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Journal of Threatened Taxa

Building evidence for conservation globally

www.threatenedtaxa.org

ISSN 0974-7907 (Online) | ISSN 0974-7893 (Print)

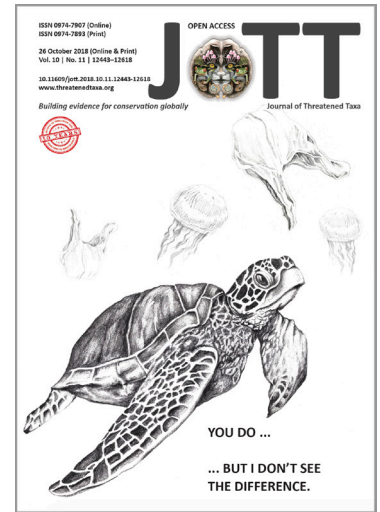
COMMUNICATION

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B. Usharani & A.J. Solomon Raju

26 October 2018 | Vol. 10 | No. 11 | Pages: 12538-12551

10.11609/jott.4008.10.11.12538-12551



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ISSN 0974-7907 (Online)
ISSN 0974-7893 (Print)



POLLINATION ECOLOGY OF *SYNEDRELLA NODIFLORA* (L.) GAERTN. (ASTERACEAE)

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Abstract: *Synedrella nodiflora* (L.) Gaertn grows almost throughout the year if the soil is damp. It produces heterogamous capitula with female ray florets anthesing on the first day and bisexual disc florets anthesing on the next three consecutive days. Disc florets are dichogamous, herkogamous, self-compatible, self-pollinating (vector-mediated) and display secondary pollen presentation through an intermediate form of brush mechanism. Ray and disc florets exhibit facultative xenogamy. Butterflies are principal pollinators while bees, wasps and flies are supplementary pollinators. Thrips *Microcephalothrips abdominalis* uses the florets as breeding and feeding sites; the feeding activity effects pollination. The ray and disc florets produce cypselas; the cypselas produced by ray florets are heavier, elliptical, membranous with upwardly-pointing teeth along the margins and two short terminal awns while those produced by disc florets are lighter, cylindrical and tangentially compressed with 2 or 3 stiff terminal divaricate awns. Seed dispersal is polychorous and represented by anemochory, anthropochory, zoochory and ombrohydrochory. Cypselas of ray florets disperse to short distances and germinate under specific germination conditions either at parental sites or in similar habitats while those of disc florets disperse farther away from parental sites and germinate readily under a wide range of conditions. Therefore, bimorphic cypselas with different germination abilities enable the plant to grow as a widespread weed but not as an invasive weed.

Keywords: Bimorphic cypselas, entomophily, polychory, secondary pollen presentation, *Synedrella nodiflora*, thripsophily.

DOI: <https://doi.org/10.11609/jott.4008.10.11.12538-12551>

Editor: Kannan C.S. Warriar, Institute of Forest Genetics and Tree Breeding, Coimbatore, India.

Date of publication: 26 October 2018 (online & print)

Manuscript details: Ms # 4008 | Received 13 January 2018 | Final received 14 September 2018 | Finally accepted 26 September 2018

Citation: Usharani, B. & A.J.S. Raju (2018). Pollination ecology of *Synedrella nodiflora* (L.) Gaertn. (Asteraceae). *Journal of Threatened Taxa* 10(11): 12538–12551; <https://doi.org/10.11609/jott.4008.10.11.12538-12551>

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Funding: Self-funded.

Competing interests: The authors declare no competing interests.

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Author Contribution: Both the authors contributed equally.

Acknowledgements: We thank the Andhra University, Visakhapatnam, for providing physical facilities to carry out this research work.



INTRODUCTION

Synedrella is a monotypic genus with only a single species, *S. nodiflora*. The generic name is derived from the Greek word “*synedros*” meaning small flowers seated together while the species name indicates the presence of flower clusters around the nodes in the upper parts of the plant (Davidse et al. 2015). It is native to tropical America and from there it has become widespread throughout the warmer regions of the world (Holm et al. 1997). It is spread throughout the Southeast Asian region, found in the plains of India, in the Andamans and West Africa. It is also found in Bangladesh, Japan, Spain, China and England (Chauhan & Johnson 2009). The plant is used as feed for livestock and in traditional medicine to treat various health problems in Ghana, Nigeria, Malaysia and Indonesia (Burkill 1985; Idu & Onyibe 2007). This plant displays floral features which are characteristic of thripsophily (Ananthakrishnan 1993). Further, it is reported that this plant with small and less attractive heterogamous heads is inhabited only by one terebrantian thrip, *Microcephalothrips abdominalis* which is able to move freely within the capitulum and also fly to other capitula of the same plant or other nearby plants. As a result, they effect both self and cross-pollination (Ananthakrishnan et al. 1981).

Kissmann & Groth (1992) reported that *Synedrella nodiflora* produces dimorphic cypselas. Rocha (1996) stated that the morphological differences between these cypselas influence dispersion strategies directly. Bradford (1990) stated that both the cypselas of *S. nodiflora* exhibit the same pattern of imbibition rates indicating no relationship to the germination rate or differences in the fruit coat permeability. Brandel (2004) reported that the germination responses between these cypselas types are not so marked because of a lack of deep innate dormancy. However, they show some differences in germination rates depending on their environment perception. The state of information available on pollination and seed ecology is insufficient to understand the pollination and propagation abilities of *S. nodiflora* as a widespread weed across tropical latitudes. In this context, the present study was contemplated to investigate the following objectives: flowering phenology, floral biology, pollination mechanism, pollinators, sexual system and seed dispersal ecology. This information presented in this paper enables us to understand the studied aspects of *S. nodiflora*.

MATERIALS AND METHODS

Populations of *Synedrella nodiflora* growing in Visakhapatnam region (17.686°N & 83.218°E) in Andhra Pradesh State, India were used for the study from 2015–2017. Observations regarding the organization of inflorescences, the spatial positioning of flowers, and their position on the plant were made since these features are regarded as important for effecting pollination by foragers. The life time of individuals of two floret types was recorded by marking twenty just open florets each and following them until fall off. Anthesis was initially recorded by observing ten marked mature capitula in the field. Later, the observations were repeated five times on different days; on each day we observed twenty marked mature capitula in order to provide an accurate anthesis schedule. Twenty mature disc florets were followed for recording the time of anther dehiscence. The presentation pattern of pollen was also investigated by recording how anthers dehisced and confirmed by observing the anthers under a 10x hand lens. The details of flower morphology such as flower sex, shape, size, colour, odour, sepals, petals, stamens and ovary were described.

