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RESEARCH ARTICLE

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Pump mechanism, secondary pollen presentation, psychophily and anemochory in *Emilia sonchifolia* (L.) DC. (*Asteraceae*)

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ABSTRACT

Emilia sonchifolia flowers profusely during August-November. The plant produces capitulum inflorescence with only disc florets presenting nectar and pollen as rewards. It is temporally dioecious with strong protandry which prevents autonomous autogamy, minimizes geitonogamy and maximizes xenogamy. The florets exhibit secondary pollen presentation using pump mechanism. The florets produce minute amount of sucrose-rich nectar, and essential and non-essential amino acids. The floral characters typify psychophily but other insects also pollinate the florets. Thrips use this plant as breeding and feeding sites; they largely contribute to geitonogamy. The high natural fruit and seed set rates recorded indicate that geitonogamy and xenogamy are functional but both modes are essentially vector-mediated. The function of dual modes of breeding suggests that the plant is self-compatible, self- as well as cross-pollinating. The fruit is typically an achene and is anemochorous. Seeds germinate only during rainy season and produce new plants within a short time to reproduce sexually. The study suggests that this plant grows in open well drained areas, important as a pioneer species and hence is useful for the restoration of ecologically degraded, damaged and deteriorated habitats.

Key words: *Emilia sonchifolia*, secondary pollen presentation, pump mechanism, psychophily, anemochory

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Introduction

Emilia is an economically important plant genus in the *Asteraceae*. It comprises of about 100 species distributed in the tropical and sub-tropical regions of the world, with the greatest species diversity in East Africa. The plants are herbaceous, annual, biennial, and perennial with much variation in floral features (Fosberg, 1972; Nordenstam, 2007). The genus Emilia is represented in Nigeria and West Africa by three species, *E. coccinea*, *E. sonchifolia* and *E. praetermissa*. It is distributed in India and Ceylon but there were no studies on the distribution of the genus in general and *E. sonchifolia* in particular (Thenmozhi et al., 2013; Kumar et al., 2015). The genus can also be found in different parts of the world. The species of this genus are edible and useful for medicinal purposes (Adedeji ,2005). Koster (1980) reported that *E. sonchifolia* is a common weed with pantropical distribution. Its origin is unknown but it occurs wild throughout the Old World, including South-East Asia. In America, it has been introduced and became naturalized in course of time. It is used as a vegetable in the whole of South-East Asia. The young, non-flowering plants are eaten raw or steamed as a side dish with rice. The older leaves or plants are cooked. The plant has many medicinal applications. It is administered internally against fever, coughs and diarrhoea as well as externally as a poultice for sores and wellings, drop for dim eyes and sore ears. In Java and Puerto Rico, the young leaves are used as a vegetable (Uphof, 1968; Martin & Ruberte, 1978). In India, it is valuable in ethno-medicine to treat diarrhoea, night blindness and sore throat, rashes, measles, inflammatory diseases, eye and ear ailments, fever, stomach tumor, malaria, asthma, liver disease, eye inflammation, earache and chest pain. The fresh stems and leaves are eaten as a salad or cooked as vegetable. In Kerala State of India, it is considered to be one among the "Ten Sacred Flowers" collectively known as "Dasapushpam" which are predominately used by the traditional healers in treating cancer and other malignant conditions. In China, the leaves are used for the treatment of dysentery, roundworm infestations, wounds and influenza, burns and snake bites. The Africans consume the leaves as a vegetable for its laxative property. The plant has been documented in the Nigerian folk medicine for the treatment of epilepsy in infants. In Malaysia, the plant is one of the popular ingredients of traditional vegetable salads "Ulam". The plant is sold in local markets as an edible wild vegetable. The flowers are fried with butter while the leaves are eaten raw.

The leaves are edible and used as a traditional salad in Bangladesh (Duke & Ayensu, 1985; Thenmozhi et al., 2013; Kumar et al., 2015). Despite its wide economic and medicinal importance, this plant species has not been investigated for its reproductive biology to understand its pollination mechanism, pollinators, breeding system, seed dispersal and how it is able to propagate sexually to survive in different habitats. Further, there is almost no information on the reproductive biology of all other species of Emilia. Keeping this in view, the present study was contemplated to investigate the floral structural and functional morphology, pollination mechanism, pollinators, sexual system and seed dispersal in *Emilia sonchifolia* (L.) DC. The results recorded have been explained in the light of relevant literature and also evaluated its importance as pioneer species in degraded, damaged and deteriorated habitats.

