

Secondary pollen presentation and psychophily in *Vernonia albicans* & *V. cinerea* (Asteraceae)

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Abstract. *Vernonia albicans* and *Vernonia cinerea* produce two or three generations from seeds during rainy season. In both, the capitula produce only disc florets. The florets are monochromatic in *V. albicans* and dichromatic in *V. cinerea*. The florets are protandrous, temporally dioecious and display secondary pollen presentation using brush mechanism to avoid autonomous pollination. The two *Vernonia* species are entomophilous. *V. albicans* is exclusively psychophilous while *V. cinerea* is principally psychophilous (pollination by butterflies). Thrips also pollinate the florets in both the species while using them as breeding and feeding sites. The fruit is cypsela and anemochorous. As the plants grow in well-drained nutrient-deficient soils of open habitats, they act as pioneer species and, hence, have the potential for use in the restoration of degraded lands.

Key words: anemochory, brush mechanism, psychophily, secondary pollination, *Vernonia albicans*, *Vernonia cinerea*

Introduction

Vernonia is a genus named after the English botanist William Vernon. It includes about 1000 species of trees, shrubs and perennials distributed in the tropical and subtropical regions of Asia, Africa and America. It has two major centers of diversification: one in southern Brazil and the other in tropical Africa. The genus is widely used as food and medicine; it is a principal source of vernolic acid in addition to sesquiterpene lactones and flavonoid compounds (Harborne & Williams 1977). In this genus, the capitula produce only one type of florets which represent disc florets (Jones 1977; Tovang & Verpoorte 2013). Cypselar features have been shown to be important for demarcation of the species of this genus (Basak & Mukherjee 2003). *V. oligocephala* flowers attract many insects, especially bees and butterflies. The seeds are enclosed in pappus and dispersed by the wind (Pooley 1998). *V. missurica* is pollinated by bumblebees, halictid bees, and miner bees; butterflies and skippers also pollinate the flowers occasionally. The flowers are capable of

self-pollination in the absence of these insects (Robinson 1999). *V. galamensis* is widely distributed in the regions of Africa. It represents a species complex of six subspecies, namely, *galamensis*, *mutomoensis*, *nairobensis*, *afromontana*, *gibbosa*, and *lushotoensis* (Gilbert 1986). It is self-fertile and is classified as a self-pollinating species (Baye & Becker 2004).

Vernonia cinerea is native to Africa, tropical and temperate Asia and Australia, but it is also widely distributed in Africa, India, Bangladesh and Sri Lanka. Almost all parts of the plant are used in traditional medicine to treat various human diseases and ailments (Nwaogaranya & Mbaekwe 2015; Bandyopadhyay & al. 2014; Shelar & al. 2014). The plant shows flowering and fruiting throughout the year and it is propagated by seed. Seeds do not have a dormancy period and germinate four days after sowing (Akobundu & Agyakwa 1998). *Vernonia albicans* is distributed in the Indian Peninsula, Malaysia, China and Sri Lanka (Pullaiah & al. 2007). It is used for treatment of filariasis (Girach & al. 1998) and eye infections by tribal people (Venkata Ratnam & al. 2010). Despite their ecological and medicinal importance, these

species have not been studied for their reproductive biology so far. Keeping this in mind, the present study has been designed to investigate the following objectives: floral structural and functional morphology, anther dehiscence and pollen presentation, growth and behavior of style during anthesis, pollination mechanism, pollination, pollinators, sexual system and seed dispersal in *Vernonia albicans* DC. and *Vernonia cinerea* (L.) Less. (subfamily Cichorioideae; tribe Vernonieae). The study provides useful information on the functionality of secondary pollen presentation, brush type pollination mechanism, entomophily, psychophily (pollination by butterflies) and anemochory that enable *Vernonia* species to grow and survive as isolated individuals or as populations in disturbed and undisturbed habitats.

