Reproductive ecology of the globally invasive Whitetop Weed, *Parthenium hysterophorus* (*Asteraceae*)

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Abstract. *Parthenium hysterophorus* L. is a weed of global significance, because of causing human and animal problems, agricultural losses, and threat to biodiversity. Particularly in this context, the information on its reproductive ecology is important so as to understand its reproductive traits that make this weed invasive at global level. The study into its reproductive ecology indicates that it displays simultaneously vegetative, flowering and fruiting phases in different habitats, depending on the age of the plant and soil environment. The inflorescence is a heterogamous capitulum which begins anthesis with ray florets opening synchronously on the first day, while the disc florets open in the next five consecutive days. The ray florets are fertile, self-compatible, self-pollinating (vector mediated) and facultatively xenogamous, while the disc florets are female-sterile and act as pollen donors. In the disc florets, their tubate corolla, nectar secretion and echinate pollen are adaptations for entomophily, while the small spheroidal and powdery pollen form is an adaptation for anemophily. Butterflies, especially nymphalids and bees, are principal pollinators, while wasps and flies are supplementary pollinators. Thrips, *Frankliniella schultzei* and *Scirtothrips dorsalis,* use flowers as breeding and feeding sites; the latter activity affects mostly self-pollination. Ray florets produce wedge-shaped cypselas crowned with persistent corolla appendages and stylar arms. Individual cypselas are liberated together with a straw-colored fruit layer and two adjacent lateral sterile disc florets, which collectively act as air sacs and aid the dispersal of cypselas.

Key words: heterogamous capitulum, female-sterile disc florets, facultative xenogamy, entomophily, anemophily, polychory

Introduction

Flan (2009) reported that *Parthenium* is a genus of North American shrubs. Ebadi (2007) mentioned it as a small genus of approximately sixteen species of shrubs, herbaceous perennials, and annuals. Hedge & Patil (1980) noted that it has twenty species and only one of these occurs in India as an exotic weed. This is *P. hysterophorus,* commonly called "Congress Weed" because its white flowers resemble the white caps worn by members of the Indian National Congress (Motooka 2003). Narwal & al. (2003) maintained that *P. hysterophorus* is believed to be a natural hybrid of *P. confertum* and *P. bipinnatifidum*. Picman & Picman (1984) stated that it is a noxious plant, native of North and South America and the West Indies. Kaur & al. (2014) wrote that it is widely distributed in many parts of the world as an invasive weed. This weed is of global significance because of being responsible for severe human and animal health problems, such as dermatitis, asthma and bronchitis, and agricultural losses, besides causing great problems for biodiversity. Gupta & al. (2016) reported this weed as a curse at global level. Joshi & al. (2016) stated that it is violently invasive, with hazardous effects across the globe. Kaur & al. (2014) mentioned a widely held belief that the seeds of this weed had come to India

with grain imported from USA under the US PL 480 scheme and then got naturalized. Rao (1956) reported the plant as a new species to India. Different methods have been employed to manage it, namely mechanical, competitive replacement (allelopathy), chemical and biological control. However, it has defied all methods for control of its proliferation. The plant generally produces allelochemicals consisting of two major groups: phenolics and sesquiterpene lactones (Patil & Hedge 1988). In South America, it does not produce parthenin but instead produces a diastereomer, hymenin, while in India, it contains large amounts of parthenin and ambrosin (Lakshmi & Srinivas 2007). Parthenin is a bitter and toxic sesquiterpene lactone, which makes the plant unpalatable and causes death to cattle, buffalo and sheep; in susceptible people, it causes allergic dermatitis, anorexia and intestinal damage (Towers & al. 1977; Towers & Subba Rao 1992). The pollen also contains parthenin, which instigates allergic rhinitis that can develop into bronchitis or asthma in humans, if the pollen enters the respiratory tract in the process of breathing (Seetharamaiah & al. 1981; Lakshmi & Srinivas 2007). There exists some sporadic information on the reproductive biology of two *Parthenium* species: *P. integrifolium* and *P. hysterophorus*. Mamood & al. (1990) reported that *P. argentatum* increases its seed yield by honeybee pollination, while Smitley (2016) wrote that this species is pollinated by bees, wasps, flies, and beetles which collect nectar and pollen from the flowers. Haseler (1976) and Navie & al. (1996) stated that *P. hysterophorus* does not reproduce by apomixis or vegetatively. Different authors noted that the pollen of *P. hysterophorus* is airborne and recorded the percentage of this airborne pollen in different Indian cities (Seetharamaiah & al. 1981; Jain 1983; Bhasale 1983; Agashe & Abraham 1988; Bhat & Rajasab 1989; Agashe & Chatterjee 1987; Nayar & al. 1990; Singh & al. 2003; Chauhan & Goyal; Ahlawat & Dahiya 2014). Gupta & Chanda (1991), however, reported the lowest number of pollen grains of *P. hysterophorus* ranging from 0 to 10 in the air across Kolkata, India. They also reported that this weed is obligately vector-dependent for pollination effected by honeybees, ants and flies. Lakshmi & Srinivas (2007) mentioned that *P. hysterophorus* is anemophilous, while Vedanthan & al. (2014) pointed out that it is entomophilous. With such a background, the present study was aimed at providing details of the reproductive ecology of *P. hysterophorous,* in order to understand as objectives the following aspects: flowering phenology, floral biology, pollination mechanism, pollinators, sexual system, and seed dispersal. This information would contribute to understanding the efficiency of sexual reproduction in *P. hysterophorous* empowering it as a widespread invasive weed, as well as to developing strategies for its control in agricultural and non-agricultural areas.

Material and methods

Study site

Populations of *Parthenium hysterophorus* L. growing in the Visakhapatnam region (17°42'N and 82°18'E), Andhra Pradesh State, India, were used for study during the period 2015–2017.

Floral biology

Observations regarding the organization of inflorescences, spatial positioning of flowers and their position on the plant were made, since these features are regarded as important for pollination by foragers. Life time of individuals of two floret types was recorded by marking twenty just opened florets each, and following their development until fall off. Anthesis was initially recorded by observing ten marked mature capitula in the field. Subsequently, the observations were repeated five times on different days, each day observing twenty marked mature capitula, in order to provide an accurate anthesis schedule. Twenty mature disc florets were watched 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 10× hand lens. The details of flower morphology such as flower sex, shape, size, colour, odour, sepals, petals, stamens, and ovary were described.

Pollen output and pollen-ovule ratio

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 provided by Cruden (1977).

Nectar analysis

Individual volumes of nectar were recorded for twenty-five ray and disc florets and then the average volume of nectar per each type of floret was determined and expressed in µl. The capitula used for this purpose

were bagged at mature bud stage, opened after anthesis and nectar squeezed from each floret into micropipette to measure its volume. On the basis of nectar volume in individual florets, the total volume of nectar secreted in a capitulum was estimated. Similarly, the sugar concentration of nectar at capitulum level was determined using a Hand Sugar Refractometer (Erma, Japan). Nectar analysis for sugar types followed the Paper Chromatography Method described in Dafni & al. (2005). The sugar content/flower is expressed as the product of nectar volume and sugar concentration per unit volume, mg/µl. This is done, first, by noting down the conversion value for the recorded sugar concentration on the refractometer scale, and then by multiplying it with the volume of nectar/flower. Table 5.6 given in Dafni & al. (2005) was followed for recording the conversion value to mg of sugars present in one µl of nectar. The dinitrosalicylic acid method was followed for the first two sugar types, and the resorcinol method for the last sugar type. The caloric reward of nectar/flower/day was measured according to 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:

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

The paper chromatography method described in Dafni & al. (2005) was applied for identifying the amino acid types in the nectar of florets.

Foraging activity and pollination

The flower visitors were collected and identified with the representative specimens available at the Department of Environmental Sciences, Andhra University, Visakhapatnam. All butterflies were further confirmed by consulting the books of Kunte (2007) and Gunathilagaraj & al. 1998), while the other insects were identitied some to the species level and a few others to the genus level only. Thrips were identified according to the key provided by Bhatti (1980) for Indian thrips. The insects were watched closely for ten hours a day for fifteen days in different months each year during the profuse flowering periods. The hourly foraging visits of each species were recorded on ten different days for thirty selected capitula. The obtained data was used for calculating the percentage of foraging visits made by each species per day, and also for calculating the percentage of foraging visits of each category of insects per day. Along with this, the insects were watched for their foraging behavior, such as mode of approach, landing, probing behaviour, the type of forage they collected, contact with essential organs resulting in pollination, and inter-plant foraging activity. The insects were captured on the flowers during 10.00–12.00 h 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 carry pollen grains or not. They were washed first in ethyl alcohol and the contents stained with aniline-blue on a glass slide and observed under microscope to count the number of pollen grains present.