Materials and Methods

Emilia sonchifolia growing in open wild areas of Visakhapatnam region, Andhra Pradesh, India (Latitude 17°42'N and Longitude 82°18'E, 45 m elevation) was used for the present study. Ten inflorescences which have not initiated flowering were tagged and followed daily to record the number of florets produced and the flowering duration. Twenty five fresh florets were used to record the floret type, sex, shape, colour, odour, symmetry, and other characters. Ten tagged inflorescences were followed to note the timing of anthesis and anther dehiscence. The presence of nectar was determined by gently pulling a floret from its calyx and firmly pressing its base against a hard surface. The micropipette was inserted into the floret base to extract nectar for measurement. The average of nectar of all open florets of ten inflorescences was taken as the total volume of nectar/floret and expressed in µl. Paper Chromatography methods described in Dafni et al. (2005) were used for nectar analysis to record the sugar types and amino acid types present. Pollen output per anther and floret was determined using the method described by Cruden (1977). Pollen grain characters were also recorded simultaneously. H2O2 test described in Dafni et al. (2005) was used to record the timing and duration of stigma receptivity. Further, the stigma physical state was also observed throughout floret life to confirm the duration of stigma receptivity. The foragers visiting the flowers were observed from morning to evening on ten different days during peak flowering phase to list of insect species. Their foraging activities were recorded for 10 min at each hour for the entire day on four different days and the data was tabulated to evaluate the activity pattern of individual species throughout the day and to calculate the percentage of foraging visits made by each category insects per day to evaluate their importance as pollinators. During the same period, their foraging behaviour such as mode of approach, landing, probing behaviour, contact with essential organs to result in pollination and inter-plant foraging activity were observed. Ten individuals of each insect species were captured while collecting pollen and/or nectar on the florets during their peak foraging activity period. They were brought to the laboratory, washed in ethyl alcohol, stained with aniline-blue on a glass slide and observed under microscope to count the number of pollen grains present and evaluate their relative pollen carryover efficiency and pollination role. Six hundred sixty one fruited florets from different inflorescences were collected to calculate the fruit and seed set rates. Seeds were found to be of two types - unfilled or half-filled and completely filled. Using this as a criterion, filled seed set was calculated. Filled seeds were designated as viable ones while the unfilled or half-filled ones as in-viable ones. Twenty inflorescences on ten plants were tagged and followed to note the duration of fruit maturation. Seed characteristics were noted to evaluate their mode of dispersal. Field visits were made to record whether the seeds germinate immediately after they are dispersed or not.

Results

Phenology

The plant is an annual straggling herb that grows primarily in sunny or slightly shaded moist cultivated and undisturbed localities (Figure 1a).

Figure 1. *Emilia sonchifolia: a. Habit, b. Flowering capitula, c. Individual plant with capitula.*

It often branches from the very base, usually purplish-green and deep rooting. The stem is slender, striate, 2-3mm in diameter, smooth or nearly so. The leaves are sessile, with alternate arrangement, dark green above and lighter green or tinged with purple beneath. They are thick, lower ones crowded, lyrate-pinnatifid; terminal lobes are large, broadly ovate-triangular with irregularly dentate margins while lateral lobes usually paired, oblong-lanceolate, both surfaces crisped-hairy. The plant appears during June/July with the onset of rainy season and disappears with the onset of winter season but it extends its growth, flowering and fruiting almost throughout the year if the soil adequately wet. Irrespective of the soil moisture status, the plant shows peak flowering during August-November. Each plant produces 15 ± 8 pendulous pedunculate flat-topped capitula terminally (Figure 1c). A capitulum is 9.5 ± 1.3 mm long, 3.2 ± 0.8 mm wide and consists of 40 ± 3 disc florets and ray florets are totally absent. The florets open acropetally within two days (Figure 1b, 2 a, b). Of the total florets produced by the capitulum, 91% of them open on day 1 and 9% on day 2 (Table 1).