Twenty mature but undehisced anthers from disc florets were collected from five randomly chosen plants and placed in a petri dish. The pollen output per anther/disc floret and pollen-ovule ratio was calculated using the protocol given by Cruden (1977). Individual volumes of nectar were recorded for 25 ray and 25 disc florets and then the average volume of nectar per each floret type was determined and expressed in μl . The capitula used for this purpose were bagged at the mature bud stage, opened after anthesis and squeezed the nectar from each floret into a micropipette to measure the volume of nectar. Based on nectar volume in individual ray and disc florets, the total volume of nectar secreted in a capitulum was calculated. Similarly, the nectar sugar concentration at the capitulum level was determined using a Hand Sugar Refractometer (Erma, Japan). Nectar analysis for sugar types was done as per the Paper Chromatography method described in Dafni et al. (2005). The sugar content/floret is expressed as the product of nectar volume and sugar concentration per unit volume, $\text{mg}/\mu\text{l}$. This was done by first noting the conversion value for the recorded sugar concentration on the refractometer scale and then by multiplying it with the volume of nectar/floret. Table 5.6 given in Dafni et al. (2005) was followed for recording the conversion value to mg of sugars present in one μl of nectar. Dinitrosalicylic acid method was followed for the first

two sugar types while Resorcinol method was followed for the last sugar type. The caloric reward of nectar/floret/day was measured as per the formula given in Heinrich (1975). He assumed that 1 mg of sugar yields 16.74 joules or 4 calories of energy and accordingly he used the formula for calculating the caloric reward of the nectar.

$$\frac{\text{Nectar volume } (\mu\text{l}) \times \text{Concentration of nectar } (\%)}{100} \times 16.74$$

Paper chromatography method described in Dafni et al. (2005) was followed for identifying the amino acid types in the nectar of ray and disc florets; the amino acid types were the same in both ray and disc florets. The flower visitors were collected and identified with the representative specimens available with the Department of Environmental Sciences, Andhra University, Visakhapatnam. All butterflies were further confirmed by consulting the books of Kunte (2007) and Gunathilagaraj et al. (1998) while other insects, some to species level while a few others to genus level only. Thrips were identified using the key provided by Bhatti (1980) for Indian thrips. The insects were observed carefully for 10 hours a day for 15 days in different months each year during the profuse flowering period. The hourly foraging visits of each species were recorded on ten different days for which thirty capitula were selected. The data obtained was used to calculate the percentage of foraging visits made by each species per day and also to calculate the percentage of foraging visits of each category of insects per day. Simultaneously, the insects were observed for their foraging behavior such as mode of approach, landing, probing behaviour, the type of forage they collected, contact with essential organs to result in pollination, and inter-plant foraging activity. The insects were captured from the capitula during 10:00–12:00 hr on five different days for pollen analysis in the laboratory. For each insect species, 10 specimens were captured and the proboscides were separated for examination to record whether they carried pollen grains or not. They were washed first in ethyl alcohol and the contents stained with aniline-blue on a glass slide and then observed under a microscope to count the number of pollen grains present.

A sample of capitula was tagged and followed for fruit set rate of ray and disc florets in open-pollinations and the same sample was used for noting the duration of fruit maturation. Seed characteristics of ray and disc florets were carefully examined to note their special adaptations for dispersal modes. Field visits were made to record whether the seeds germinate immediately

after they are dispersed or not. Field observations on seed germination and seedling formation were made to record the approximate number of generations produced during the rainy season.

RESULTS

Phenology

The plant is an erect, branched, ephemeral herb with long internodes and swollen nodes (Image 1a). The lower parts of the stems root at the nodes in damp soil conditions. The shallow tap root system is strongly branched. It grows in humid places, shaded and nutrient rich soils, crop fields, wastelands, roadsides, lawns and disturbed areas. The stems are ribbed, dichotomously branched, sub-angular, smooth to sparsely hairy. The leaves occur in opposite pairs, ovate to elliptic, finely hairy with short petioles and joined by a ridge across the stem. It propagates only by seed. Individual plants complete their life cycle within 4–5 months. The seeds germinate and produce new plants as soon as they are dispersed from the mother plants and in effect, the plants show vegetative, flowering (Image 1b) and fruiting phases simultaneously in different habitats. However, the plant shows prolific growth during the rainy season and displays peak flowering from October–November.

Flower morphology

A plant produces several capitula and their numbers vary depending upon the age, number of branches and nutrient condition of the soil. But, it produces an average of 22.6 ± 4.6 capitula. The capitula are sessile and borne either singly or as groups of 2–8 to nodes in leaf axils; they are covered by two green herbaceous involucre bracts. Each capitulum consists of odorless outer ray florets and central disc florets and each floret type is enclosed by 3–5 mm long erect bracts. Ray florets vary from 5–8 (7.3 ± 1.31) while disc florets vary from 11–15 (13.06 ± 1.50); they are produced in the ratio of 1:2. The calyx is reduced to pappus of 2–3 barbed and strong bristles in both types of florets. The corolla is tubate, zygomorphic, yellow and tipped with one ligulate lobe in ray florets and five actinomorphic lobes in disc florets. The ray floret is 8.1 ± 0.7 mm long and 2.0 ± 0.3 mm wide while disc floret is 8.2 ± 0.6 mm long and 1.2 ± 0.3 mm wide. The ray florets lack stamens but have well developed pistil with ovary and style which is terminated into two smooth stylar arms (Image 1h,i). The disc florets have four stamens with yellow filaments and dark brown anthers. The stamens are epipetalous