Observations on fruiting, seed dispersal and seed germination

Five hundred capitula were tagged and followed for fruit set rate in ray florets in open-pollinations and for noting down the duration of fruit maturation. The capitula were collected, brought to the laboratory and ray florets were separated from each capitula prior to their observation under microscope to record the number of filled cypselas. Seed characteristics of the ray florets were carefully examined to note down their special adaptations for dispersal mode. 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 carried out to record the approximate number of generations produced during the rainy season.

Results

Phenology

The species was an erect, aromatic, puberulous, annual herbaceous plant. It showed two distinct phases: juvenile and rosette representing the vegetative phase, and adult and mature representing the reproductive phase. The reproductive phase displayed a strongly branched erect stem with a deep tap-root system and flowering. The plant grew across the year, as long as there was moisture, and continued flowering and fruiting until senescence. However, robust vegetative growth and concentrated flowering occured during the rainy season from July to November (Fig. 1a). The species propagated only by seed. Individual plants completed their life cycle within 9–10 months in farmlands and within 7–8 months in all other habitats, but extend-

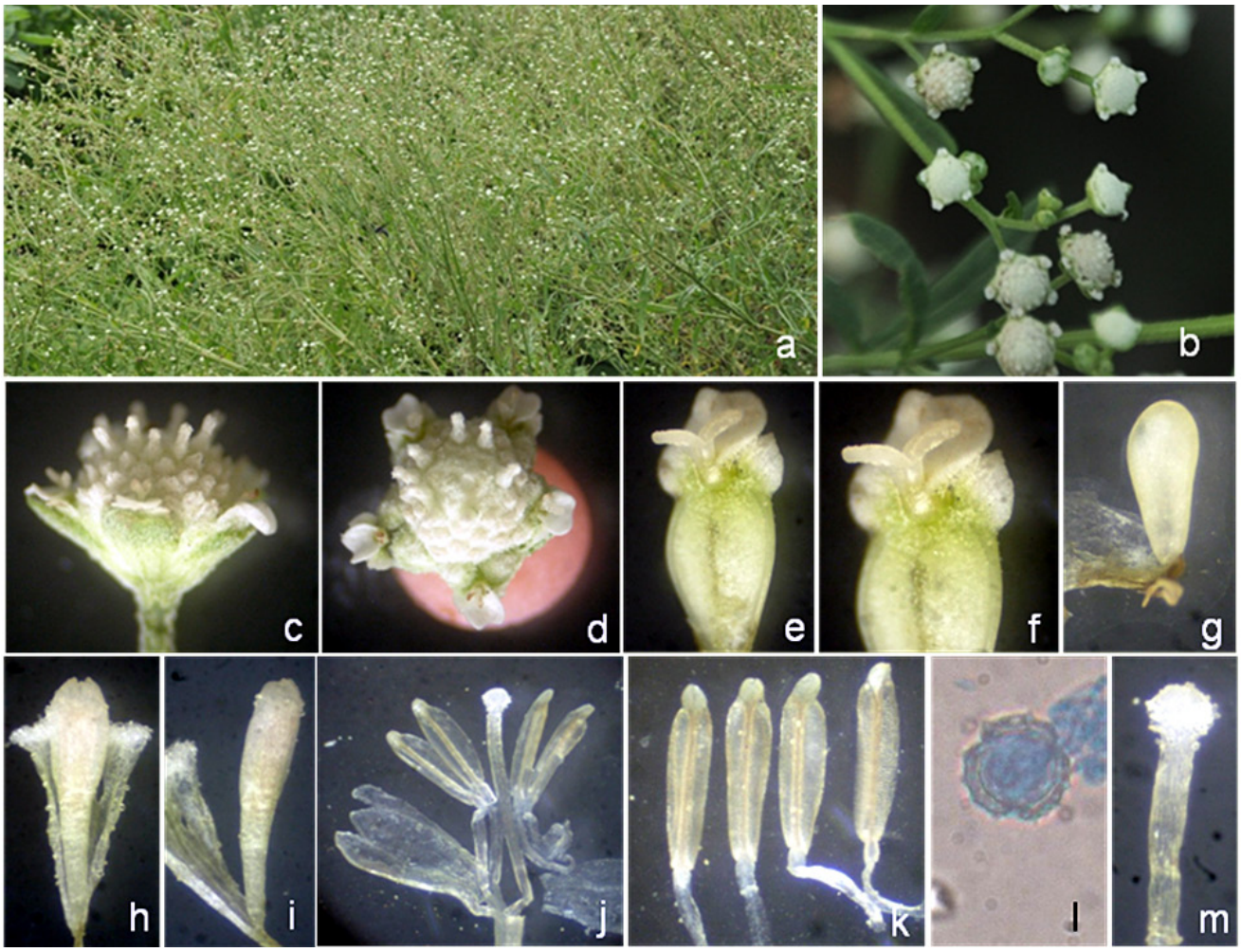

Fig. 1. *Parthenium hysterophorus:* **a.** Flowering phase, **b.** Capitula, **c.** Capitulum in anthesis phase, **d.** Top view of anthesing capitulum, **e. & f.** Ray floret with stylar arms, **g.** Ovule, **h. & i.** Disc floret bud, **j.** Relative positions of spheroid stigma and connate anthers in disc floret, **k.** Anthers of disc florets, **l.** Pollen grain of the disc florets, m. Spheroid stigma of the disc florets.

ed beyond this period, if moisture was available in the soil. The seeds germinated and produced new plants immediately after their dispersal, owing to which the plants showed simultaneously the vegetative, flowering and fruiting phases in different habitats.

Flower morphology

The inflorescence was a terminal and axillary pedunculate scorpioid cyme bearing a heterogamous capitula (Fig. 1b). A plant produced 802.6 ± 134.8 capitula. The capitulum was pentangular and consisted of five outer, narrowly ovate, puberulous involucral bracts, five thin inner obovate bracts, five outer female ray florets (seldom six or seven), and 75.7 ± 16.4 central staminate disc florets; the ratio of ray to disc florets was 1:15. Each ray floret was subtended by two disc florets on either side. Ray florets were ligulate, white, odorless, truncate to emarginate, 2 mm long, 4 mm across and zygomorphic; they had a well-developed pistil consisting of a bicarpellary, unilocular ovary with a single basal anatropous ovule (Fig. 1g) and exerted style with two linear and smooth whitish-green arms. Disc florets were odourless, white-green, 2 mm long and actinomorphic. The corolla was tubate, 4-lobed towards apex and infundibuliform. There were four stamens, epipetalous, fused near base of the corolla tube, creamy-white, 1.2–1.4 mm long, and the anthers were basifixed, tipped deltate appendages at the tip, connate laterally and dithecous (Fig. 1k). The pistil consisted of 1 mm long rudimentary ovary without ovule, 2 mm long style and 1 mm long spheroid stigma. The calyx represented by pappus was absent in both ray and disc florets. The floral features indicated that ray florets were morphologically and functionally female, while disc florets were morphologically bisexual and functionally staminate.