Table 1. *Anthesis as a function of time in Emilia sonchifolia*

Time (h)	No. of florets anthesed				
	Day 1	%	Day 2	%	Total
06:00	-	-	-	-	-
07:00	8	18	-	-	18
08:00	9	21	-	-	21
09:00	11	26	1	2	28
10:00	4	9	2	5	14
11:00	3	7	1	2	9
12:00	2	5	-	-	5
13:00	2	5	-	-	5
14:00	-	-	-	-	-
15:00	-	-	-	-	-
16:00	-	-	-	-	-
17:00	-	-	-	-	-
18:00	-	-	-	-	-

Flower morphology

The capitulum is protected by 8.8 ± 1.9 mm long, 3.4 ± 0.6 mm wide green involucres. The disc florets are small (9.1 ± 1.2 mm long, 1.6 ± 0.4 mm wide), pink or purplish, odourless, actinomorphic, bisexual and nectariferous. The calyx is reduced to bristles and represented by white soft hair like structures. The corolla is tubular (3.1 ± 0.5 mm long, 1mm wide) tipped with five lobes (1.6 ± 0.5 mm long, 1.2 ± 0.4 mm wide). Stamens are five (2.3 ± 0.4 mm long, 1 mm wide), white, epipetalous and display syngenesious condition; the anthers are 1.2 ± 0.4 mm long, 1 mm wide), dithecous and apex appendiculate. The anthers are positioned along the sinuses of the corolla lobes (alternate to the lobes). The anther filaments are free from the corolla just above the tube and the two thecae (pollen sacs) of each stamen are connate with the thecae of adjacent stamens producing a tube that surrounds the style. Pollen is shed to the interior of this tube (introrse dehiscence). The ovary is green (3.1 ± 0.5 mm long, 1 mm wide), slightly hairy, bicarpellary, unilocular with a single ovule on basal placentation (Figure 2k,l). The style is 5.1 ± 0.7 mm long and is terminated into 2 pubescent stigmatic arms. A nectariferous disc is present at the base of style inside the corolla tube. The style with its aligned stylar arms extend beyond the height of anthers; the stylar arms stand almost erect and diverge partially exposing the inner hidden stigmatic surfaces.

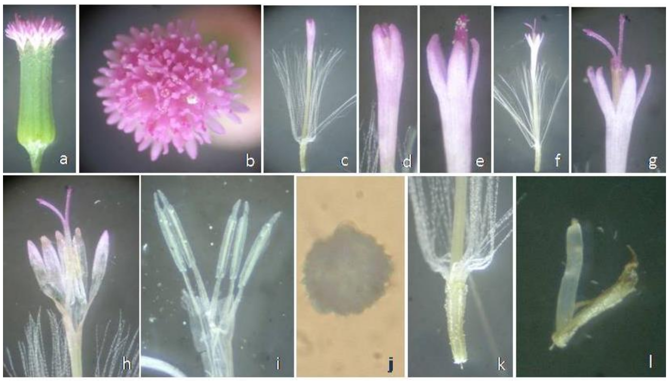

Figure 2. *Emilia sonchifolia: a. Anthesing capitulum, b. Top view of anthesed capitulum, c-g. Different stages of anthesis of disc floret, h. Relative positions of stylar arms and syngenecious anthers, i. Dehisced anthers, j. Pollen grain, k. Ovary, l. Ovule.*

Floral biology

The disc florets open during early morning 0700-1300 h on clear sunny days (Table 1; Figure 2c-g). The flowers open completely on sunny days while they are partially open on rainy days. Individual disc florets take about 3 hours to open from mature bud phase. The anthers dehisce by longitudinal slits during mature bud phase and hence the florets are protandrous (Figure 2i). At mature bud stage, the style with its aligned branches lies below the anthers. During and immediately after anthesis, the style grows and passes through the tube formed by the fused anthers pushing the pollen up. At this stage, the inner stigmatic surfaces are un-receptive and not exposed; this situation prevents the occurrence of autogamy. Such a form of pollen presentation is referred to as "secondary pollen presentation mechanism" represented by pump mechanism which ensures the pollen availability to insects visiting the capitulum on daily basis. The pollen grains are white, spheroidal, polyporate, echinate and 35.45 ± 3.79 µm in size (Figure 2j). The pollen output per anther is 49 ± 4.65 and per floret is 245. The pollen-ovule ratio is 245: 1. The style with its aligned branches gradually diverge in the early hours of 2nd day; then the inner stigmatic surfaces attain receptivity and remain so until the end of that day. A disc floret produces 1.2 µl of nectar which rises up as it accumulates in the floret due to narrow corolla tube. The sugar types present in the nectar include sucrose and glucose with the first one as dominant. The nectar contains eight essential amino acids which include arginine, histidine, lysine, isoleucine, methionine, threonine, tryptophan and valine; the first three amino acids are dominant. All non-essential amino acids tested are present in the nectar. The disc florets wither away after two days. After the initiation of fruit formation, the withered petals and stamens gradually fall off.