Image 1. *Synedrella nodiflora*

a. Habit, b. Plant in flowering phase, c. Capitulum, d. Anthesing capitulum, e–g. Different stages of anthesis in capitulum, h. Ray floret, i. Ray floret with bifid stigma, j. Disc florets, k. Disc floret with unreceptive stigma, l. Disc floret with receptive stigma, m. Syngeneisous anthers, n. Relative positions of stamens and stigma, o. Pollen grain. © A.J. Solomon Raju

and anthers are ditheous, fertile, united and cohered forming a hollow cylinder representing syngenesious condition (Image 1m). The anther has its connective prolonged into a hood and tend to separate when the flower withers. The pistil is well developed with ovary and long style which is terminated into two linear-lanceolate stylar arms covered abaxially at the base with sweeping hairs. A nectariferous disc is present at the base of the style inside the corolla tube. The style with its aligned arms extend beyond the height of anthers (Image 1j,k,n); the stylar arms diverge and curve inwards exposing the hidden stigmatic surfaces and finally over-arching the florets (Image 1l). In both floret types, the ovary is bicarpellary, syncarpous and unilocular with one anatropous ovule on basal placentation. The floral features indicate that ray florets are female and disc florets are bisexual.

Floral biology

The ray and disc florets open during early morning from 07:00-09:00 hr on clear sunny days (Image 1c–g) (Table 1). The florets open completely on sunny days while they are partially open on rainy days. In a capitulum, the ray florets open first and all of them open simultaneously; the disc florets open concentrically inwards from the next day for three successive days with 38% opening on day 1 and 31% each on day 2 and day 3 (Table 1). Individual ray and disc florets take about three hours to open from mature bud phase. The disc florets are protandrous with anther dehiscence taking place during mature bud stage by longitudinal slits. The narrow anthers are united to form a hollow space into which pollen is liberated. At the mature bud stage the style with its aligned stylar arms lies below the anthers, its forked arms are converged at this stage. During and immediately after anthesis, the style grows, elongates

Table 1. Anthesis of disc florets as a function of time in *Synedrella nodiflora*

Time (h)	No. of disc florets anthesed						Total
	Day 1	%	Day 2	%	Day 3	%	
06:00	-	-	-	-	-	-	-
07:00	2	15	1	8	1	8	31
08:00	2	15	2	15	2	15	45
09:00	1	8	1	8	1	8	24

First, all ray florets open at once on the first day of anthesis of capitulum. The next day onwards disc florets open for three consecutive days. Total No. of disc florets per capitulum 13

and passes through the anther tube brushing the pollen with its sweeping hairs. At this stage, the inner stigmatic surfaces are un-receptive and not exposed, the functional situation of which prevents the occurrence of autogamy. Such a form of pollen presentation is referred to as “secondary pollen presentation mechanism” which ensures the pollen availability to insects visiting the capitula on a daily basis. The style with its aligned branches gradually diverge in the early hours of the second day; then the inner stigmatic surfaces attain receptivity and remain so until the end of that day. The stylar arms curve downwards completely exposing the receptive stigmatic surfaces. Ray florets display stigma receptivity by diverging the stylar arms day-long on the day of anthesis only. The pollen grains are bright yellow, spheroidal, tricolporate, $35.96 \pm 0.04 \mu\text{m}$ in size and echinate. The pollen grains are 134.13 ± 21.16 per anther, 536.53 ± 84.66 per floret and $6,975$ per capitulum (Image 10). The pollen-ovule ratio is 955:1. The ray and disc florets are nectariferous. A ray or disc floret produces $1.3 \mu\text{l}$ of nectar which rises up as it accumulates in the floret due to the narrow corolla tube. The beginning of nectar secretion coincided with anthesis in ray florets and with anther dehiscence in disc florets; its secretion ceased by the evening of day 1 in ray florets while it ceased by the evening of day 2 coinciding with cessation of stigma receptivity. A capitulum produces an average volume of $22.4 \mu\text{l}$ of nectar during its lifespan; the nectar sugar concentration is $27 \pm 1.6\%$ with 0.4mg of sugar containing 1.6 calories of energy at floret level and 6.67mg sugar containing 26.68 calories of energy at capitulum level. The sugar types present in the nectar include sucrose, glucose and fructose; they are present in that order of dominance. The nectar contains five essential amino acids (arginine, histidine, lysine, tryptophan and threonine) and six non-essential amino acids (cysteine, glycine, serine, aspartic acid, glutamic acid, hydroxyproline, alanine, cystine and proline); they

are present in that order of dominance. The ray and disc florets wither away on the 3rd day and fall off on the 4th day. The tubate corolla in ray florets and the tubate corolla and stamens in disc florets gradually fall off following fertilization and initiation of fruit formation.

Pollination mechanism

The ray florets devoid of stamens act as female and they expose the stigmatic region prominently by unfolding stylar arms immediately after anthesis against the ligulate petal to receive pollen from the foragers on par with disc florets. The disc florets present the stamens and stylar arms at different positions. The anthers dehisce inwardly and discharge pollen grains into the anther tube during mature bud stage. At this stage, the style lies below the basal part of the anthers. During and immediately after anthesis, the style with its aligned stylar arms elongates within the anther tube and brushes the pollen out of the anther tube by stylar hairs called “sweeping hairs” presenting the pollen only on the abaxial surface at the base of stylar arms (sterile portions). Such a pollen presentation pattern is indicative of secondary pollen presentation functional through an intermediate mechanism representative of brush mechanism. The stylar arms are in closed state on day 1 and the inside stigmatic surfaces are un-receptive, there is no possibility for the occurrence of autogamy. The staminate phase ends at 1700 h and the sterile portion of the stylar arms has residual pollen at that time. This is followed by the retraction of filaments and the consequent partial retraction of anthers into the corolla tube. The pistillate phase starts in the early hours of the second day, the stigmatic surfaces attain receptivity, gradually diverge and curve downwards within three hours totally exposing the inner stigmatic surfaces; the stigmatic surfaces remain receptive until the end of that day. The brush type pollen presentation mechanism, staminate phase on day 1 and pistillate phase on day 2 appear to have evolved to prevent autogamy and promote cross-pollination. However, the anthesis of disc florets for three consecutive days in the same and different capitula on the same plant facilitates the occurrence of vector-mediated self-pollination. Therefore, the secondary pollen presentation mechanism and the sexual system function do not insulate completely from the occurrence of self-pollination and hence the flowers set fruit and seed through self- as well as cross-pollination.