Floral biology

The ray and disc florets opened in early morning, at 08.00–09.00 h (Table 1) (Fig. 1c, d, h, i). The florets opened completely on sunny days and only partially on rainy days. In the capitulum, ray florets opened first, all of them and simultaneously on the same day at 08.00 h. Disc florets opened concentrically inwards in five consecutive days: 22 % opening on day 1st, 27 % on day 2nd, 23 % on day 3rd, 22 % on day 4th, and 6 % on day 5th. Each day, most disc florets opened at 08.00 h; 69 % of all disc florets in the capitulum opened at 08.00 h, and 31 % opened at 09.00 h over a period of five days (Table 1). Individual ray and disc florets took about three hours to open from the mature bud phase. Ray florets commenced stigma receptivity almost immediately after anthesis by diverging the stylar arms (Fig. 1e, f) and ceased receptivity by the evening of the 3rd day. Disc florets were protandrous, with anther dehiscence taking place during the mature bud stage by longitudinal slits. At the mature bud stage, the style with its spheroid stigma lay below the anthers (Fig. 1j, m). During and immediately after anthesis, the style grew, elongated and passed through the anther tube, brushing the pollen with its slightly hairy stigma. As the pistil was sterile, the presentation of pollen by the stigma above the anthers and the corolla tube enabled the insects to pick up the pollen and carry it; these pollen-laden insects effected pollination in ray florets of the same or different capitula, on the same or different plants, if visited by them subsequently. Pollen grains were white, powdery, radially symmetrical, isopolar, spheroidal, tri-colporate, zono-aperturate, sculpture supratectal, 22.3 ± 3.9 µm, echinate (6–7 spines between the colpi) (Fig. 1l). The pollen grains were 209.6 ± 29.8 per anther, 838.4 ± 119.4 per disc floret, 63 466 per capitulum and 50 899 732 per plant. The pollen-ovule ratio was 12 693:1. The ray and disc florets were nectariferous. A ray or disc floret produced 0.8 µl of nectar, which rose up slightly as it accumulated in the floret due to the narrow corolla tube. Nectar secretion began with anthesis and ceased by the end of the same day in both ray and disc florets. A capitulum produced an average volume of 64.8 µl of nectar during its lifespan; the nectar sugar concentration was 31 ± 1.8 %, with 0.3 mg of sugar containing 1.2 calories of energy at floret level, and 22.60 mg sugar containing 90.4 calories of energy at capitulum level. The sugar types present in the nectar included sucrose, glucose and fructose; they were present in that order of dominance. The nectar contained five essential amino acids (tryptophan, arginine, histidine, lysine, and threonine) and eight non-essential amino acids (glutamic acid, aspartic acid, cysteine, cystine, glycine, serine, hydroxyproline, and proline); they were present in that order of dominance. The ray and disc florets remained intact until fruits matured in ray florets. Each fruited or unfruited ray floret, along with the disc florets situated on both its sides, detached as a unit for dispersal. All disc florets detached as a single unit and fell off in the vicinity of the parental plants.

Table 1. Anthesis as a function of time in *Parthenium*

Time (h)	Number of anthesed disc florets										
	Day 1	%	Day 2	%	Day 3	%	Day 4	%	Day 5	%	Total
07:00	–	–	–	–	–	–	–	–	–	–	–
08:00	9	12	16	21	12	16	9	12	5	7	68
09:00	7	9	6	8	4	5	5	7	2	3	32

Total no. of disc florets per capitulum 75.7.

Pollination mechanism

Ray florets devoid of stamens acted as female and exposed the stigmatic region prominently by unfolding stylar arms immediately after anthesis against the ligulate petal to receive pollen from the foragers. Disc florets presented the stamens and spheroid stigma at different positions. The anthers dehisced inwardly and discharged pollen grains into the connate anther area during mature bud stage. At this stage, the style elongated and passed through the connate anther area, while the stigma with its hairs captured a few pollen grains and presented them outside the tubular corolla. Thus, the pollen presented by the stigma was carried away by the probing foragers which subsequently effected pollination, while probing the ray florets for forage. Since the disc florets were female-sterile, they acted as staminate florets, for which no special pollen presentation mechanism was required. Therefore, the ray florets, being female, essentially needed pollen from the disc florets for pollination, for which pollen vectors were essential.

Thrips breeding, feeding and pollination

The thrips species *Frankliniella schultzei* and *Scirtothrips dorsalis* (Thysanoptera: Thripidae) oviposited in the early bud stage of florets in the capitula. The larvae emerged from the eggs in synchrony with the anthesis and nectar production in both ray and disc florets. For their growth, centripetal development of the capitulum was found to provide continuous availability of pollen and nectar for six days. The thrips were found to feed on pollen and nectar, especially from disc florets. They

were dusted with pollen in their upward and downward movements within the corolla tube of the disc florets. The pollen grain surface facilitated the larvae to carry 80 to 137 pollen grains and the adults to carry 93 to 213 pollen grains on their body setae, wings and legs. The thrips dispersed the pollen on the stigmatic region of the stylar arms of ray florets and the spheroid stigma of disc florets due to their active movement, rubbing their abdomens on the stigmatic surface, cleansing their body parts with their hind legs, and also by their wing combing mechanism. Since disc florets are functionally staminate, any pollen deposition on their stigma does not contribute to pollination. Thrips effect self-pollination within the capitulum due to the pollen transfer from disc to ray florets; they also effect geitonogamous pollination by pollen transfer to ray florets of different capitula on the same plant and xenogamous pollination to ray florets of different plants, which are usually situated closely.

Insect foraging activity

Capitulum was the unit of attraction for insect foragers. Within the capitulum, the white ligulate petal of ray florets acted as chief attractant. The ray and disc florets were foraged by bees, wasps, flies, and butterflies. The bees and butterflies were the consistent and regular foragers, while all wasps and flies were inconsistent foragers. The bee foragers were *Apis cerana* (Fig. 2a), *A. florea* (Fig. 2b) and *Trigona iridipennis* (Fig. 2c). The wasps were *Scolia quadripustulata* (Fig. 2d) and one unidentified species (Fig. 2e). The fly was *Musca domestica* (Fig. 2f). The butterflies were *Junonia lemonias* (Fig. 2g), *Danaus chrysippus* (Fig. 2h), *Euploea core* (Nymphalidae), and *Freyeria trochylus* (Lycaenidae) (Fig. 2i) (Table 2). Of these, all bees foraged for both pollen and nectar, while all other foragers only for nec-

Table 2. List of insect foragers on *Parthenium hysterophorus.*

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
	Scoliidae	*Scolia*	*quadripustulata* F.	Blue Winged Wasp	Nectar
		Wasp (Unidentified)			Nectar
Diptera	Muscidae	*Musca*	*domestica* L.	House Fly	Nectar
Lepidoptera	Nymphalidae	*Junonia*	*lemonias* L.	Lemon Pansy	Nectar
		Danaus	*chrysippus* L.	Plain Tiger	Nectar
		Euploea	*core* Cramer	Common Indian Crow	Nectar
	Lycaenidae	*Freyeria*	*trochylus* Freyer	Grass Jewel	Nectar

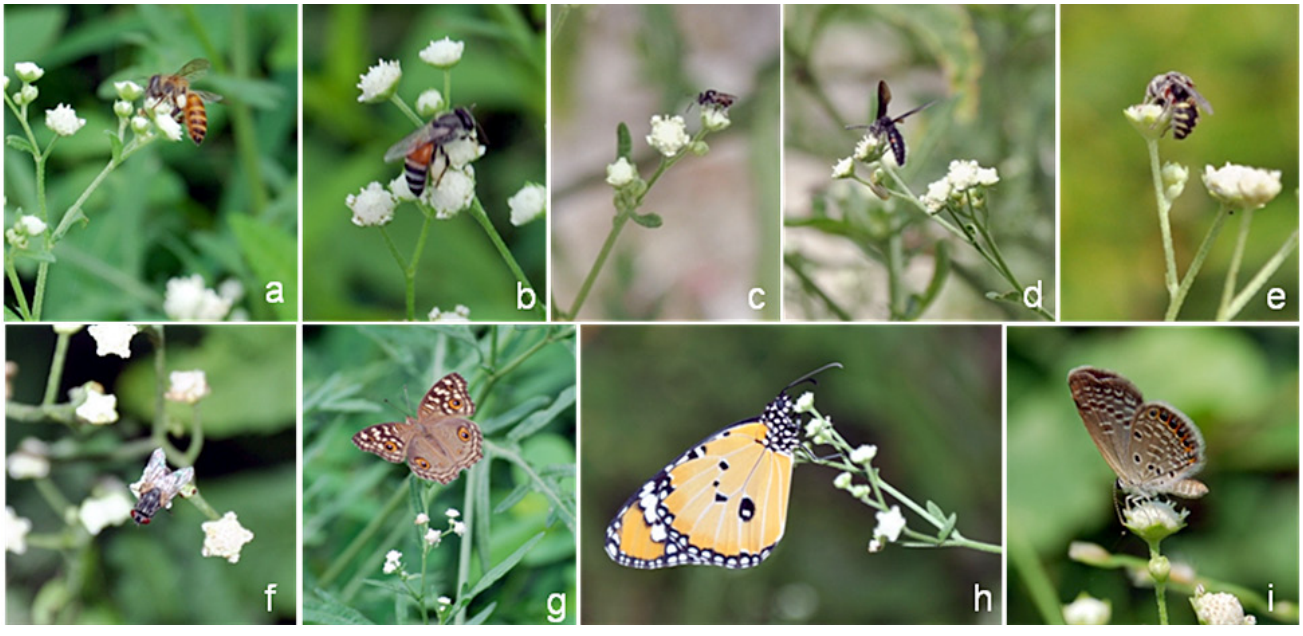

Fig. 2. *Parthenium hysterophorus*: **a.** *Apis cerana*, **b.** *Apis florea*, **c.** *Trigona iridipennis*, **d.** *Scolia quadripustulata*, **e.** Wasp (unidentified), **f.** *Musca domestica*, g. & h. Nymphalids – **g.** *Junonia lemonias*, **h.** *Danaus chrysippus*, **i.** Lycaenid, *Freyeria trochylus*.