Pollination mechanism

The disc florets present the stamens and stigmas at different positions. The anthers mature, dehisce inwardly releasing the pollen grains into the anther tube. As the style grows and elongates within the anther tube it pushes the pollen grains out of the anther tube by stylar hairs situated at the tip of the stylar branches (Figure 2h). Such a pollen presentation is indicative of pump mechanism of secondary pollen presentation. The stylar branches are aligned at that stage and positioned above the anther ring and the inner stigmatic surfaces are not receptive on the day of anthesis. Since the stigmatic surfaces are hidden, there is no possibility of autogamy on the day of anthesis and by the end of that day most of the pollen would be dispersed by insects. On the 2nd day, stylar branches diverge partially in almost erect position exposing the stigmatic surfaces. In this position, the stigmatic surfaces are receptive and remain so until the end of the same day. The secondary pollen presentation mechanism represented by pump mechanism, and 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 a small percentage of disc florets on the 2nd day in the same capitulum and of different capitula on the same plant facilitates the occurrence of vector-mediated self-pollination. Therefore, the secondary pollen presentation mechanism and the sexual system functional in this species do not insulate completely from the occurrence of self-pollination and hence the flowers set fruit and seed through self-pollination and cross-pollination.

Foraging activity

The capitulum is the unit of attraction for the insects. Insects visiting the capitula consist of wasps, flies and butterflies and all foraged for nectar only (Table 2). Wasps and flies, each represented by a single species; the wasp is the Scoliid, *Campsomeris annulata* (Figure 3a), the fly is the Syrphid, *Eristalinus sp* (Figure 3b). The butterflies are represented by 1 pierid species (*Catopsilia pomona* -Figure 3c) and 7 lycaenid species (*Castalius rosimon*, *Zizula hylax* - Figure 3d, *Zizeeria karsandra*, *Zizina otis*, *Freyeria trochylus*, *Chilades laius* - Figure 3e and *C. pandava* -Figure 3f). The florets offer nectar and pollen for the visiting insects. All these insects approached the flowers in upright position, landed on the flat-topped capitulum and then probed individual florets for nectar. Of these insects, wasps and flies were found to be uncommon and also not consistent foragers while butterflies were common and consistent foragers during the peak flowering season. Of these insects, butterflies made 83%, wasps 12% and flies 5% of total foraging visits (Figure 5). The foraging activity pattern of all these insects showed a definite pattern with reference to foraging schedule. They foraged flowers during 0800-1700 h with peak foraging during 1000-1100h coinciding well with the standing crop of nectar by that time (Figure 4). These insects foraged several florets of a capitulum in a single visit and made multiple visits to the few capitula produced by individual plants in quest of nectar. They also made visits to capitula of different closely and distantly spaced plants. Such a foraging behavior was considered to be promoting both self- as well as cross-pollination to a great extent. The body washings of all foraging insects collected from the flowers during peak foraging period revealed that they carry pollen ranging from

Figure 3. *Emilia sonchifolia: a. Campsomeris annulata, b. Eristalinus sp., c. Pierid, Catopsilia pomona, d-f. Lycaenids - d. Zizula hylax, e. Chilades laius, f. Chilades pandava, g-h. Seed dispersal, i. Seed with pappus, j. Seeds.*

Table 2. *List of insect foragers on Emilia sonchifolia.*

Order	Family	Genus	Species	Common Name	Forage sought
Hymenoptera	Scoliidae	*Campsomeris*	*annulata* F.	Sand Wasp	Nectar
	Syrphidae	*Eristalinus*	sp.	Hoverfly	Nectar
Lepidoptera	Pieridae	*Catopsilia*	*pomona* F.	Lemon Migrant	Nectar
	Lycaenidae	*Castalius*	*rosimon* F.	Common Pierrot	Nectar
		Zizula	*hylax* F.	Tiny Grass Blue	Nectar
		Zizeeria	*karsandra* Moore	Dark Grass Blue	Nectar
		Zizina	*otis* F.	Lesser Grass Blue	Nectar
		Freyeria	*trochylus* Freyer	Grass jewel	Nectar
		Chilades	*laius* Stoll	Lime Blue	Nectar
		Chilades	*pandava* Horsfield	Plains Cupid	Nectar