Thrips breeding, feeding and pollination

Thrips species, *Microcephalothrips abdominalis*



Image 2. *Synedrella nodiflora*

a. *Trigona iridipennis* collecting nectar, b. *Trigona iridipennis* collecting pollen, c. *Xylocopa latipes* collecting nectar, d. *Ceratina* sp. collecting nectar, e. *Ceratina smaragdula* collecting nectar, f. *Nomia* sp. collecting nectar, g. *Lasioglossum* sp. collecting nectar, h. *Rhynchium* sp. collecting nectar, i. *Ammophila* sp. collecting nectar, j. *Sarcophaga* sp. collecting nectar, k. *Eristalinus* sp. collecting nectar. © A.J. Solomon Raju.

Table 2. List of insect foragers on *Synedrella nodiflora*

Order	Family	Genus	Species	Common name	Forage sought	
Hymenoptera	Apidae	<i>Trigona</i>	<i>iridipennis</i> Smith	Stingless Honey Bee	Pollen + Nectar	
		<i>Ceratina</i>	sp.	Small Carpenter Bee	Pollen + Nectar	
		<i>Ceratina</i>	<i>smaragdula</i> F.	Small Carpenter Bee	Pollen + Nectar	
	Anthophoridae	<i>Xylocopa</i>	<i>latipes</i> L.	Large Carpenter Bee	Nectar	
	Halictidae	<i>Nomia</i>	sp.	Alkali Bee	Pollen + Nectar	
		<i>Lasioglossum</i>	sp.	Sweat Bee	Pollen + Nectar	
	Vespidae	<i>Rhynchium</i>	sp.	Black Potter Wasp	Nectar	
	Sphecidae	<i>Ammophila</i>	sp.	Digger Wasp	Nectar	
	Diptera	Sarcophagidae	<i>Sarcophaga</i>	sp.	Flesh Fly	Nectar
		Syrphidae	<i>Eristalinus</i>	sp.	Hover Fly	Nectar
Lepidoptera		Pieridae	<i>Eurema</i>	<i>hecabe</i> L.	Common Grass Yellow	Nectar
	<i>Leptosia</i>		<i>nina</i> F.	Psyche	Nectar	
	Lycaenidae	<i>Zizula</i>	<i>hylax</i> F.	Tiny Grass Blue	Nectar	
		<i>Pseudozizeeria</i>	<i>maha</i> Kollar	Pale Grass Blue	Nectar	
		<i>Zizeeria</i>	<i>karsandra</i> Moore	Dark Grass Blue	Nectar	
		<i>Everes</i>	<i>lacturnus</i> Godart	Indian Cupid	Nectar	
		Hesperiidae	<i>Pelopidas</i>	<i>mathias</i> F.	Small Branded Swift	Nectar

(Thysanoptera: Thripidae) oviposited during early bud stage of florets of capitula. The larvae emerge from the eggs in synchrony with anthesis and nectar production in both ray and disc florets. The centripetal development of the capitulum was found to provide continuous availability of pollen and nectar for three days for their growth. The thrips were found feeding on pollen and

nectar, especially from disc florets. They were dusted with pollen in their upward and downward movements within the corolla tube of disc florets. The echinate pollen surface facilitated the thrips to carry 180 to 345 pollen grains on their body setae, wings and legs. The thrips dispersed the pollen on the stigmatic region of the stylar arms of both ray and disc florets due to their active

movements, rubbing the abdomen on the stigmatic surface, cleansing of their body parts with their hind legs and also by their wing combing mechanism. Since the disc floret is staminate on day 1 and pistillate on day 2, the foraging activity of thrips within that floret does not contribute to self-pollination but may contribute to self-pollination between disc florets of the same or different capitula of the same plant. Further, self-pollination may also take place in ray florets due to deposition of pollen of disc florets of the same capitulum by thrips. As the plant occurs as small or large populations, thrips could fly to migrate to the capitula of other closely spaced plants and effect cross-pollination.

Insect foraging activity

The capitulum is the unit of attraction for insect foragers. Within the capitulum, the yellow ligulate petal of ray florets acts as chief attractant. The ray and disc florets were foraged by bees, wasps, flies and butterflies. The butterflies were the consistent and regular foragers while all others were inconsistent foragers and also they forage especially during the peak flowering season. The bees were *Trigona iridipennis* (Image 2a,b), *Ceratina* sp. (Image 2d), *Ceratina smaragdula* (Image 2e), *Xylocopa latipes* (Image 2c), *Nomia* sp. (Image 2f) and *Lasioglossum* sp. (Image 2g). The wasps were *Rhynchium* sp. (Image 2h) and *Ammophila* sp. (Image 2i). The flies were *Sarcophaga* sp. (Image 2j) and *Eristalinus* sp. (Image 2k). The butterflies included *Eurema hecabe* (Image 3a), *Leptosia nina* (Image 3b) (Pieridae), *Zizula hylax* (Image 3c), *Pseudozizeeria maha* (Image 3d), *Zizeeria karsandra*, *Everes lacturnus* (Image 3e) (Lycaenidae) and *Pelopidas mathias* (Image 3f) (Hesperiidae) (Table 2). Of these, all bees except *Xylocopa* sp. foraged for both pollen and nectar while *Xylocopa* sp. and all other foragers foraged for nectar only. All these insects approached the flowers in upright position, landed on the flat-topped capitulum and then probed ray and disc florets for nectar. They foraged several florets in a single visit and made multiple visits to several capitula on the same plant in quest of forage. They made frequent visits to capitula of different closely and distantly spaced plants to collect forage. Such a foraging behavior was considered to be promoting both self- and cross-pollination. The foraging activity pattern of insects showed a definite pattern with reference to foraging schedule. They foraged flowers during 08:00-16:00/17:00 hr with peak foraging during 10:00-12:00 hr (bees, wasps and flies) and during 10:00-11:00 hr (butterflies) coinciding well with the standing crop of nectar by that time (Figs. 1,2). Bees made 42%, wasps 13%, flies 11% and butterflies 34% of total foraging

visits (Fig. 3). The body washings of insects collected from the flowers during peak foraging period revealed that all insects carry pollen but bees carry the highest number of pollen grains. Further, the mean number of pollen grains varied with each insect species (Table 3).