Material and methods

Vernonia albicans and *Vernonia cinerea* which grow in the Visakhapatnam region (Latitude 17°42'N and Longitude 82°18'E, 45 m elevation), Andhra Pradesh, India, were selected for a study in the period of June 2014 – December 2016. The inflorescence type and the number of florets per inflorescence were noted down. Ten inflorescences, which have not commenced flowering, were tagged and followed daily to record flower production per inflorescence and flowering duration. Twenty-five fresh florets were used to record the floret morphometrics and features and to examine them in relation to the forage collection activity of insects. Twenty inflorescences, which have not commenced flowering, were tagged and watched to record an accurate anthesis schedule, and the timing and mode of 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. A micropipette was inserted into the floret base to extract nectar and measure its volume/floret. The protocols provided by Dafni & al. (2005) were followed for nectar analysis for sugar types and amino acids, pollen output/floret, pollen grain features, and stigma receptivity duration.

The insect species were observed by naked eye and by binoculars; they were identified by tallying with the identified specimens available at the Department of Environmental Sciences, Andhra University, Visakhapatnam. Butterflies were identified by consulting the books of Kunte (2007) and Gunathilagaraj & al. (1998). The methodology described by Dileepu

Kumar & al. (2017) was followed to record the daily foraging activity rate, observe foraging behavior and determine pollen carryout capacity of each insect species, so as to evaluate their role in pollination.

A sample of fruited florets from different inflorescences was collected. The fruit set was calculated on the basis of the seed status in each fruited floret. Seeds were found to be of two types: unfilled or half-filled, and completely filled. Using this as a criterion, the filled seed set was calculated. Filled seeds were designated as viable ones and the unfilled or half-filled as inviable. A sample of inflorescences was tagged and watched for noting down the duration of fruit maturation. Seed characteristics were observed to evaluate their mode of dispersal. Casual field visits were made to record whether the seeds germinate immediately after they are dispersed or not.

Results

Vernonia albicans

Phenology: The plant is an erect annual herb with striate branches. It grows primarily on bare slopes and in forest undergrowth. Leaves are alternate, ovate-lanceolate, pubescent above, tomentose below. 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 is adequately wet. Irrespective of the soil moisture status, the plant shows peak flowering during September–December (Fig. 1a). Each plant produces 35–40 paniced heads consisting of pendulous pedunculate flat-topped capitula in leaf axils, as well as in terminal portions. A capitulum is 12±1.3 mm long, 7±0.8 mm wide, tomentose outside and consists of 27±3 disc florets, while ray florets are totally absent. The florets open acropetally within two days (Fig. 1b,c). Of all florets produced by the capitulum, 76% open on the first and 24% on the second day (Table 1).

Flower morphology: The capitulum is protected by 5.5±0.7 mm long, 4.0±0.5 mm wide green involucre. The disc florets are small (8.1±0.5 mm long, 1.9±0.3 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 (4.1±0.3 mm long, 1 mm wide) tipped with five glabrous lobes (1.6±0.5 mm long, 1.2±0.4 mm wide). Stamens are



Fig. 1. *Vernonia albicans*: a. Individual plant in flowering phase, b. & c. Flowering inflorescences, d. Cypsela dispersal, e. Seedlings.

five (1.8 ± 0.4 mm long, 1 mm wide), white, epipetalous, and syngenesious; the anthers are 1.2 mm long, 1 mm wide, creamy-white, ditheous, with appendiculate apex. 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 pro-

Table 1. Anthesis as a function of time in *Vernonia albicans* and *Vernonia cinerea*.

Time (h)	<i>Vernonia albicans</i>			<i>Vernonia cinerea</i>						
	Day 1	%	Day 2	%	Total	Day 1	%	Day 2	%	Total
06:00	-	-	-	-	-	-	-	-	-	-
07:00	-	-	-	-	-	-	-	-	-	-
08:00	1	3	-	-	3	1	4	-	-	4
09:00	2	7	-	-	7	2	7	-	-	7
10:00	7	23	2	7	30	6	22	1	4	26
11:00	8	26	3	10	36	10	37	2	7	44
12:00	3	10	2	7	17	2	7	1	4	11
13:00	2	7	-	-	7	1	4	1	4	8
14:00	-	-	-	-	-	-	-	-	-	-
15:00	-	-	-	-	-	-	-	-	-	-
16:00	-	-	-	-	-	-	-	-	-	-
17:00	-	-	-	-	-	-	-	-	-	-
18:00	-	-	-	-	-	-	-	-	-	-

ducing a tube that surrounds the style. Pollen is shed to the interior of this tube (introrse dehiscence). The ovary is green (1.1 mm long, 1 mm wide), hairy, bicarpellary, unilocular with a single ovule on basal placentation. The style is 6.4 ± 0.5 mm long and terminates into two pubescent stylar arms with inside stigmatic surfaces. A nectariferous disc is present at the base of style inside the corolla tube. The style with its aligned arms extends beyond the height of anthers; the stylar arms diverge and curve inwards exposing the hidden stigmatic surfaces and finally over-arching the florets.