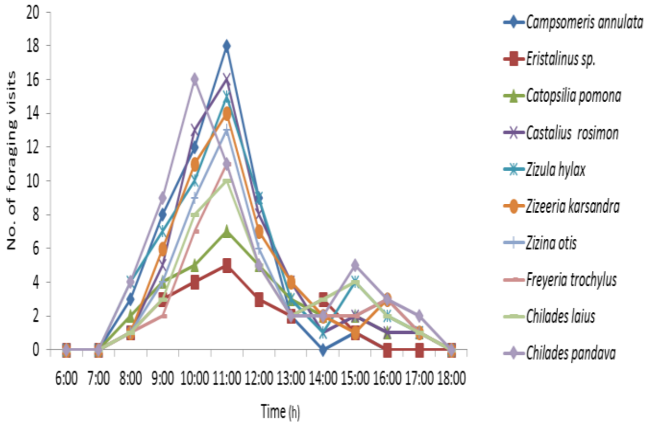

Figure 4. *Hourly foraging activity of insect foragers on Emilia sonchifolia.*

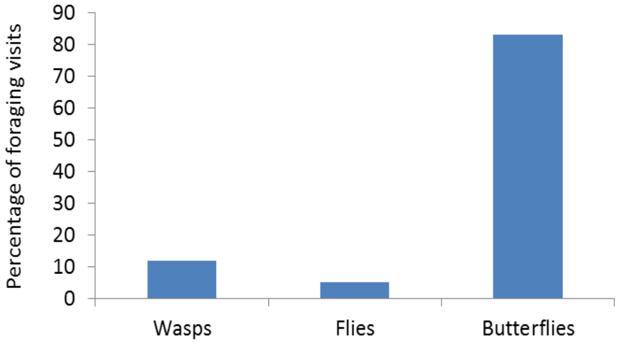

Figure 5. *Percentage of foraging visits of different categories of insect foragers on Emilia sonchifolia.*

5 to 36. Individual species showed variation in the number of pollen grains carried by them. The mean number of pollen grains recorded varied from 18 to 26 (Table 3).

Therefore, butterflies were considered to be the principal pollinators while the wasp and the fly were considered to be supplementary pollinators. Apart from all these insects, thrips were found in mature buds and emerged out during anthesis. They were resident foragers and collected both pollen and nectar from disc florets. The thrips were found to use the disc buds for breeding and disc florets for forage after anthesis. Since the disc florets are staminate on day 1 and pistillate on day 2, their foraging activity within capitulum does not contribute to self-pollination within or between florets of the same capitulum. However, there is a possibility for such a form of pollination if pollen is viable and self-pollen is deposited on the stigmatic surfaces of disc florets of the same capitulum by thrips while collecting forage during post-anthesis period.

Fruiting ecology and seed dispersal

The fertilized flowers produce single-seeded fruits within two weeks. Individual capitula produced 31 ± 5 fruits and 23 ± 8 seeds. In open-pollinations, fruit set is 63.69% out of which filled seed set is 73.63%. The fruit is an oblong, brownish, 3-4 mm long dry indehiscent ribbed achene with a pappus of white hairs which are up to 8 mm long. The pappus aids in the dispersal of seeds and seed dispersal occurs primarily by wind (Figure 3g-j). Further, the seeds stick readily to hair and clothing and hence they are also dispersed by humans. Seed dispersal occurs principally on clear sunny days and during dry spells of the rainy season. Seeds show dormancy and germinate only during rainy season which starts in June. Seeds settled or buried near the soil surface germinate readily and produce new plants, especially in open or partly shaded areas characterized by adequate soil moisture. Field observations indicated that long dry spells during rainy season caused withering of seedlings and even young plants.