Fruiting ecology and seed dispersal

The fertilized disc florets produce single-seeded cypselas within two weeks. Natural cypselas set is 86% in ray florets and 98% in disc florets (Table 4). In ray florets, the cypselas is 3–5 mm long, 2.5–3.1 mm wide, pale brown, oval, tangentially flattened with upwardly-pointing teeth along the marginal wing and 2 short terminal awns (Image 3g). In disc florets, the cypselas is 4–5 mm long, 1.8–2.5 mm wide, cylindrical, thickened, 4-sided and tangentially compressed with 2 or rarely 3 terminal stiff divaricate awns (Image 3h). The cypselas of disc florets detach earlier than those produced from ray florets. The stiff echinate structures of cypselas of both types of florets enable them to stick readily to hair, fur, clothing and animal skin for dispersal; the cypselas of disc florets being light in weight disperse easily to long distances than those of ray florets which are comparably heavy. Wind dispersed the cypselas efficiently when ambient air is dry. Water also acted as an efficient dispersal agent for the dispersal of cypselas during the

Table 3. Pollen recorded in the body washings of insect foragers on *Synedrella nodiflora*

Insect species	Sample size (N)	Number of pollen grains		
		Range	Mean	S.D
<i>Trigona iridipennis</i>	10	56-134	106.7	21.08
<i>Ceratina</i> sp.	10	25-56	37.6	8.54
<i>Ceratina smaragdula</i>	10	21-63	48.5	11.78
<i>Xylocopa latipes</i>	10	17-50	29.8	9.47
<i>Nomia</i> sp.	10	20-53	35.7	10.13
<i>Lasioglossum</i> sp.	10	15-49	34.4	8.79
<i>Rhynchium</i> sp.	10	11-42	28.2	8.31
<i>Ammophila</i> sp.	10	8-25	15.9	5.27
<i>Sarcophaga</i> sp.	10	10-31	20.5	6.00
<i>Eristalinus</i> sp.	10	11-26	18.4	4.08
<i>Eurema hecabe</i>	10	21-54	37.9	8.64
<i>Leptosia nina</i>	10	8-27	20.2	5.61
<i>Zizula hylax</i>	10	5-24	21.7	6.86
<i>Pseudozizeeria maha</i>	10	11-28	21.5	4.60
<i>Zizeeria karsandra</i>	10	9-36	26.4	7.47
<i>Everes lacturnus</i>	10	10-32	23.2	5.97
<i>Pelopidas mathias</i>	10	7-24	15.7	4.37

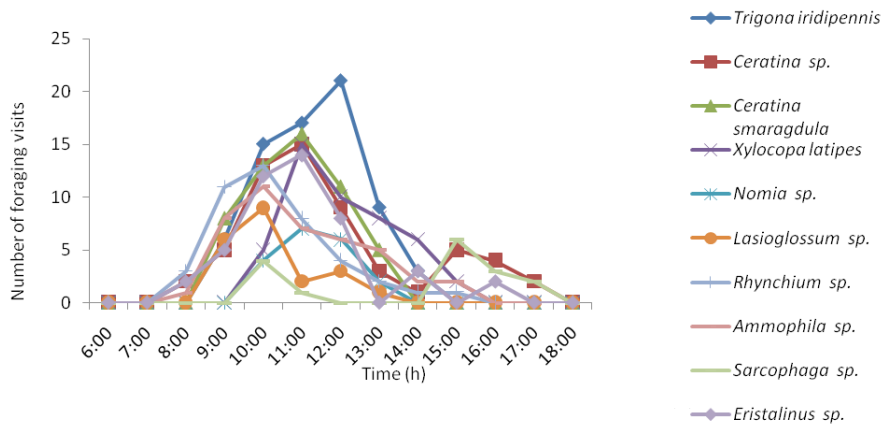


Figure 1. Hourly foraging activity of bees, wasps and flies on *Synedrella nodiflora*

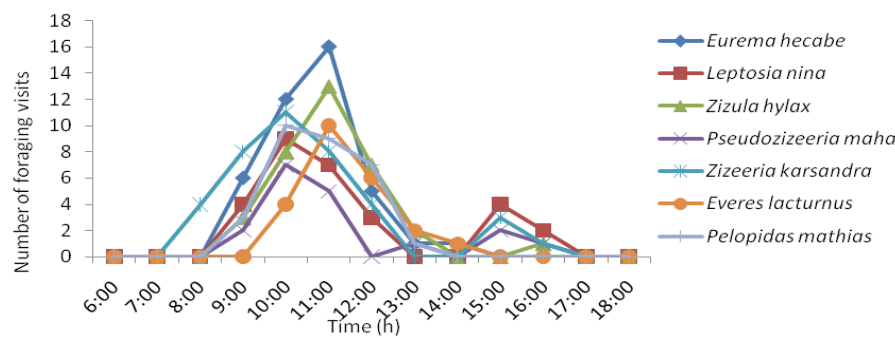


Figure 2. Hourly foraging activity of butterflies on *Synedrella nodiflora*

Table 4. Natural cypsela set in *Synedrella nodiflora*

Ray florets			Disc florets		
No. of florets sampled	No. of florets set cypsela	Cypsela set (%)	No. of florets sampled	No. of florets set cypsela	Cypsela set (%)
98*	84	86	258**	253	98

*Sample size: 14; **Sample size: 20

rainy season. Therefore, zoochory, anthropochory, anemochory and ombrohydrochory are the functional forms of seed dispersal in this plant.