tar. All these insects approached the flowers in upright position, landed on the flat-topped capitulum and then probed the ray and disc florets for nectar. They foraged several florets in a single visit and made multiple visits to several capitula of the same plant in quest of forage. They made frequent visits to the capitula of different closely and distantly spaced plants to collect forage. Such foraging behavior promoted both self- and cross-pollination. The foraging activity pattern of insects showed a definite pattern with reference to the foraging schedule. They foraged flowers between 08.00–15.00 h, with peak foraging between 09.00–12.00 h (bees, wasps and flies) (Fig. 4) and between 09.00–10.00 h (butterflies) (Fig. 5), which coincided well with the standing crop of nectar by that time. Bees accounted for 33 %, wasps for 22 %, flies for 7 %, and butterflies for 38 % of all foraging visits (Fig. 6). The body washings of insects collected from flowers during the peak foraging period revealed that all insects carried pollen but bees carried the highest number of pollen grains. Furthermore, the mean number of pollen grains varied with each insect species (Table 3).

Fruiting ecology and seed dispersal

Capitula produced mature dry cypselas from the fertilized ray florets within two weeks (Fig. 3a, b). A natural cypsela set accounted for 91 %. Unfertilized ray florets (Fig. 3h, i) and disc florets remained in place until the ray florets set fruit and, thereafter, fell off as a single unit (Fig. 3c-e). The cypselas were black, wedge shaped, flattened, 2 mm long, 1–2 mm wide, with thin white scales, and crowned by persistent corolla ap-

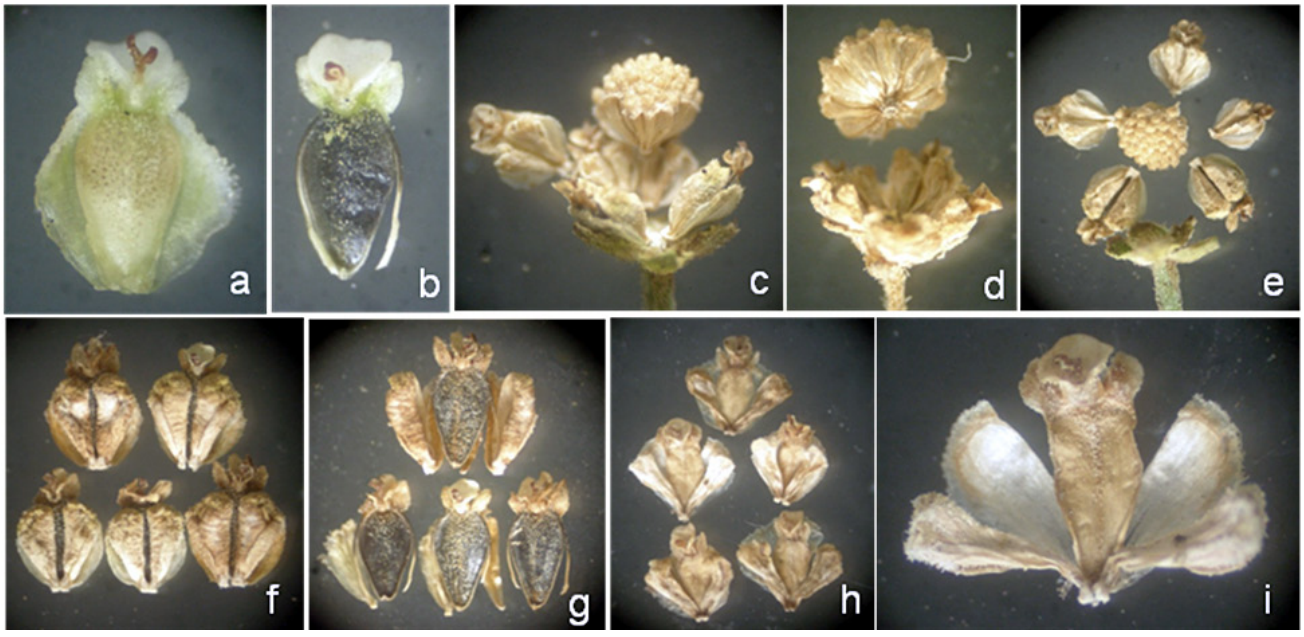

Fig. 3. *Parthenium hysterophorus*: **a.** Maturing fruit of ray floret, **b**. Mature fruit of ray floret, **c-e.** Detachment of the disc florets as a unit from the fruited ray florets, **f. & g.** Fertilized fruits of the ray florets with black wedge-shaped seeds, **h. & i.** Unfertilized ray florets.

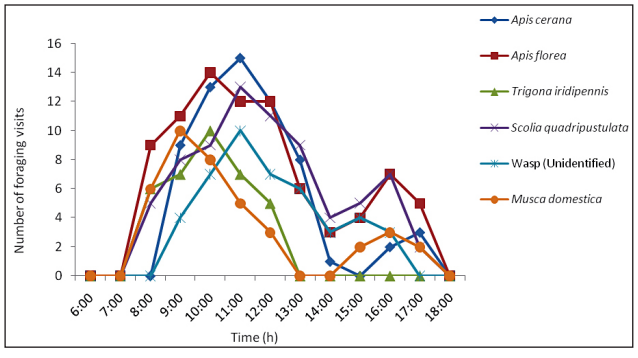

Fig. 4. Hourly foraging activity of bees, wasps and fly on *Parthenium hysterophorus.*

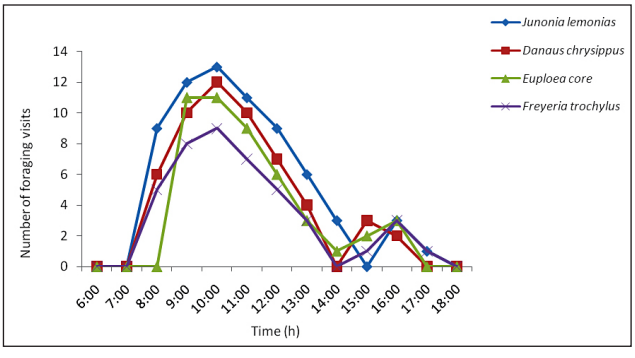

Fig. 5. Hourly foraging activity of butterflies on *Parthenium hysterophorus.*

Table 3. Pollen recorded in the body washings of insect foragers on *Parthenium hysterophorus*.

Insect species	Sample size (N)	Number of pollen grains		
		Range	Mean	S.D.
Apis cerana	10	68–173	122.4	31.1
Apis florea	10	53–156	108.9	26.4
Trigona iridipennis	10	36–124	91.6	22.4
Scolia quadripustulata	10	14–67	40.3	13.3
Wasp (Unidentified)	10	8–33	22.4	7.2
Musca domestica	10	16–45	31.8	7.1
Junonia lemonias	10	24–63	42.7	9.3
Danaus chrysippus	10	21–57	40.1	8.6
Euploea core	10	26–54	42.8	7.2
Freyeria trochylus	10	7–29	20.4	5.8

pendages and stylar arms (Fig. 3f, g). Each cypsela was enclosed in a straw-coloured fruit layer and fused at base to two adjacent lateral sterile disc florets. Each cypsela, together with the corolla, style, two adjacent disc florets which appeared as spathulate appendages, and subtending bract was shed as a unit. This fruit layer, along with the spathulate appendages, acted as an air sac and aided the cypsela dispersal by wind.