Table 3. Pollen recorded in the body washings of insect foragers on *Emilia sonchifolia*

Insect species	Sample size (N)	Number of pollen grains		
		Range	Mean	S.D
Wasps				
Campsomeris annulata	10	08-36	26.2	9.31
Butterflies				
Castalius rosimon	10	11-29	21.3	6.53
Zizula hylax	10	07-26	19.6	6.51
Zizeeria karsandra	10	12-34	20.2	7.23
Zizina otis	10	09-31	19.3	7.76
Freyeria trochylus	10	05-25	18.9	6.93
Chilades laius	10	10-26	19.1	5.13
Chilades pandava	10	07-29	18.7	7.33

Discussion

Wee (1970) reported that *Emilia sonchifolia* thrives under a wide range of conditions from the full sunlight of open grassland, waste areas, roadsides or wide-spaced arable crops, to the partial shade of perennials. The present study shows that it grows primarily in sunny moist well drained soils both in cultivated and un-disturbed localities. It shows patchy distribution in open sunny areas while scattered distribution as isolated individuals in partly shaded areas. Marks (1983) reported that *E. sonchifolia* germinates in soils with adequate moisture during the growing season in Nigeria. The plant completes its life cycle in about 90 days. The present study shows that *E. sonchifolia* seeds germinate following the first monsoon showers in June/July and produce new plants. Flowering occurs during August - November and then the plant gradually disappears in areas where soil is deficient in moisture. But, the plant continues to flower and fruit in areas where the soil has adequate moisture. Therefore, it can be said that soil moisture plays an important role in providing stimulus for the growth and reproduction in *E. sonchifolia*. Olorode & Olorunfemi (1973) mentioned that *E. sonchifolia* and *E. coccinea* hybridize with each other in natural conditions in Africa. *E. sonchifolia* flowers are mauve or rarely white; however, flower colour varies greatly around the world and particular care is required when considering this character. Chetty et al. (2008) reported that *E. sonchifolia* and *E. scabra* occur intermingled with each other in the same habitat. The present study shows that the two species mostly form separate distinct patches although occur in the same habitats. Both the species flower simultaneously and produce purple to pinkish flowers. Whether the two species hybridize naturally with each other or not is not known. The flower colour in *E. sonchifolia* is not variable and is consistently pink or purple in the study area. However, field studies on flower colour variation in *E. sonchifolia* in different areas are suggested to confirm whether the plant consistently produce purple flowers or not. Marks & Akosim (1984) stated that *E. sonchifolia* produces ray and disc florets. But, the present study revealed that *E. sonchifolia* produces several capitula consisting of only disc florets presenting nectar and pollen as rewards. The close association of many florets renders the capitulum more conspicuous and attractive to insect visitors. The plant has the disadvantage of non-production of ray florets which further increase the conspicuousness of the capitulum due to outward directed rays, whose colour frequently differs from that of the disc florets. The disc florets form a flat surface consisting of many protruding reproductive organs. The aggregation of disc florets into a capitulum is biologically the equivalent of a single flower. It permits the pollinating insects to crawl over the disc florets and pollinate many florets in the shortest possible time, which compensates for the biological disadvantage of having only one ovule in each floret. Each capitulum consisting of several disc florets enables pollinator insects to reduce flight time, search time and hence each such visit paid by them is energetically rewarding.

Secondary pollen presentation system is widespread in angiosperms. It is an important characteristic of the family *Asteraceae* (Howell et al., 1993). It has been described as a strategy to improve accuracy in pollen removal and deposition, which will result in the enhancement of the male and female fitness (Ladd, 1994) and this mechanism seems to occur within *Campanulaceae* and *Asteraceae* by means of stigmatic lobes curvation (Carana, 2004). In the present study, *E. sonchifolia* is protandrous and the pollen is shed from the anthers onto the tip of the style in the bud stage when the style branches are joined and stigmatic surfaces are not receptive. This type of pollen presentation is the characteristic of pump mechanism (Torres & Galetto, 2007). As the style grows out of the anther tube, the tip of the style arms present pollen for pollination. The receptive papillate stigmatic surface is hidden between the two appressed style arms, preventing self pollination. After the pollen presentation, during the functionally female phase of the floret which occurs on day 2, the style arms separate partially exposing the receptive papillae for the receipt of pollen. The style arms serve dual purpose; they are 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). From day three onwards the florets enter the senescence stage in *E. sonchifolia*. The secondary pollen presentation system functional in *E. sonchifolia* is therefore an evolved mechanism that enhances the efficiency and accuracy of pollen exportation and/or pollen reception, thus increasing male and/or female fitness of the plant (Ladd, 1994).