Floral biology: The disc florets open early in the morning 08:00–13:00 h on clear sunny days (Table 1). The flowers open completely on sunny days and only partially on rainy days. Individual disc florets take about three hours to open from the mature bud phase. The anthers dehisce by longitudinal slits during mature bud phase and, hence, the florets are protandrous. At the mature bud stage, the style with its aligned stylar arms lies below the anthers. During and immediately after anthesis, the style grows, elongates and passes through the tube formed by the fused anthers brushing the pollen with its external stylar hairs. At this stage, the inner stigmatic surfaces are unreceptive and not exposed, which functionally prevents autogamy. Such a form of pollen

presentation is referred to as "secondary pollen presentation mechanism" which ensures the pollen availability to insects visiting the capitula on daily basis. The style with its aligned branches gradually diverges in the early hours of the 2nd day; then the inner stigmatic surfaces attain receptivity and remain so until the end of that day. The stylar arms curve inwards towards the center of the floret, completely exposing the receptive stigmatic surfaces. The pollen grains are creamy-white, spherical to rounded, radially symmetrical, lophate, tricolpate, echinate and $31.54 \pm 5.61 \mu\text{m}$ in size. The pollen output per anther is 49 ± 1.12 and per flower 245. The pollen-ovule ratio is 245:1. A disc floret yields $1.3 \mu\text{l}$ of nectar, which rises up as it accumulates in the floret due to the narrow corolla tube. The sugar types present in the nectar include sucrose, glucose and fructose; they are present in that order of dominance. The nectar contains the essential amino acids such as arginine, histidine, lysine, leucine, threonine, tryptophan, isoleucine, methionine, phenylalanine and valine; the first five amino acids are dominant. It also contains non-essential amino acids such as alanine, amino-butyric acid, aspartic acid, cysteine, cystine, glutamic acid, glycine, hydroxyproline, proline, serine, and tyrosine. The disc florets wither away after two days. After the fruit formation begins, the withered petals and stamens gradually fall off.

Pollination mechanism: The disc florets present the stamens and stigmas at different positions. The anthers dehisce inwardly and discharge pollen grains into the anther tube during mature bud stage. At this stage, the style lies below the basal part of the anthers. During and immediately after anthesis, the style with its aligned stylar arms elongates within the anther tube and brushes the pollen out of the anther tube predominantly by external stylar hairs called "sweeping hairs", which brush the pollen only on the outside of the style and stylar arms. Such a pollen presentation pattern is indicative of secondary pollen presentation functional by brush mechanism. Since the stylar arms are in a closed state and the inside stigmatic surfaces are unreceptive, there is no possibility for autogamy. In the early hours of the 2nd day, the stigmatic surfaces attain receptivity, gradually diverge and curve downwards, totally exposing the inner stigmatic surfaces within three hours; the stigmatic surfaces remain receptive until the end of that day. The secondary pollen presentation mechanism represented by brush mechanism and the staminate phase on the first day and pistillate phase on the second day appear to have evolved to prevent autogamy and promote cross-pollina-

tion. However, the anthesis of disc florets for two consecutive days in the same and different capitula on the same plant facilitates the occurrence of vector-mediated self-pollination. Therefore, the secondary pollen presentation mechanism and the sexual system functional in this species do not insulate completely from the occurrence of self-pollination and, hence, the flowers set fruit and seed through self- as well as cross-pollination.