Cypselas were viable, non-dormant and germinated within a week, if the soil was damp. The percentage of cypsela germination varied with the season: 85 % in the rainy season and 76 % in the dry season. The plant produced four or five successive cohorts of seedlings during the rainy season, and two or three successive cohorts of seedlings during the dry season. The seedlings produced adult plants at the end of the 4th week, began flowering since then and continued flowering and fruiting, depending on the soil moisture and nutrient status.

Discussion

Jeffrey (2009) has stated that the *Asteraceae* members produced capitula consisting of outer ray florets and inner disc florets. The ray florets attracted pollinators, while the disc florets took up the reproductive function and, hence, improved the chances for reproductive success and facilitated a more flexible basis for the breeding system evolution than a single flower did. Furthermore, this author has pointed out that a particularly diverse trait in the capitulum was the perianth symmetry exhibited by the ray and disc florets; the ray florets displayed zygomorphic symmetry, while the disc florets displayed actinomorphic symmetry. The present study shows that *P. hysterophorus* used ray florets for pollinator attraction and seed production, and disc florets exclusively for pollen production and supply to ray florets. Torices & al. (2011) have stated that the expression of floral sexuality was associated with changes in symmetry, which had important consequences for the evolution of reproductive biology in *Asteraceae*. This generalization was absolutely true for *P. hysterophorus,* because the outer zygomorphic ray florets were female, while the inner actinomorphic disc florets were staminate. Chapman & Abbott (2009) have reported that the presence of outer ray florets had a marked effect for attractiveness of pollinators, cross-pollination rate and fitness for the plant. In *P. hysterophorus*, the ray florets played dual roles of pollinator attraction and seed production. Since disc florets were not involved in seed production, the plant was compelled to use only ray florets to increase fitness as an invasive weed. However, a plant with a fixed number of ray florets, usually five per capitulum, could not produce abundant seed. On the other hand, a plant with numerous scorpiod cymes, each cyme with several capitula, produced profuse seed through the ray florets.

Torices & al. (2011) have reported that the *Asteraceae* family possessed all major sexual systems, except for andromonoecy. However, hermaphrotidism and gynomonoecy were the most common. In *P. hysterophorus,* the morphology of ray and disc florets indicated gynomonoecy but actually it was monoecy, because of the function of ray florets as female and of disc florets as staminate. This example of the evolution of monoecy from hermaphroditism contradicted the hypothesis put forward by Torices & al. (2011) that the most likely pathway to monoecy from hermaphroditism was via andromonoecy and not via gynomonoecy, since the latter required unrealistically high amounts of seed production by the ray florets. In *P. hysterophorus*, the capitulum began anthesis with ray florets on day 1st and with disc florets from day 2nd for five consecutive days. Such a pattern of anthesis facilitated the occurrence of vector-mediated autogamy in ray florets on the 2nd and 3rd day of anthesis of the capitulum, because the ray florets showed stigma receptivity for three consecutive days and on these days the pollen was available from the disc florets. The pollen available from the disc florets on the 4th and 5th day facilitated the occurrence of geitonogamy or xenogamy. The highest fruit set recorded in open-pollinat-

ed ray florets indicated that the plant was self-compatible and self-pollinating. This study disagrees with the conclusions of Verma & Singla (1990), who reported that *P. hysterophorus* was self-incompatible. However, these authors had noted that this weed displayed pseudo-selfcompatibility attributed largely to gametophytic factors rather, than to sporophytic factors. The recorded fruit set rate in this study does not agree with their findings. Furthermore, the fertilized ray florets did not have any resource competition for the seed set, since the disc florets were not involved in seed production. This was in agreement with the concept of sex allocation theory that the flowers in 'optimal positions' would allocate proportionally more resources to female structures, whereas flowers in 'suboptimal positions' would become relatively male-biased (Primack & Lloyd 1980; Mazer & Dawson 2001), suggesting architectural constraints that produced a decreasing resource gradient from the outermost to the innermost florets in *Asteraceae* (Torices & Mendez 2010). Therefore, *P. hysterophorus* is a species in which the sexual system has evolved to monoecy by aborting female sex in the central disc florets and this sexual system enables the plant to avoid resource constraint and to produce healthy and viable seeds from the fertilized ray florets.

Cruden (1977) reported that the pollen/ovule ratio was the highest in obligately xenogamous species and decreased from obligate xenogamy, facultative xenogamy, facultative autogamy, and obligate autogamy to cleistogamy. Erbar & Langlotz (2005) have produced similar reports about these breeding systems functional in the *Asteraceae*: the pollen/ovule ratio ranged from 262 to 12 890 in obligate xenogamy, from 114 to 8214 in facultative xenogamy or facultative autogamy, and from 33 to 373 in obligate autogamy. The pollen/ovule ratio recorded for *P. hysterophorus* (12 693:1) in this study fell into the range of the pollen/ovule ratio reported for obligate xenogamy provided by Erbar & Langlotz (2005) but it was not in compliance with the facultative xenogamous breeding system functional in this species, which is characterized by minimization of autogamy (vector-mediated) and geitonogamy and maximization of xenogamy. The high pollen/ovule ratio in this species appeared to be a consequence of abortion of the female sex in disc florets. Furthermore, Erbar & Langlotz (2005) have not provided details on the sexual systems of the species used by them, while documenting the pollen/ovule ratios for the different breeding systems functional in some *Asteraceae*. Therefore, detailed studies into the functional sex in ray and disc florets in relation to the pollen/ovule ratio are required so as to evaluate the functional sexual systems in the *Asteraceae*. In *P. hysterophorus*, facultative xenogamy facilitated genetic variation through xenogamy, in order to ensure thriving in a heterogeneous and variable environment (Hsu 2006), while geitonogamy and autogamy facilitated the increase of population in the currently growing sites or other sites with similar environment. Therefore, facultative xenogamy is a "fail-safe mode of the breeding system" that enabled *P. hysterophorus* to grow as an invasive weed in a wide variety of habitats and expand its distribution range to any possible extent.

Florets opening in the morning are a common feature among the *Asteraceae* (Proctor & Yeo 1978) and this usually occurs before 08.00 h (Mani & Saravanan 1999**).** In *P. hysterophorus*, anthesis of both ray and disc florets occured in the morning between 08.00 and 09.00 h. In the capitulum, ray florets opened 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 extended receptivity until the evening of the 3rd day facilitating vector-mediated autogamy on the 2nd and the 3rd day, after which the pollen of disc florets anthesing on the 4th and the 5th day was available for geitonogamy or xenogamy only. In *Asteraceae*, the secondary pollen presentation mechanism is an important characteristic associated with protandry (Howell & al. 1993), but it is an ancestral feature in this family (Jeffrey 2009). This pollen presentation mechanism has been considered 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 *P. hysterophorus* were functionally staminate and, hence, there was no need of a special pollen presentation mechanism to prevent spontaneous autogamy.