The cypselas of both ray and disc florets are viable and germinate within a week after their dispersal from the parental plants if the soil is damp and fertile (Image 3i). Cypselas of both floret types sowed in different pots filled with fertile soil produced seedlings within a week; germination rate is 60% in ray floret cypselas and 80% in disc floret cypselas. The seedlings have epigeal germination. The hypocotyl is 10–18 mm long, purplish and hairless. The cotyledons are elliptic, 5–9 mm long, purplish and shortly stalked. The paired juvenile leaves are similar to adult leaves but smaller. After two weeks, they were transplanted to natural soil and followed for their life cycle, which is nearly four months. The

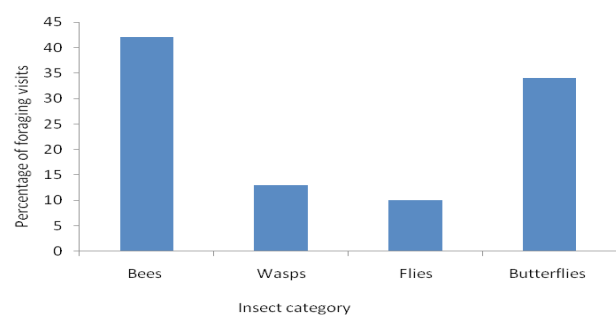


Figure 3. Percentage of foraging visits of different categories of insects on *Synedrella nodiflora*

observations indicated that both types of cypselas produce identical individuals and produce both types of cypselas.



Image 3. *Synedrella nodiflora*

a & b. Pierids - a. *Eurema hecabe*, b. *Leptosis nina*, c-e. Lycaenids ; c. *Zizula hylax*, d. *Pseudozizeeria maha*, e. *Everes lacturnus*, f. Hesperiid, *Pelopidas mathias*, g. Ray floret seeds, h. Disc floret seeds, i. Emergence of seedlings during rainy season. © A.J. Solomon Raju.

DISCUSSION

Synedrella nodiflora is a herbaceous weed and grows in soils with sufficient moisture for its rapid germination, growth, flowering and seed set. It grows in a very wide range of habitats and tolerates most forms of cultivation because of its short life cycle (Holm et al. 1997). As an exotic species, it is widely distributed in both natural habitats and cultivated fields in India (Ansari et al. 2016). It is one of the widespread weeds endangering the native flora (Singh et al. 2002) and causing a menace in cultivated fields due to its invasiveness (Singh et al. 2010). Despite this situation created by this weed, there are no studies on this species as to how it is able to grow and invade varied habitats. The present study shows that *S. nodiflora* is a therophyte and produces new sets of populations continuously in damp soils of forest and

agricultural systems. As a result, it displays vegetative, flowering and fruiting phases simultaneously in different habitats throughout the year. But, the rainy season is the best period for its prolific growth in any habitat because the soil is damp and contains nutrients due to decomposition of organic matter at this time. Peak flowering occurs during October-November in different populations. Therefore, it can be said that soil moisture and nutrient content greatly influence the growth and population size of this weed in different habitats.

Jeffrey (2009) stated that Asteraceae members produce capitula consisting of peripherally located ray florets and centrally located disc florets. The ray florets are highly specialized in pollinator attraction while disc florets assume the reproductive function and hence improve the chances for reproductive success and facilitate a more flexible basis for breeding system

evolution than does a single flower. Further, this author stated that a particularly diverse trait in the capitulum is the perianth symmetry exhibited by peripheral ray and central disc florets; the ray florets display zygomorphic symmetry while disc florets display actinomorphic symmetry. The present study shows that *S. nodiflora* uses nectar-less ray florets for pollinator attraction and reproductive function, and nectariferous disc florets exclusively for reproductive function. The position of several florets in a capitulum as a unit enables the plant to maximize reproductive success. Torices et al. (2011) stated that the expression of floral sexuality is associated with changes in symmetry, which has important consequences for the evolution of reproductive biology in Asteraceae. This generalization is absolutely true in *S. nodiflora* because the peripheral zygomorphic ray florets are female while the actinomorphic disc florets are bisexual. Chapman & Abbott (2009) reported that the presence of peripheral ray florets shows a marked effect on attractiveness to pollinators, cross-pollination rate and fitness for the plant. In *S. nodiflora*, the highest fruit set recorded in both ray and disc florets indicate that ray florets attract pollinator fauna and enhance both self and cross-pollination rate in both types of florets enabling the plant to increase fitness as an invasive weed.

Allen et al. (2011) reported that dichogamous protandry and self-incompatibility are functional in Asteraceae; self-incompatibility occurs at the stigmatic surface either by failure of germination of self-pollen grains or by the arrest of pollen tube growth. Harder et al. (2000) noted that dichogamous protandry reduces rates of self-fertilization and enhances out-crossing. Nettancourt (2001) stated that self-incompatibility is another evolutionary strategy to avoid self-fertilization and inbreeding. The present study shows that *S. nodiflora* is dichogamous, protandrous, self-compatible and self-pollinating. But, disc florets have a mechanism to prevent spontaneous self-pollination but not vector-mediated self-pollination. In disc florets, the staminate phase on day 1 and pistillate phase on day 2 characterize temporal dioecy. These florets are also herkogamous as they have a physical barrier between the site of pollen deposition and stigmatic region; herkogamy favors xenogamy, and pollination occurs during pistillate phase. The occurrence of self-pollination, however, is possible due to the centripetal opening of florets in the capitulum on consecutive days. In this study, fruit set standing at 86% in ray florets and 98% in disc florets in open-pollinations indicate the function of self-compatibility and self-pollination in this plant. The pollen/ovule ratio recorded for *S. nodiflora* (955:1) in

this study falls in the range of pollen/ovule ratio (244.7–2,588) for facultative xenogamy provided by Cruden (1977) and hence this plant has facultative xenogamous breeding system with low self-incompatibility. In this breeding system, xenogamy enables plants to increase genetic heterogeneity which favors their establishment in heterogeneous and variable environment (Hsu 2006) while geitonogamy facilitates to increase their population in the currently growing sites or other sites with similar environment. Therefore, the widespread and invasive character of *S. nodiflora* could be attributable to low self-incompatibility and facultative xenogamy.