Foraging activity: The capitulum is the unit of attraction for insects. The disc florets presented by capitula were foraged consistently for nectar by butterflies, especially during the peak flowering season. The foraging butterflies represented three families: *Pieridae*, *Nymphalidae* and *Lycaenidae* (Table 2). Pierid butterflies included *Catopsilia pomona* (Fig. 2a), *C. pyranthe* (Fig. 2b) and *Eurema hecabe* (Fig. 2c). Nymphalid butterflies were *Acraea violae* (Fig. 2d), *Junonia lemonias*, *J. hierta*, *J. almana*, *Tirumala limniace* (Fig. 2e), *Danaus chrysippus* and *Euploea core* (Fig. 2f). Lycaenid butterflies were *Castalius rosimon* (Fig. 2g), *Leptotes plinius* (Fig. 2h), *Zizina otis* (Fig. 2i), *Everes lacturnus* (Fig. 2j), *Chilades pandava* and *Spindasis elima* (Fig. 2k). Among the butterflies, nymphalids accounted for 47%, lycaenids for 30% and pierids for 23% of all foraging visits (Fig. 12). All butterflies approached the flowers in upright position, landed on the flat-topped capitulum and then probed individual florets for nectar. The foraging activity pattern of butterflies showed a definite pattern

Table 2. List of butterfly foragers on *Vernonia albicans*.

Order	Family	Genus	Species	Common Name	Forage sought
Lepidoptera	Pieridae	<i>Catopsilia</i>	<i>pomona</i> F.	Common Emigrant	Nectar
		<i>Catopsilia</i>	<i>pyranthe</i> L.	Mottled Emigrant	Nectar
		<i>Eurema</i>	<i>hecabe</i> L.	Common Grass Yellow	Nectar
	Nymphalidae	<i>Acraea</i>	<i>violae</i> F.	Tawny Coster	Nectar
		<i>Junonia</i>	<i>lemonias</i> L.	Lemon Pansy	Nectar
		<i>Junonia</i>	<i>hierta</i> F.	Yellow Pansy	Nectar
		<i>Junonia</i>	<i>almana</i> L.	Peacock Pansy	Nectar
		<i>Tirumala</i>	<i>limniace</i> Cramer	Blue Tiger	Nectar
		<i>Danaus</i>	<i>chrysippus</i> L.	Plain Tiger	Nectar
		<i>Euploea</i>	<i>core</i> Cramer	Common Indian Crow	Nectar
	Lycaenidae	<i>Castalius</i>	<i>rosimon</i> F.	Common Pierrot	Nectar
		<i>Leptotes</i>	<i>plinius</i> F.	Zebra Blue	Nectar
		<i>Zizina</i>	<i>otis</i> F.	Lesser Grass Blue	Nectar
		<i>Everes</i>	<i>lacturnus</i> F.	Indian Cupid	Nectar
<i>Chilades</i>		<i>pandava</i> Horsfield	Plains Cupid	Nectar	
		<i>Spindasis</i>	<i>elima</i> Moore	Shot Silver Line	Nectar