In *E. sonchifolia*, the capitulum form of inflorescence, narrow tubular corolla, production of nectar, pollen accessibility to foragers within and outside the corolla tube and pollen characteristics such as spheroidal shape, porate apertures and echinate exine suggest that the plant is adapted for insect pollination. In *E. praetermissa* also, the pollen grains are spheroidal, polyporate aperturate and echinate; these characteristics are considered as structural adaptations for effective pollination by insects (Mbagwu et al., 2009). Therefore, the pollen grain characteristics recorded in these two species suggest that the disc florets have perfectly evolved for entomophily in order to prevent autogamy, minimize geitonogamy and maximize xenogamy.

Burkhardt (1964) and Faegri & van der Pijl (1979) characterized butterfly-flowers. Flowers conforming to this type usually possess large, white, pink, red, yellow or blue, narrow, tubular flowers with deep nectaries and often yellow rings or other markings on the petals which function as nectar guides. Baker & Baker (1982; 1983) described 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 *E. sonchifolia*, the capitula characteristically produce only pink bisexual disc florets. The florets in a capitulum slightly vary in number but the number stands approximately at 40. They produce minute amount of sucrose-rich nectar which is concealed and positioned at the base of the narrow corolla tube. Further, the nectar is a potential source of eight essential amino acids which include arginine, histidine, lysine, isoleucine, methionine, threonine, tryptophan and valine, and also of all non-essential amino acids tested in this study. Therefore, the characteristics of disc florets conform to butterfly pollination syndrome.

In *E. sonchifolia*, the capitula attract butterflies, wasps, flies and thrips. The butterflies visiting the florets represent almost lycaenid family of lepidoptera suggesting mutualistic interaction between lycaenids and disc florets of this plant. As the florets are very small, tubate and aggregated in capitula, the small lycaenid butterflies qualify to be appropriate pollinators. Since the disc florets possess narrow corolla tube, the butterflies require skill to carefully insert the proboscis into each floret in order to access nectar. The visiting butterflies have this skill and collect nectar efficiently from several florets in a single visit. In such an act, their proboscis gains contact with the tip of the stylar arms dusted with pollen grains and the dehisced anthers inside the corolla tube effecting pollination. The pollen carried on their proboscis and forehead parts is sufficient to pollinate individual disc florets since the latter produce only one ovule per floret. The standing crop of nectar at plant or population level is commensurate with the requirement of the lycaenid butterflies because the latter being small-bodied do not require huge quantity of nectar. In areas where the plant has patchy distribution, the butterflies frequent the capitula of flowering individuals hopping from capitulum to capitulum on the same or different plants. But, in areas where the plants occur as isolated and scattered individuals, the butterflies do not make frequent visits to them. In areas of patchy distribution, the lycaenid butterflies frequent visits to several closely and distantly spaced plants and hence enhance cross-pollinate rate. Their foraging schedule and the peak foraging activity period coincide well with the availability of standing crop of nectar. The consistent foraging activity of lycaenid butterflies evidenced on *E. sonchifolia* suggests that they use this plant as a major nectar source and the relationship between the two partners conform to psychophily.

The present study indicated that wasps and flies also visit *E. sonchifolia* capitula for nectar and pollinate the florets. But, they are not consistent foragers and hence are only supplementary pollinators. Thrips use this plant as breeding and feeding sites. They emerge during anthesis from mature buds, move in and out of the florets collecting pollen and nectar due to which geitonogamy occurs. In closely spaced individuals, the thrips may also fly to the capitula of the nearest plants and effect cross-pollination. Apart from this, their nectar feeding activity reduces the availability of nectar at capitulum level; in effect the lycaenid butterflies are compelled to make multiple visits to the same or different plants in quest of nectar. Therefore, thrips by consuming the nectar appear to be promoters of cross-pollination by the actual pollinators.