Varatharajan & Daniel (1984) reported that thrips had intimate association with the capitula of *Asteraceae*. Laughlin (1977) wrote that in *Asteraceae* duration of growth and development of thrips synchronized well with the centripetal development of florets. Thereby thrips, which were mostly pollen feeders, efficiently used the capitulum for their growth and survival. Ananthakrishnan & al. (1981) stated that the heterogamous capitula of *Asteraceae* facilitated the

free movement of both larvae and adults in-between the individual florets, and adults carried maximum pollen load on the body. In the present study, *Frankliniella schultzei* and *Scirtothrips dorsalis* have been found to use *P. hysterophorus* for its breeding and feeding. Larval emergence was in synchrony with the timing of anthesis of the capitulum which occured for six consecutive days. Larvae and adults moved freely up and down within and between ray and disc florets in search of pollen and nectar; the larvae carried less pollen, while the adults carried more pollen because of variation in the surface area of the body. Furthermore, they used the stylar arms in ray florets and the spheroid stigma in disc florets for take-off and landing, during which the stigmatic area was dusted with pollen. The feeding activities of larvae and adult thrips within the capitulum contributed to self-pollination. As thrips emerged continuously in synchrony with sequential anthesis within the capitulum, the available forage became insufficient to meet their food requirements and in effect they migrated to other capitula on the same plant or nearby plants in search of forage, which enhanced the chances of cross-pollination. Ananthakrishnan & al. (1981) stated that thrips living in the heterogamous capitula of *Asteraceae* with solitary inflorescences spent more energy for their visits to other flowers, where there was plenty of food. In *P. hysterophorus,* the scorpioid cymes, each consisting of several capitula, enabled the thrips to minimize energy expenditure for visiting and to acquire more energy from the forage they collected from different capitula of the same plant. Such an interaction between *P. hysterophorus, Frankliniella schultzei* and *Scirtothrips dorsalis* benefited both partners, the former in pollination and the latter in breeding and feeding. Different authors have also reported *P. hysterophorus* as the breeding and feeding host plant for *Scirtothrips dorsalis, Frankliniella schultzei, Megalurothrips usitatus*, *Haplothrips gowdeyi,* and *Thrips palmi* in Andhra Pradesh (Upendhar & al. 2007), *T. tabaci* in South India (Jayanthi Mala 2013), and *T. subnudula* in India (Mound & Masumoto 2005).

Different authors have reported that the pollen of *P. hysterophorus* was airborne and also have documented that 7 % to 69 % percent of this airborne pollen was trapped at various altitudes from 1.8 m to 915 m in Bangalore (Seetharamaiah & al. 1981; Agashe & Abraham 1988; Agashe & Chatterjee 1987), at 1.5 m in Aurangabad (Bhasale 1983), at 9 m in Gulbarga (Bhat & Rajasab 1989), at 10 m in Delhi (Singh & al. 2003), and at 1.8 m in Rohtak City (Haryana) in India. These studies indicate that *P. hysterophorus* releases a copious amount of pollen into the air and disperses almost within the range of one kilometer. The present study indicates that the high concentration of *Parthenium* pollen in the air reported by these authors could be due to misidentification of its pollen, because the pollen grains of *Asteraceae* are mostly identical and the pollen of several species of this family was also airborne. This observation was further substained by the report of Gupta & Chanda (1991) that the pollen grains of *P. hysterophorus* ranged from 0 to 10 only in the airspora trapped at 5.5 m in different places of Kolkata. The report indicated further that the airborne pollen grains were almost nil even at this height and, hence, there was no scope for *P. hysterophorus* pollen to be dispersed to greater heights. Lewis & al. (1987–1988) reported that *P. hysterophorus* pollen was not transported over great distances but tended to remain airborne in appreciable quantities only near the source plants and thus a large amount could not be trapped from air. Gupta & Chanda (1991) wrote that chemical composition of the pollen indicated that it contained certain amino acids and significant percentage of total carbohydrate, protein and lipide content, though the proportion of saturated fatty acids was higher than of the unsaturated fatty acids. Opute (1975) pointed out that predominance of the saturated fatty acids would make the pollen heavy and, hence, not ideal for dispersal by wind. The present study shows that the pollen grain features of *P. hysterophorus,* namely their small size, spheroid shape and powder form were adaptations for anemophily, while the suptratectal sculpture and presence of a few spines between the colpi were adaptations for entomophily. Echinate pollen grains were very distinct in entomophilous *Asteraceae*. Furthermore, the spheroid stigma did not facilitate easily the release of pollen from anthers, which were situated within the corolla tube. In line with this, the pollen grains per capitulum and plant recorded in this study were also optimal: 63 466 per capitulum and 50 899 732 per plant. This study contradicts the report of Lewis & al. (1987–1988), who pointed out that a capitulum produces 168 192 pollen grains, the report of Gupta & Chanda (1991) of a capitulum producing 345 600 pollen grains, and of Vedanthan & al. (2014) reporting that a plant produces 625 million pollen grains. The pollen grain characters, along with more

nutrient constituents, were more favourable for entomophily than anemophily. Anemophily was probably more effective during the dry season and long dry spells in the rainy season due to the powdery form of pollen and its easy detachment from the insect carrier in flight. Therefore, it could be stated that *P. hysterophorus* is ambophilous.

Different authors reported that *P. hysterophorus* was a source of nectar and pollen for insects without any mention of their role in pollination. It was a nectar source for *Xylocopa brasilianorum* in Puerto Rico (Jackson 1986). In India, it has been reported as a major or important pollen source for honeybees, especially in periods of high floral scarcity (Satyanarayana & al. 1992; Bhusari & al. 2005; Dalio 2013), and both a nectar and pollen source for honeybees (Chaudhari 2015; Dama & al. 2016). This weed has been reported as ambophilous as it was mainly pollinated by insects and partially by wind (Gupta & Chanda 1991), as anemophilous (Lakshmi & Srinivas 2007) and entomophilous as it was pollinated by honeybees, ants, houseflies, and some members of the Diptera (Vedanthan & al. 2014). In the present study, it was found that the floral characters of *P. hysterophorus,* such as white tubular flowers with nectar situated at the corolla base, characterize entomophily (Faegri & van der Pijl 1979). Furthermore, the nectar sugar types indicating sucrose-rich nectar in the flowers of *P. hysterophorus* were typical of the "true butterfly flowers" (Baker & Baker 1982;1983). The nectar was also a source of certain essential and non-essential amino acids. In line with this, throughout the year *P. hysterophorus* was principally pollinated by butterflies followed by bees. Wasps and flies also acted as pollinators but they arweree not consistent foragers. The anthesis and nectar presentation schedules coincided well with the foraging schedules of pollinator insects. Nectar feeding by thrips reduced the standing crop of nectar and drove the pollinator insects to visit numerous capitula from as many plants as possible in quest of nectar and such a foraging activity was useful for promoting cross-pollination, in order to achieve genetic variation by the weed.

Several reports indicated that *P. hysterophorus* pollen was allergenic and caused allergic dermatitis, asthma and bronchitis in humans (Seetharamaiah & al. 1981; Lakshmi & Srinivas 2007; Kaur & al. 2014). However, there was no information on the effects of pollen in pollen-feeding insects, especially honeybees. In this context, Dalio (2013) has stated that the adverse effect of pollen on adult honeybees, their brood or on hive products should be investigated, since the pollen is allergic to human beings. Furthermore, the adverse effect of pollen on all other pollinator insects should be investigated too. The present study indicates that the human health problems relating to the pollen of this weed arose mostly in the dry season, due to emission of powdery pollen by wind or by pollen-carrying insects, and release of bio-particles, due to withering and decomposition of the aerial parts of the plant in areas where the soil was dehydrated.

The present study shows that *P. hysterophorus,* with an average number of 802 capitula per plant, produced approximately 3700 seeds (cypselas) from the ray florets, which suggested that the plant was not a prolific seed producer. This finding does not comply with Navie & al. (1996), who reported that *P. hysterophorus* was a prolific seed producer turning out 15 000–25 000 seeds per plant, nor with Lakshmi & Srinivas (2007), who claimed that this weed produced up to 25 000 seeds per plant. The high seed set rate recorded by these authors was impossible, because only ray florets produced seed, while disc florets were staminate and did not produce seed.

The present study has shown that *P. hysterophorus,* with a minimum life span of seven months and a maximum life span of 10 months, produced continuously several batches of seed, if the soil was damp. Fertilized ray florets produced seeds within two weeks. Disc florets remained in place until the seeds set in ray florets and then fell off collectively as a single unit. The seed was a wedge-shaped cypsela crowned with persistent corolla appendages and stylar arms. It was shed together with a straw-coloured fruit layer and two adjacent lateral sterile disc florets. These structures acted collectively as air sacs and aided the cypsela dispersal by wind. Monaco & al. (2001) have reported that *P. hysterophorus* was anemochorus, zoochorous, anthropochrous, and ombrohydrochorous. Annapurna & Singh (2003) have pointed out that soil environment influenced the seed mass and seed production in *P. hysterophorus*. Furthermore, these authors have also stated that the fundamental functional traits of seeds in this weed varied with soil environment and that these variations enabled it to adjust to a variety of habitat conditions. Dhileepan (2012) has reported that reproductive output correlated with plant size which, in turn, was related to soil environment. Pan-

dey & al. (2003) have written that the reproductive output was influenced by season: it was low in winter as compared to summer in *P. hysterophorus*. These studies indicate that seasonal differences and soil environment have a strong bearing on the reproductive output and this information signifies that *P. hysterophorus* is flexible in using different habitats, which ensures it as a successful invasive weed. The present study also indicates that *P. hysterophorus* was growing successfully in different habitats in the study site and has become invasive in the process.