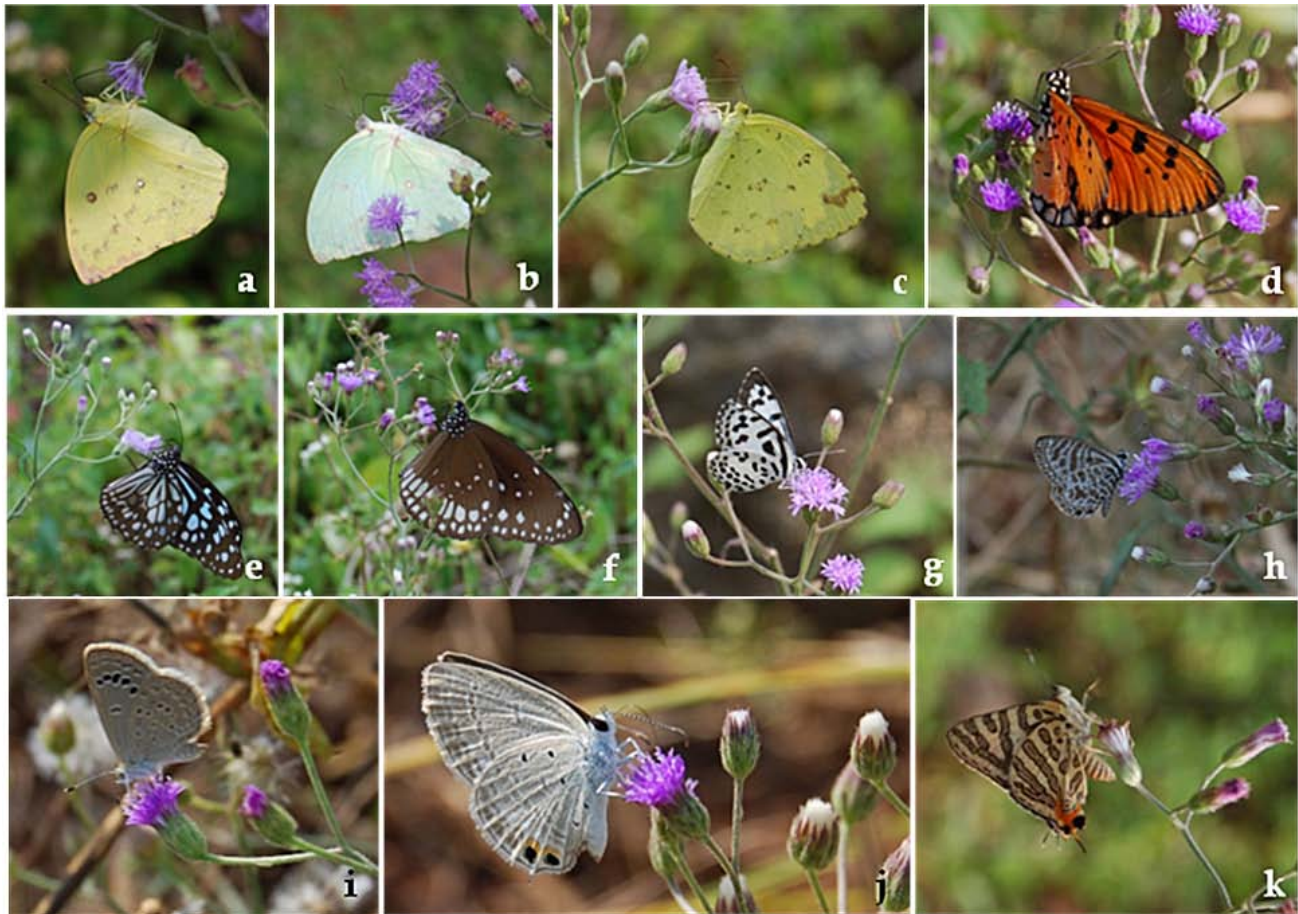


Fig. 2. *Vernonia albicans*: a-c. Pierids – a. *Catopsilia pomona*, b. *Catopsilia pyranthe*, c. *Eureka hecabe*, d-f. Nymphalids – d. *Acraea violae*, e. *Tirumala limniace*, f. *Euploea core*, g-k. Lycaenids – g. *Castalius rosimon*, h. *Leptotes plinius*, i. *Zizina otis*, j. *Everes lacturnus*, k. *Spindasis elima*.

with reference to foraging schedule. They foraged flowers during 08:00–17:00 h with peak foraging during 14:00–15:00 h coinciding well with the standing crop of nectar by that time (Fig. 7-9). They 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 the capitula of different closely and distantly spaced plants. Such a foraging behavior was considered to be promoting to a great extent both self- and cross-pollination. The body washings of butterflies collected from the flowers dur-

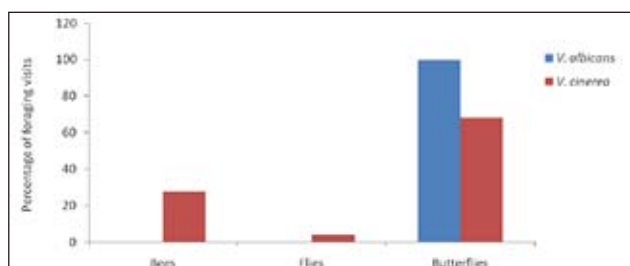


Fig. 12. Percentage of foraging visits of different categories of insects on *Vernonia albicans* and *V. cinerea*.

ing the peak foraging period revealed that they carried pollen grains ranging from 6 to 71. Individual species showed variation in the number of pollen grains carried by them. The mean number of pollen grains recorded varied from 18 to 45 (Table 3). Therefore, butterflies were considered to be the exclusive pollinators.

Apart from all these insects, thrips were found in mature buds and emerged out during the 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.