Lane (1996) stated that six different sexual systems exist within the heads of members of *Asteraceae* - monoecy, dioecy, gynodiecy, andromonoecy, gymnomonoecy, and hermaphroditism. All these conditions derive from differences of sexuality of ray and disc flowers which are often correlated with overall morphology. In the present study, *E. sonchifolia* with capitula producing only disc florets are morphologically hermaphroditic but functionally temporally dioecious. Because, the florets dehisce anthers during bud stage and the stigmatic surfaces of stylar arms attain receptivity on the following day. In effect, the florets display staminate phase on the day of anthesis and pistillate phase on the following day. The display of alternate phases of staminate and pistillate by the florets constitutes temporal dioecy, a sexual system evolved in this species to prevent autonomous selfing and minimize vector-mediated selfing, especially geitonogamy. Each capitula of *E. sonchifolia* opens all its disc florets on two successive days presenting staminate and pistillate phase florets; this situation facilitates the occurrence of geitonogamy with the aid of insects. Further, the simultaneous presence of staminate and pistillate phase florets in several capitula on the same plant provides ample opportunities for the occurrence of geitonogamy. The high natural fruit and seed set rates recorded for this species indicate that geitonogamy and xenogamy are functional but both modes are essentially vector-mediated. The function of dual modes of breeding suggests that the plant is self-compatible, self- as well as cross-pollinating. The pollen output rate per floret/capitulum additionally substantiates the same (Cruden, 1977). Such a breeding system is usually found in plants that occur in disturbed areas. In such plants, the number of flowers visited by pollinators may determine the proportion of the seed set that is selfed or out-crossed, and this will affect the levels of inbreeding (Baker, 1974). *E. sonchifolia* has the ability to grow both in disturbed and undisturbed areas and reproduce sexually in order to thrive well seasonally and also throughout the year if favourable soil conditions exist.

Leuszler et al. (1996) reported that the *Asteraceae member*, *Echinacea angustifolia* produces achenes from both out-crossed and self-pollinated florets, but out-crossed florets produce significantly more filled achenes. Self-pollinated florets produce mostly unfilled achenes and exhibit lower fitness than those produced from out-crossed achenes. These authors attributed the production of unfilled achenes to inbreeding depression. Marks & Akosim (1984) distinguished two types of seeds in *Emilia sonchifolia* based on the colour of achene. The female outer circle of ray florets of a flower head produce reddish-brown achenes while those from inner hermaphrodite florets are off-white. The present study showed that *E. sonchifolia* produces only disc florets and hence the report by Marks & Akosim (1984) that seeds are produced from ray and disc florets is totally false. The plant produces both filled and unfilled achenes; the percentage of the latter is significant suggesting that both selfed and crossed florets produce fruit and unfilled ones are produced mostly from selfed ones. Each single-seeded fruit is the product of separate selection and fertilization by individual pollination. The pollination mechanism functional in this species ensures the necessary genetic variability to the numerous offspring produced in the same capitulum, and preserve the morphological stability of the genetically fixed characteristics.

Funk et al. (2005) reported that the plants that exhibit anemochory predominantly occur in open areas. This study shows that *E. sonchifolia* is predominantly distributed in open sunny areas than in shaded areas. The achenes consisting of seed capped by a cluster of pappus are highly fragile and become airborne when mature and dry with the slightest gust of wind and fly like a parachute across different habitats and regions. Such a form of seed dispersal typifies anemochory. Anemochory is adaptive and effective for *E. sonchifolia* due to its predominant occurrence in open sunny areas. However, anemochory is effective in this species only on clear sunny days and long dry spells during rainy season. Therefore, the rainy season is not ideal timing for the dispersal of seeds of this plant. The ambient weather appears to be limiting factor for the expansion and distribution of the species as a major weed. Field studies indicate that *E. sonchifolia* is a minor weed and has limitations in producing huge populations both in disturbed and un-disturbed habitats.

E. sonchifolia is used as a vegetable and for treating various human ailments in the whole of South-East Asia, India, China, Bangladesh and Africa. In Malaysia, the plant is sold in local markets as an edible wild vegetable (Uphof, 1968; Martin & Ruberte, 1978; Duke & Ayensu, 1985; Thenmozhi et al., 2013; Kumar et al., 2015). Its wide use in all these countries suggest that it is an economically important minor weed and can be used as a potential wild vegetable and for treating various human diseases. During rainy season, the seeds germinate and readily produce the whole plant within a short period if the soil is sufficiently wet. It supports local lycaenid butterflies and also other visiting foragers with nectar during its flowering season. The plant can be cultivated or allowed to grow where it is not a menace because it is not invasive and does not produce huge populations. Since it usually occurs in open sunny places with little herbaceous cover consisting of low ground species such as *Justicia procumbens*, *Spermacoce hispida*, *S. articularis*, *S. pusilla*, *Justicia procumbens*, *Hedyotis brachiata*, *H. corymbosa*, *Boerhaavia diffusa*, *Merremia tridentata* etc., it can be considered as a pioneer species for the enrichment of soil fertility and used in eco-restoration programs.

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