
Lepidoptera	Pieridae	Catopsilia	pomona F.	Common Emigrant	Nectar
		Catopsilia	pyranthe L.	Mottled Emigrant	Nectar
		Eurema	hecabe L.	Common Grass Yellow	Nectar
		Anaphaeis	aurota F.	Pioneer	Nectar
	Nymphalidae	Acraea	violae F.	Tawny Coster	Nectar
		Junonia	lemonias L.	Lemon Pansy	Nectar
		Hypolimnas	misippus L.	Danaid Egg Fly	Nectar
		Tirumala	limniace Cr.	Blue Tiger	Nectar
		Danaus	chrysippus L.	Plain Tiger	Nectar
		Euploea	core Cr.	Common Indian Crow	Nectar
	Lycaenidae	Leptotes	<i>plinius</i> F.	Zebra Blue	Nectar
		Everes	lacturnus Godart	Indian Cupid	Nectar
		Chilades	pandava Horsfield	Plains Cupid	Nectar
	Hesperiidae	Borbo	cinnara Wallace	Rice Swift	Nectar



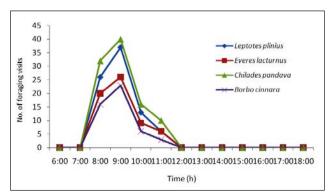
**Fig. 7.** Hourly foraging activity of bees and wasps on *Sida cordio-folia* (average of foraging visits on four different days during wet season in 2012 and 2013).



**Fig. 8.** Hourly foraging activity of Pierid butterflies on *Sida cordio-folia* (average of foraging visits on four different days during wet season in 2012 and 2013).



**Fig. 9.** Hourly foraging activity of Nymphalid butterflies on *Sida cordiofolia* (average of foraging visits on four different days during wet season in 2012 and 2013).



**Fig. 10.** Hourly foraging activity of Lycaenid and Hesperiid butterflies on *Sida cordiofolia* (average of foraging visits on four different days during wet season in 2012 and 2013).

for effecting and promoting cross-pollination. The bees and the wasp were either coated with pollen all over during forage collection, while the proboscis and/or forehead of the butterflies were sprinkled with pollen too. These insects invariably contacted the stamens and stigmas, while probing and collecting the forage and this contact was considered their contribution to pollination, wether self- or cross-pollination.

**Flower predation**: The beetle *Mylabris phalerata* fed on the flowers, especially the petals, stigmas and anthers. Flower predation rate was 37.5%; the flowers were partly or fully consumed by this beetle. Such flowers subsequently withered and fell off without producing fruit.

Fruiting ecology and seed dispersal: The fruit growth and development begins immediately after pollination and fertilization. The calyx turns into persistent fruiting calyx. The fruits mature within a week and show colour shifts from green to darkbrown towards maturity. They are small, hard, 4 mm long, 6-8 mm wide and normally produce 10 seeds. In open pollinations, the fruit set is 98% and the seed set is 87% (Table 4). The mature fruits split apart into 10 segments and dehisce dry seeds into the air during January/February. The seeds are wedge-shaped, brown to black, smooth, obovoid with three angles, 2 mm long and topped with two sharp awns. The fallen seeds remain in the soil, germinate and produce new plants during monsoon or wet season. Since the seeds are minute, they disperse effectively during dry season by wind and during wet season by rain water. Furthermore, they also disseminate by attaching to the fur of animals and to the clothes of human beings. As the plant is a short-lived annual, it reproduces exclusively by seed.