Floret opening in the morning is a common feature among the Asteraceae (Proctor & Yeo 1978), and it usually occurs before 08:00hr (Mani & Saravanan 1999). In *S. nodiflora* also, anthesis of both ray and disc florets occurs in the morning from 07:00–0900 hr. Within a capitulum, ray florets open first exposing simultaneously the white ligulate petal and the receptive stigmatic region by unfolding the stylar arms to receive pollen from other capitula of the same or different plants. These florets cease stigma receptivity by the end of the same day and become non-functional to receive pollen from the next day onwards. The disc florets open concentrically on three consecutive days but each floret shows staminate and pistillate phases on two consecutive days to avoid spontaneous autogamy and minimize geitonogamy. In Asteraceae, secondary pollen presentation mechanism is an important characteristic associated with protandry (Howell et al. 1993) but it is an ancestral feature in this family (Jeffrey 2009). This pollen presentation mechanism has been considered to be a strategy to improve accuracy in pollen removal and deposition in order to enhance male and female fitness (Ladd 1994). In the present study, the disc florets of *S. nodiflora* display this form of pollen presentation. In these florets, the pollen shed from the anthers is brushed by the sterile sweeping hairs present at the base of the abaxial side of stylar arms when the style branches are joined and inner stigmatic surfaces are not receptive. This pollen presentation mechanism is an intermediate mechanism representative of brush mechanism *sensu* Leins & Erbar (2006). As the style grows out of the anther tube, the outer sweeping hairs of the style arms present pollen for pollination. The receptive papillate stigmatic surface is hidden between the two appressed style arms, preventing self pollination. During the functionally female phase of the floret which occurs on day 2, the style arms separate exposing the receptive papillae for the receipt of pollen. The style arms serve as secondary pollen presenters in the staminate phase and expose

receptive stigmatic surfaces for pollen during pistillate phase. This type of active pollen presentation is typical of disc florets of Asteraceae (Ladd 1994). The secondary pollen presentation system functional in *S. nodiflora* appears to have evolved to enhance the efficiency and accuracy of pollen exportation and/or pollen reception, thus increasing male and/or female fitness of the plant (Yeo 1993).

Varatharajan & Daniel (1984) reported that thrips have an intimate association with the capitula of Asteraceae. Laughlin (1977) reported that in Asteraceae, the duration of growth and development of thrips synchronizes well with the centripetal disc floral development whereby thrips, which are mostly pollen feeders, efficiently use the capitulum for their growth and survival. Kirk (1997) noted that thrips puncture the pollen coat and drain the grains; individual thrips consume more than 800 pollen grains per day. Abrol (2012) noted that thrips carry pollen ranging from 129–180 pollen grains but the pollen loads carried vary with the larvae and adults with the latter carrying an increased load due to greater surface area such as wing fringes, abdominal setae, as well as the antenna. Grimaldi & Engel (2005) stated that the higher the pollen production the greater the level of pollen carrying capacity. Ananthakrishnan (1982) reported that the pollen carrying capacity could also depend upon the pollen surface and architecture. Pollen grains attached to the body setae, wings and legs of thrips are dispersed on the stigma by way of their active movement, rubbing the abdomen on the stigmatic surface, cleansing of their body parts with their hind legs and also by their wing-combing mechanism. Kirk (1997) reported that thrips use the stigma for landing and take-off. During this process, thrips place the pollen directly on the stigma. The impressive petal colour and corolla tube of a small flower form is an ideal site to attract thrips for oviposition, enabling the emerging larvae to become dusted with pollen in their upward and downward movement eventually leading to pollination. Ananthakrishnan et al. (1981) reported that heterogamous capitula of Asteraceae facilitate free movement of both larvae and adults in between the individual florets, and adults carry a maximum pollen load on the body. In the present study, *Microcephalothrips abdominalis* is the only thrips species which uses *S. nodiflora* capitula for its breeding. The larvae emerge in synchrony with the timing of anthesis of capitulum which occurs for four consecutive days. The larvae and adults move freely up and down within and between ray and disc florets in search of pollen and nectar; the larvae carry less pollen while the adults carry more pollen because of variation in the surface area of

the body. Further, they use stylar arms for take-off and landing during which the stigmatic area is dusted with pollen. The feeding activities of larvae and adult thrips within the capitulum contribute to self-pollination. As there is a continuous emergence of thrips in synchrony with sequential anthesis within the capitulum, the available forage becomes insufficient to meet their food requirement and in effect they migrate to other capitula on the same plant or nearby plants in search of forage due to which, chances of cross-pollination are enhanced. Ananthakrishnan et al. (1981) stated that the thrips living in the heterogamous capitula of Asteraceae with solitary inflorescences spend more energy for their visits to other flowers where the food is plenty. In *S. nodiflora*, the solitary as well as grouped capitula borne in leaf axils enable thrips to optimize energy expenditure to visit and acquire more energy from the forage they collect from different capitula within the plant. Such an interaction between *S. nodiflora* and *M. abdominalis* benefits both partners, the former in pollination and the latter in breeding and feeding.

In *S. nodiflora*, the peripheral nectar-less yellow ray florets attract foragers. In ray florets, the stylar arms with exposed receptive stigmatic region standing above the tubular portion of the corolla is an adaptation for easy pollen deposition and pollination by the foragers which visit the disc florets for pollen and/or nectar. In the central yellow disc florets, the narrow tubular corolla containing nectar, pollen accessibility to foragers within and outside the corolla tube, and pollen characteristics such as spheroidal shape, tri-colporate apertures and echinate exine are adaptations for insect-pollination. Wodehouse (1935) stated that the echinate trait of the pollen grains is a special adaptation for adherence to insect vectors. Therefore, the characteristics of both ray and disc florets suggest that this plant is adapted for insect-pollination.

Faegri & Pijl (1979) described the floral characters of butterfly-pollination. They usually possess large, white, pink, red, yellow or blue, narrow, tubular flowers with deep nectaries and nectar guides. Baker & Baker (1982; 1983) categorized two categories of flowers with reference to flower-butterfly relationships. The first category is “true butterfly flowers” which are characterized by deep, narrow corolla tubes with relatively copious sucrose-rich nectar. The second category is “bee and butterfly flowers” which are characterized by short-tubed corolla with hexose-rich nectar. In *S. nodiflora*, the nectar of disc florets is sucrose-rich with moderate sugar concentration and sugar content, and has some essential and non-essential

amino acids. These characteristics of disc florets conform to “true butterfly pollination syndrome”. The tubular corolla of ray florets lacking nectar and stamens and having functional pistil indicates that it is adapted for butterfly-pollination by deception.