The present study also shows that *P. hysterophorus* cypselas did not have a dormancy period and germinated any time, if moisture was available in the soil. This weed was photo- and thermo-insensitive and survived under extreme environmental conditions (Lakshmi & Srinivas 2007). Its seeds also possessed the ability to remain viable in the soil for many years (Monaco & al. 2001). Rapid germination rate was important for seedling establishment and could provide competitive advantage (Baker 1972). In areas where there was a dense population of *P. hysterophorus*, its seedlings emerged quickly and formed a dense carpet that inhibited the establishment of other species (Navie & al. 2004). The weed also had innate dormancy which prevented a large portion of seeds from germinating after the first rainfall, because some leaching of germination inhibitors was required before germination (Picman & Picman 1984). Such inhibitors were important for preventing the untimely germination of seeds and this characteristic enabled the weed to maintain some of the seeds as reserve (Navie & al. 2004). With such characters, the weed was able to colonize and invade rapidly a wide variety of habitats and to outcompete other vegetation in its vicinity. As a consequence, it caused changes in the above-ground vegetation, as well as the in underground soil nutrients. It outcompeted native and non-native palatable plants that were important to livestock. The changes in vegetation and soil nutrients could lead to ultimate changes at other trophic levels and alter the ecosystem function in forest ecosystems. In the course of time, there would be a breakdown in flower-animal interactions, pollination syndromes and seed dispersal syndromes.

The present study maintains that *P. hysterophorus* displays simultaneously vegetative, flowering and fruiting phases in different habitats depending on the age of the plant and on soil environment. The inflorescence is a heterogamous capitulum with fertile, self-compatible and self-pollinating, vector-mediated ray florets and female-sterile disc florets. The ray florets are pollinated by both insects and wind. Seeds are non-dormant and germinate, if the soil environment is favourable. With such reproductive traits, the weed has attained an invasive status at global level, due to its ability to grow in different habitats by modifying the vegetative and reproductive morphological and functional traits.

References

Agashe, S.N. & Abraham, J.N. 1988. Pollen calendar of Bangalore City – Part 1. – Indian J. Aerobiol., **1**: 35-38.

Agashe, S.N. & Chatterjee, M. 1987. Aircraft sampling of the upper airspora. – In: **Boehm, G. & Leuschner, R.M.** (Eds), Advances in Aerobiology. Proc. 3rd Intl. Conf. Aerobiology, Basel 1986, pp. 411-414, Birkhauser, Basel.

Ahlawat, M. & Dahiya, P. 2014. Risk of pollen allergy in Rohtak city (Haryana), India: a pollen calendar. – Plant Archives, **14**: 177-184.

Ananthakrishnan, T.N., Varatharajan, R. & Gopinathan, K. 1981. Seasonal periodicity of thrips infesting some *Compositae* in relation to pollination. – Proc. Indian Nat. Sci. Acad., **B47**: 811-815.

Annapurna, C. & Singh, J.S. 2003. Variation of *Parthenium hysterophorus* in response to soil quality: implications for invasiveness. – Weed Research, **43**: 190-198.

Baker, H.G. 1972. Seed weight in relation to environmental conditions in California. – Ecology, **53**: 997-1010.

Baker, H.G. & Baker, I. 1982. Chemical constituents of nectar in relation to pollination mechanisms and phylogeny. – In: **Nitecki, M.H.** (Ed.) Biochemical Aspects of Evolutionary Biology, pp. 131-171, The University of Chicago Press, Chicago.

Baker, H.G. & Baker, I. 1983. A brief historical review of the chemistry of floral nectar. – In: **Bentley, B. & Elias, T.** (Eds) The Biology of Nectaries, pp. 126-152, Columbia University Press, New York.

Bhasale, S.S. 1983. Studies in airspora of Aurangabad. Ph.D. Thesis, Marathwada University, Aurangabad, p. 335.

Bhat, M.M. & Rajasab, A.H. 1989. Efficiency of vertical cylinder spore trap and seven-day volumetric Burkard spore trap in monitoring airborne pollen and fungal spores. – Grana **28**: 147-153.

Bhatti, J.S. 1980. Species of the genus *Thrips* from India (Thysanoptera). – Syst. Entomol., **5**: 109-166.

Bhusari, N.V., Mate, D.M. & Makde, K.H. 2005. Pollen of Apis honey from Maharashtra. – Grana **44**: 216-224.

Chapman, M.A. & Abbott, R.J. 2009. Introgression of fitness genes across a ploidy barrier. – New Phytol., **186**: 63-71.

Chaudhari, S.V. 2015. Occurrence and distribution of *Zygogramma bicolorata* Pallister (*Coleoptera: Chrysomelidae*): the biocontrol agent of *Parthenium hysterophorus* L. in Rahuri Taluka. – Intl. J. Bioassyas, **4**: 4356-4361.

Chauhan, S.V.S. & Goyal, R. 2006. Pollen calendar of Agra City with special reference to allergenic significance. – J. Env. Biol., **27**: 275-281.

Cruden, R.W. 1977. Pollen-ovule ratios: a conservative indicator of breeding systems in flowering plants. – Evolution, **31**: 3246.

Dafni, A., Kevan, P.G. & Husband, B.C. 2005. Practical Pollination Biology. Enviroquest Ltd., Cambridge, p. 583.

Dalio, J.S. 2013. Foraging activity of *Apis mellifera* on *Parthenium hysterophorus*. – ISOR J. Pharm. Biol. Sci., **7**: 1-4.

Dama, L.B., Gaikwad, N.G., Valsange, A.B., Varade, M.G., Sonawane, S.R., Mane, P.P. & Vinchurkar, A.S. 2016. Melissopalynology: tool to study biodiversity in crude honey collected from South Solapur, M.S., India. – Asian J. Multidisciplinary Stud., **4**: 34-36.

Dhileepan, K. 2012. Reproductive variation in naturally occurring populations of the weed *Parthenium hysterophorus* (*Asteraceae*) in Australia. – Weed Science, **60**: 571-76.

Ebadi, M. 2007. Pharmacodynamic Basis of Herbal Medicine. CRC Press, Taylor & Francis Group, New York, p. 700.

Erbar, C. & Langlotz, M. 2005. Pollen to ovule ratios: standard or variation. A compilation. – Bot. Jahrb. Syst., **126**: 71-132.

Faegri, K. & Pijl, L. 1979. The Principles of Pollination Ecology. 3rd ed. Pergamon Press, New York, p. 244.

Flan, C. (Ed.). 2009. Global Compositae Checklist.

Gunathilagaraj, K., Perumal, T.N.A., Jayaram, K. & Ganesh Kumar, M. 1998. Field Guide: Some South Indian Butterflies. Niligiri Wildlife and Environmental Association, Niligiri, p. 274.

Gupta, S. & Chanda, S. 1991. Aerobiology and some chemical parameters of *Parthenium hysterophorus* pollen. – Grana, **30**: 497-503.

Gupta, S.K., Monika., Gupta, V. & Deepika. 2016. An overview of airborne contact dermatitis. – Air Water Borne Diseases, 5: 128-130.

Haseler, W.H. 1976. *Parthenium hysterophorus* L. in Australia. – PANS., **22**: 515-517.

Hedge, B.A. & Patil, T.M. 1980. Physiological studies on *Parthenium hysterophorus* L. under different ecological conditions. – Biogiyanam, **6:** 15-19.

Howell, G.J., Slater, A.T. & Knox, R.B. 1993. Secondary pollen presentation in angiosperms and its biological significance. – Aust. J. Bot., **41:** 417-438.

Hsu, H.M. 2006. Implication of the invasiveness of *Bidens pilosa* var. *radiata* Sch. Bip. by studying its superiority over *Bidens bipinnata* L. MS Thesis, National Taiwan University, Taipei, p. 106.