## Discussion

The three *Sida* species exhibit almost the same flowering phenology, floral morphology, floral biology, sexual, breeding and pollination systems, fruiting behavior and seed dispersal. They complete their vegetative and reproductive events in quick succession during rainy season and disperse seeds by the onset of dry season. The plants occur in the same habitat, side by side or scattered, or in patches representing pure populations. Their simultaneous flowering, anthesis and anther dehiscence schedules, and the same floral structural and functional characteristics would attract almost the same insect species to their flowers. However, the solitary state of flowers, production of few flowers per day and per plant, production of nectar in traces, and low pollen output per flower do not keep the visiting insects for long on the same flower or plant and in effect, the flower visitors move quickly from flower to flower within and between populations of the three Sida species alternately to collect the floral rewards, due to which there is a possible occurrence of deposition of mixed pollen on all these three species. Furthermore, these species provide floral rewards for a brief period in the forenoon, after which the flowers close back and fall off the next day. Therefore, the negative effects of concurrent flowering, flower opening and anther dehiscence schedules, and nectar presentation schedules on reproductive success through biotic pollinators appear to be counteracted by the production of a few flowers with traces of nectar and low pollen productivity, in order to use the same insect species for pollination of Sida species occurring in the same habitat.

In all three Sida species, the solitary flowers stand out visually. They are cup-like, with ovary well protected by the short staminal column formed by the fusion of filaments. The staminal column and free styles resemble a shaving-brush and this entire structure springs up from the center of the flower. They are well exposed and enable the flower visitors to enter freely to collect the forage and, while collecting the forage, the visitors touch the floral sex organs due to which pollination occurs with certainty. Faegri & van der Pijl (1979) described the characteristics of melittophilous flowers. They include yellow or blue colour, pleasant odour, pollen shedding during the day, strong landing platform, nectar guides, and production of small quantities of nectar that is hidden in the basal part of the sepals. However, in all three Sida species, the flowers without perceptible smell are yellow, shed pollen during the forenoon period, provide landing platform and offer traces of nectar that is covered by thin hairs at the base of sepals. With these characteristics, the Sida species attract bees, wasps and butterflies to their flowers as soon as they are open in the morning and the foragers collect the forage with great ease for a brief period due to closure of the petals by noon. The bees use these plants as principal pollen source while wasps and butterflies use them as nectar source during which they contact the anthers and stigmas and pollinate the flowers. Since nectar is produced in traces at flower and even plant level, these insects in a quest for nectar move quickly from flower to flower within and between populations and in effect, promote crosspollination. The prominent finding in case of butterfly visits is that papilionids do not use Sida species as a nectar source. In case of hesperiids, only one species, Borbo cinnara utilizes these plants as a nectar source. Pierids, nymphalids and lycaenids are important as pollinators of these plants. Nevertheless, hymenopterans and lepidopterans are involved in the pollination and, hence, hymenopterophily and psychophily exist in the Sida species. Venkata Rao (1955) explained the process of pollination in Sida species. In these plants, the pollen grains that reach the capitate stigmas germinate quickly, produce pollen tubes in a polysiphonous manner and penetrate through the transmitting tissue of the style and enter the ovule in a porogamous manner. Subsequently, fertilization occurs.

In India, the honey bees Apis dorsata, A. cerana and A. florea are widely distributed (Batra 1997). All three species are economically and commercially important. They provide livelihood opportunities and employment for many traditional communities who live in the hilly and rural areas. Furthermore, they are important as pollinators of agricultural crops and wild plants. Traditional beekeeping is practiced with A. cerana and A. florea in most areas, but they are not as popular as the introduced European honey bee, A. mellifera. A. mellifera is more aggressive and efficient in forage collection than the other two honey bee species and, hence, it is an excellent producer of honey. In recent years, A. mellifera has become naturalized in certain areas and has replaced A. cerana and A. florea. In effect, the distribution range of the latter two honey bee species is shrinking. A. dorsata is not manageable and, hence, beekeeping with this species is ruled out. Nevertheless, Sida species with their huge population size and profuse flowering during the wet season are potential pollen and nectar sources for all these honey bees.