In the present study, butterflies are the consistent and regular foragers throughout the year for *S. nodiflora*. The capitula attract butterflies belonging to pieridae, lycaenidae and hesperiidae but lycaenids are the principal pollinators. It is interesting to note that papilionid butterflies never visited the capitula. The small, narrow tubate ray and disc florets aggregated into capitula are appropriate for pollination by butterflies which efficiently handle several florets to collect nectar successfully in a single visit. In such an act, their proboscis gains contact with the dehisced anthers situated inside the corolla tube and also with the pollen adhered to sweeping hairs during staminate phase in disc florets. The proboscis is the carrier of pollen and the number of pollen grains carried by them vary with the length of proboscis and the time of nectar collection. In pistillate phase of disc florets, the butterflies with their proboscis contact the exposed stigmatic regions and in effect transfer and deposit pollen at this region effecting pollination. Further, the butterflies with pollen-laden proboscis pollinate the ray florets while probing their tubular corolla lacking nectar. In both disc and ray florets, self-pollination occurs due to simultaneous occurrence of staminate and pistillate phases in different disc florets, and only pistillate phase in ray florets at capitula and plant level. The standing crop of nectar at plant or population level is commensurate with the requirement of the butterflies as sufficient volume of nectar is available at capitulum level. The butterflies frequent the capitula of the same and/or different closely or distantly spaced individuals and promote cross-pollination. Their foraging schedule and the peak foraging activity period coincide well with the availability levels of standing crop of nectar. The consistent foraging activity of butterflies on this plant suggests that they use this plant as an important nectar source. Therefore, *S. nodiflora* is principally psychophilous.

In the present study, it is found that bees, wasps and flies also use the disc florets of *S. nodiflora* as pollen and/or nectar sources, especially during peak flowering season. The foraging behavior of the bees indicated that they are successful mostly as pollen collectors due to a slight mismatch between the length of their tongue and the length of the corolla tube to collect the deeply seated nectar. In case of wasps and flies, their proboscis length easily facilitates nectar collection from the disc florets.

All these insects also probe the ray florets for nectar without any discrimination although there is no nectar; their visits to ray florets result in pollination. All these insects carry pollen on their body, transfer and effect self- and cross-pollination. Since they show foraging activity mainly during the peak flowering period, they serve as supplementary pollinators. Nectar feeding by the larvae and adults of *M. abdominalis* leads to reduced levels of nectar and make all nectar feeding insect species to increase foraging activity across populations to meet their nectar requirement and in effect, both self- and cross-pollination rates are enhanced.

Different authors reported that *Synedrella nodiflora* produces two types of fruits (Banerji & Pal 1959; Kissmann & Groth 1992; Rocha 1996). The present study also found that *S. nodiflora* produces two types of cypselas within a capitulum. The cypselas produced from ray florets are heavier, elliptical, membranous with upwardly-pointing teeth along the margins and two short terminal awns while those from disc florets are lighter, cylindrical and tangentially compressed with 2 or 3 stiff terminal divaricate awns. Chauhan & Johnson (2009) stated that the heavier cypselas produced from ray florets could be related to the inclusion of additional carbohydrate resources by the plant to help in the plant emergence while Brandel (2007) attributed the presence of superior mass in the cypselas produced from ray florets to the pericarp wing which is developed as an alternative structure for dispersion. The present study shows that the differences in morphological features of these two types of cypselas favour spatial dispersion having different strategies which promote spreading in various sites. In a capitulum, the cypselas of disc florets detach first and disperse to farther sites while those of ray florets disperse later in the vicinity of mother plants. The morphological features such as marginal and terminal teeth in ray floret cypselas and terminal teeth in disc floret cypselas enable them to be dispersed by animals and humans. Further, wind during dry season and water during rainy season also disperse them farther away. Therefore, the morphological features of cypselas of *S. nodiflora* are adapted for dispersal by multiple vectors, the situation of which is referred to as “polychory” involving zoochory, anthropochory, anemochory and ombrohydrochory.

The present study shows that the cypselas of both ray and disc florets of *S. nodiflora* are viable and germinate within a week after their dispersal from the mother plants and produce new plants. This situation indicates that both types of cypselas do not have dormancy. Similarly, Bradford (1990) reported

that both cypselas types in this plant do not have any difference in the fruit coat permeability and hence germination responses between them are almost the same; both cypselas types germinate immediately after dispersal. On the contrary, Brandel (2004) reported some differences in germination rates of the two cypselas types in *S. nodiflora* and related these differences to the ability of cypselas to environment perception. Turner (1994) also reported that fresh cypselas of both types of florets germinate quickly in a wide range of conditions. The buried cypselas to 10cm depth in soil remain viable for one year. Chauhan & Johnson (2009) reported that in *S. nodiflora*, the cypselas germinate immediately but ray floret cypselas if buried in soil would remain dormant for several months and germinate when favourable conditions exist. The present study indicates that heterocarpy in *S. nodiflora* is a mixed strategy in which disc floret cypselas successfully germinate under different conditions in time and space and ray floret cypselas germinate in restricted environment, usually near mother plants or the same habitats. The ability of disc floret cypselas offers the chance to colonize new sites, free from sibling competition or other local sources of stress, whereas the remainder of the offspring stays in the same habitat (Imbert & Ronce 2001). Interestingly, both types of cypselas produce identical plants and also produce bimorphic cypselas within the capitulum during flowering period suggesting that they are genotypically identical but different only by morphology which is configured by environmental situations. The study suggests that *S. nodiflora* with bimorphic cypselas and the associated traits is able to grow as a widespread weed in different habitats and expand its distribution range. This plant is considered to be a menace in agro-ecosystems. But it is an important food source for bees, wasps, flies and butterflies. Therefore, it may be an important component of agro-ecosystems because it plays a significant role in sustaining communities of insects that contribute to crop growth. Nevertheless, the information detailed here on the reproductive system of this weed is important to plan a management control schedule.

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ISSN 0974-7907 (Online); ISSN 0974-7893 (Print)

October 2018 | Vol. 10 | No. 11 | Pages: 12443–12618

Date of Publication: 26 October 2018 (Online & Print)

DOI: 10.11609/jott.2018.10.11.12443-12618

www.threatenedtaxa.org

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