Jackson, G.C. 1986. Additional host plants of the Carpenter Bee, *Xylocopa brasilianorum* (L.) (Hymenoptera: Apoidea) in Puerto Rico. – J. Agric. Univ. P.R., **70:** 255-265.

Jain, A.K. 1983. Allergenic pollen grains of *P. hysterophorus* Linn. in the atmosphere of Gwalior (MP). – Proc. Indian Nat. Sci. Acad., **B59**: 55-58.

Jayanthi Mala, B.R. 2013. Off-seasonal survival of onion thrips, *Thrips tabaci* Lindeman infesting onion (*Allium cepa*). – Insect Environ., **19**: 193-194.

Jeffrey, C. 2009. Evolution of *Compositae* flowers. – In: **Funk, V., Susanna, A., Stuessy, T.F. & Bayer, R.J.** (Eds) Systematics, Evolution, and Ciogeography of *Compositae*, pp. 131-138, International Association for Plant Taxonomy, Vienna.

Joshi, A., Bachheti, R.K., Sharma, A. & Mamgain, R. 2016. *Parthenium hysterophorus* L. (*Asteraceae*): A boon or curse? (A Review). – Oriental Journal of Chemistry, 32: 1283-1294.

Kaur, M., Aggarwal, N.K., Kumar, V. & Dhiman, R. 2014. Effects and management of *Parthenium hysterophorus:* a weed of global significance. – Intl. Scholarly Res. Notices, **1**: 1-12.

Kunte, K. 2007. India – A Lifescape: Butterflies of Peninsular India. Universities Press, Hyderabad.

Ladd, P.G. 1994. Pollen presenters in the flowering plants – form and function. – Bot. J. Linn. Soc., **115**: 165-195.

Lakshmi, C. & Srinivas, C.R. 2007. *Parthenium:* a wide-angle view. – Indian J. Dermatol. Venereol. Leprol., **73**: 296-306.

Laughlin, R. 1977. The gum tree thrips, *Isoneurothrips australis* Bagnall. Survival at different temperature and humidities and their relation to capacity for survival. – Aust. J. Ecol., **2**: 391-398.

Lewis, W., Dixit, A.B. & Wedner, H.J. 1987-1988. Reproductive biology of *Parthenium hysterophorus* (Asteraceae). – J. Palynol., **23-24**: 73-78.

Mamood, A.N., Ray, D.T. & Waller, G.D. 1990. Seed set in Guayule (*Parthenium argentatum*, Asteraceae) in relation to insect pollination. – Economic Bot., **44**: 440-444.

Mani, M.S. & Saravanan, J.M. 1999. Pollination ecology and evolution in *Compositae* (*Asteraceae*). Science Publishers, New Hampshire, p. 166.

Mazer, S.J. & Dawson, K.A. 2001. Size-dependent sex allocation in *Clarkia unguiculata* (*Onagraceae*): ontogenetic and genetic variation. – Am. J. Bot., **88:** 819-831.

Monaco, J.T., Weller, S.C. & Ashton, F.M. 2001. Weed Biology and Ecology. Acad. Publ., New York, p. 605.

Motooka, P. 2003. Weeds of Hawaii Pastures and Natural Areas: an Identification and Management Guide. College of Tropical Agricultural and Human Resources. University of Hawaii, Manoa, p. 316.

Mound, L.A. & Masumoto, M. 2005. The genus *Thrips* (Thysanoptera, Thripidae) in Australia, New Caledonia and New Zealand. – Zootaxa, **1020**: 1-64.

Narwal, S.S., Palaniraj, R., Sati, S.C., Kadian, HS. & Dahiya, D.S. 2003. Allelpopathic plants: 8. *Parthenium hysterophorus* L. – Allelopathy J., **11**: 151-170.

Navie, S.C., McFadyen, R.E., Panetta, F.D. & Adkins, S.W. 1996. The biology of Australian weeds. 27. *Parthenium hysterophorus* L. – Plant Prot. Q., **11**: 76-88.

Navie, S.C., Panetta, F.D., McFadyen, R.E. & Adkins, S.W. 2004. Germinable soil seed banks of Central Queensland rangelands invaded by the exotic weed *Parthenium hysterophorus* L. – Weed Biol. Manag., **4**: 154-167.

Nayar, J., Kumar, A. & Ramanujam, C.G.K. 1990. Monitoring of *Parthenium* pollen in the atmosphere of Hyderabad and its environs. – J. Indian Inst. Sci., **70**: 435-439.

Opute, E.I. 1975. Lipid and sterol composition of the pollen of the West African Oil Palm. *Elaeis guinneensis*. – Phytochem., **14**: 1023-1026.

Pandey, D.K., Palni, L.M.S. & Joshi, S.C. 2003. Growth, reproduction, and photosynthesis of ragweed parthenium (*Parthenium hysterophorus*). – Weed Sci., 51: 191-201.

Patil, T.M. & Hedge, B.A. 1988. Isolation and purification of sesquiterpene lactone from the leaves of *Parthenium hysterophorus* L. Its allelopathic and cytotoxic effects. – Curr. Sci., 57: 1178-1181.

Picman, J. & Picman, A.K. 1984. Autotoxicity in *Parthenium hysterophorus* and its possible role in control of germination. – Biochem. Syst. Ecol., **12**: 287-292.

Primack, R.B. & Lloyd, D.G. 1980. Andromonoecy in the New Zealand montane shrub Manuka, *Leptospermum scoparium* (Myrtaceae). – Am. J. Bot., **67**: 361-368.

Proctor, M.C.F. & Yeo, P. 1978. The Pollination of Flowers. William Collins Sons & Co. Ltd., Glasgow, p. 195.

Rao, R.S. 1956. *Parthenium,* a new record for India. – J. Bombay Nat. Hist. Soc., **54**: 218-220.

Satyanarayana, M.C., Mohana Rao, G. & Singh, T.S.M.S. 1992. Studies on pollen sources of *Apis cerana* Fabr. and *Apis mellifera* L. bees at Muzaffarpur, Bihar, India. – Apidologie, **23:** 33-46.

Seetharamaiah, A.M., Viswanath, B. & Subba Rao, P.V. 1981. Atmospheric survey of *Parthenium hysterophorus*. – Ann. Allergy, **47**: 192-196.

Singh, A.B., Pandit, T. & Dahiya, P. 2003. Changes in airborne pollen concentrations in Delhi, India. – Grana, **42**: 168-177.

Smitley, D. 2016. Protecting and enhancing pollinators in urban landscapes for the US North Central Region. – Michigan State University Extension Bulletin, E3314.

Torices, R. & Mendez, M. 2010. Fruit size decline from the margin to the center of capitula is the result of resource competition and architectural constraints. – Oecologia, **164**: 949-958.

Torices, R., Mendez, M. & Gomez, J.M. 2011. Where do monomorphic sexual systems fit in the evolution of dioecy? Insights from the largest family of angiosperms. – New Phytol., **190**: 238-248.

Towers, G.H.N. & Subba Rao, P.V. 1992. Impact of the pantropical weed, *Parthenium hysterophorus* L. on human affairs. – In: Proc. 1st Intl. Weed Control Congress, Weed Sci. Soc. pp. 134-138, Melbourne, Australia.

Towers, G.H.N., Rodriguez, E., Bennett, F.D. & Subba Rao, P.V. 1977. Biology and chemistry of *Parthenium hysterophorus* L., a problem weed in India. – J. Sci. Industr. Res., (India) **36**: 672-684.

Upendhar, S, Singh, T.V.K. & Prasada Rao, R.D.V.J. 2007. Survey of the occurrence of various thrips and sunflower necrosis disease in Andhra Pradesh. – Indian J. Plant Protection, **35**: 73-75.

Varatharajan, R. & Daniel, M. 1984. Studies on soil pupation in some phytophagous thrips. – J. Soil Biol. & Ecol., **4**: 116-123.

Vedanthan, P.K., Nelson, H., Agashe, S.N., Mahesh, P.A. & Katial, R. (Eds) 2014. Text Book of Allergy for the Clinician. CRC Press, Taylor & Francis Group, New York. p. 496.

Verma, S.C. & Singla, R.K. 1990. Some observations on fertility and incompatibility in *Parthenium hysterophorus* L. (*Asteraceae*). – Plant Cell Incompatibility Newsletter, 22: 82-91.