Rocha-Filho & Melo (2011) reported that, in the case of bees the presence of floral resources in an area is an essential condition when selecting a nest site. Rozen (1984) observed that the solitary bee, *Anthophorula sidae*, builds nests in a site covered by *Sida* species so as to use the latter as pollen and nectar sources. Solomon Raju & al. (2009) reported that the stingless bee, *Trigona iridipennis*, builds nests in plac-

es covered by the luxuriant growth of Sida acuta. This bee gathers the pollen of this plant and its pollen pots are filled with it. Also, in the present study, this bee species builds nests in places carpeted by the prolific growth of S. acuta, S. cordata and S. cordifolia. It collects pollen voraciously and loads the pollen pots with the pollen of these plants along with other yellow-coloured pollen from other plants growing in these areas. Honey bees also collect Sida pollen voraciously and deposit it in their hives. Ceratina bees, small carpenter bees, also gather pollen for use in brood development. The pollen contains the same amino acids in all three Sida species. The pollen grains are sources of six essential amino acids: threonine, valine, methionine, iso-leucine, lysine, and phenylalanine, and eight non-essential amino acids: alanine, aspartic acid, cysteine, cysteine, glutamic acid, hydroxyproline, proline, and serine. DeGroot (1953) reported that honey bees require ten essential amino acids, sixout of which are present in the pollen of these plants, plus some non-essential amino acids. The pollen also has a small amount of protein content. It is thus nutritionally important. Therefore, these bees use Sida species as important pollen sources and their pollen collecting activity, although contributing to pollination, may greatly reduce the availability of pollen for pollination purpose. In this case, the limited and fixed number of ovules per flower, and capitate stigmas with large surface area covered by short and soft hairs in these plants are presumed important in the context of pollination by insects. A few pollen grains deposited on each stigma are sufficient to fertilize a single ovule in each carpel and the hairy stigma keeps the deposited pollen grains intact, in order to enable the latter to germinate and fertilize the ovule (s).

In all three *Sida* species, such characters as protandry, self-compatibility, short period of open flowers, low energy investment for nectar and pollen production, low pollen-ovule ratio, and brief period of stigma receptivity suggest that the plant is optionally autogamous with an open option for allogamy or cross-pollination (Cruden 1977). The flowers facilitate the occurrence of delayed autonomous selfing by the curling of styles which enables the stigmas touch the anthers and also by the bending of stamens upward late in flowers causing the anthers to collide with the stigma (Lloyd & Schoen 1992). The movement of styles and anthers aimed at resulting in autogamy is further facilitated by the closure of free petals before

noon. Delayed autonomous selfing is regarded to be adaptive because it apparently assures seed production when pollinators are scarce, y& allows outcrossing to predominate, when they are abundant (Wyatt 1983). If vector-mediated outcross-pollination occurs substantially before autonomous self-pollination, outcross fertilization may predominate owing to the time advantage of the earlier deposited outcross pollen grains. In such a case, self-fertilization would be facultative, although the deposition of self-pollen occurs regardless of prior outcrossing. Alternatively, pollination per se can be facultative, if the facilitating movement of flower parts occurs only in the absence of prior vector-mediated pollination. Furthermore, rain-assisted autogamy may also occur due to the falling rain drops into the flowers on rainy days, during which the insect activity on the flowers is either negligible or totally absent (Pansarin & al. 2008); this form of autogamy is presumed important in all three Sida species due to their flowering during rainy season. Such floral behavior is a "fail-safe strategy" to assure the Sida species achieve pollination and set fruit and seed in the absence of insects. The natural fruit set and seed set rates recorded in all three Sida species also substantiate the function and success of the mixed breeding system, a character essentially required for these annual weeds for the invasion and establishment of their populations in different open habitats.

Sida species have been reported as host plants for certain beetles and butterflies. The chrysomelid beetle, Calligrapha pantherina, is folivorous and causes complete defoliation in weeds. It feeds especially on the leaves of Sida species. It is used to control S. rhombifolia, S. spinosa and S. acuta in Australia (Pacala 1986; Forno & al. 1992). Another chrysomelid beetle, Podagrica submetallica, uses S. cordifolia and S. rhombifolia as larval host plants; it feeds on the leaves, petals and pollen of open flowers of these plants in Northeastern Queensland (Hawkeswood & Jolivet 2002). The cotton mealy bug, Phenacoccus solenopsis, is polyphagous and uses a number of weeds as host plants. One such important weed is Sida acuta, which occurs on a wide range of soil types and reproduces by seeds (Vennila & al. 2013). The nymphalid butterflies such as Junonia hierta, J. orithya, J. lemonias, J. alamana, and J. iphita use S. cordifolia as larval host plants in India (Tiple & al. 2011). In the present study, a meloid beetle, Mylabris phalerata, feeds on the petals, anthers and stigmas of S. acuta and S. cordifolia and in effect, such flowers subsequently fall off; the percentage of flower predation is considerably high, it is 43 % in the former and 37.5 % in the latter species. This beetle, therefore, has negative effect on the reproductive success of these two plants. In case of *S. cordata*, an unidentified insect has been found to use its fruits for brood development. This insect appears to be feeding on the seeds during larval stage and then pupating on the surface of fruit pericarp. The fruits used by it are defective and, hence, the insect has been considered to be affecting negatively the reproductive success of the plant. Predation of flowers by the beetle and of fruits by the unidentified insect appears to be functional in the control of *Sida* species.

In Sida species, fruit and seed attributes are identical both in their morphological and functional characteristics. Fruits mature quickly, split apart and disperse seeds into the air during early part of the dry season. The seeds possess the characteristics adapted to dispersal by various means such as wind, humans, animals, and rain water. As a result, they migrate effectively to long distances during the dry season and, depending on the rain fall intensity, rain water also disseminates seeds to other places. Animal and human forms of dispersal are predominant in the tropics and have the potential to help restore plant diversity on degraded sites in a reasonable period of time, thereby helping to defray restoration costs (Joseph 1997). As soon as the rains occur during rainy season, the seeds of Sida species germinate, establish and colonize new areas. Self-compatibility favours these plants after long-distance dispersal (Cox 1989) and also the delayed autogamy is advantageous in maximizing their capacity for rapid spread onto a newly available site without precluding the ability to exchange genes with the population at large when it develops (Klips & Snow 1997).

Machado & Sazima (2008) stated that weeds serve as keystone floral resources favouring the maintenance of populations of different species of insects by providing them with pollen and nectar. Tiple & al. (2011) also stated that wild plants such as weeds are crucial for maintaining insect species, especially butterflies and, hence, it is vital to conserve the biotopes of these insects. The present study agrees with the statements made by these authors in that the *Sida* species with their luxuriant growth play a key role in maintaining the populations of bees and butterflies by providing them both with pollen and nectar. The ability of these

plants to grow on a wide range of soil types, both in polluted and non-polluted areas, is another advantage in considering them as initial stabilizers of degraded habitats and indicators of pollution levels. In fact, a study by Ogunkunle & Fatoba (2013) detailed certain modifications and adaptations in Sida acuta growing in polluted areas with, for instance, cement pollution. These authors have stated that several epidermal modifications such as increase in trichome density, high stomatal density, increased stomatal index, and reduced stomatal size are good indicators that the level of atmospheric pollutants has become hazardous for this species. These modifications are useful biological markers for the presence of cement dust pollutants in the leaves of S. acuta. These could be adaptive features for tolerating the high cement dust pollution of the area. Increased number of trichomes may aid S. acuta in filtering out particulate matter and in insulating the leaflet surface from detrimental pollutants, which otherwise may enter the leaf and disrupt metabolic activities in the plant tissues. High stomatal density in S. acuta from a cement polluted site is another adaptive response to the cement dust pollution. Therefore, further studies into the herbaceous weeds, including Sida species, are suggested, in order to use them as indicators of pollution levels in industrial or urban areas and subsequently for considering their roles in combating environmental pollution. True that Sida species are weeds and thus are risky, but they still have unappreciated roles in the restoration of degraded, damaged and polluted areas. Keeping this in mind, comprehensive studies are suggested in a holistic way on the interactions between Sida species and insects, and their roles in environment amelioration.

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