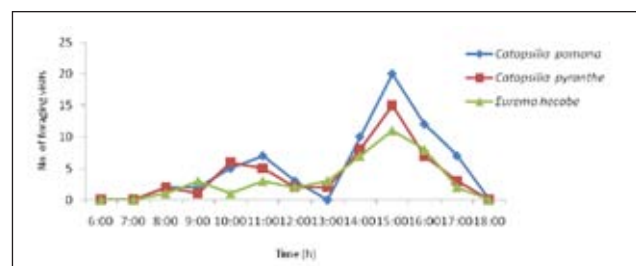


Fig. 7. Hourly foraging activity of Pierid butterflies on *Vernonia albicans*.

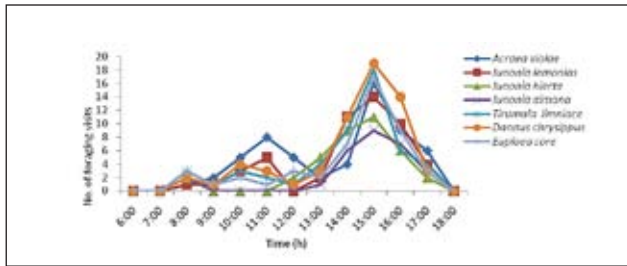


Fig. 8. Hourly foraging activity of Nymphalid butterflies on *Vernonia albicans*.

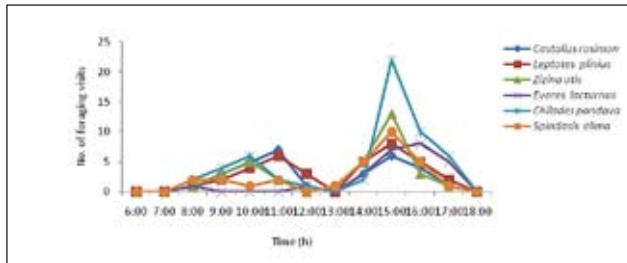


Fig. 9. Hourly foraging activity of Lycaenid butterflies on *Vernonia albicans*.

Table 3. Pollen recorded in the body washings of butterflies on *Vernonia albicans*.

Butterfly species	Sample size (N)	Number of pollen grains		
		Range	Mean	S.D
<i>Catopsilia pomona</i>	10	16–47	29.7	8.51
<i>Catopsilia pyranthe</i>	10	14–51	31.5	11.65
<i>Eurema hecabe</i>	10	21–58	35.5	10.77
<i>Acraea violae</i>	10	15–61	38.7	13.85
<i>Junonia lemonias</i>	10	20–53	36.5	8.77
<i>Junonia hierta</i>	10	12–40	29.7	7.54
<i>Junonia almana</i>	10	9–34	19.5	6.62
<i>Tirumala limniace</i>	10	24–71	45.6	13.11
<i>Danaus chrysippus</i>	10	21–60	41.8	11.60
<i>Euploea core</i>	10	17–54	36.9	12.51
<i>Castalius rosimon</i>	10	11–32	20.4	5.52
<i>Leptotes plinius</i>	10	8–30	21.5	7.18
<i>Zizina otis</i>	10	9–26	19.3	4.76
<i>Euresis lacturnus</i>	10	10–32	20.8	6.81
<i>Chilades pandava</i>	10	6–30	20.3	6.51
<i>Spindasis elima</i>	10	8–24	18.3	4.71

Since the disc florets are staminate on the first and pistillate on the second day, their foraging activity within the 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-deposited on the stigmatic surfaces of the disc florets of the same capitulum by thrips, while foraging during the post-anthesis period.

Fruiting ecology and cypselas dispersal: The fertilized flowers produce single-seeded cypselas within

two weeks. An individual capitulum produced 24 ± 4 cypselas and 22 ± 4 seeds. In open pollinations, fruit accounted for 70.89%, of which the filled seed claimed 67.36%. The cypselas is oblong, brownish, 4.8 mm long, densely adpressed, hairy, indehiscent, angled with outer setose and inner barbellate pappus of white hairs, which are up to 2–4 mm long. The pappus aids in the dispersal of cypselas and their dispersal occurs primarily by wind (Fig. 1d). Furthermore, the cypselas stick readily to hair and clothing and, hence, they are also dispersed by humans. Cypselas dispersal occurs principally on clear sunny days and during dry spells of the rainy season.

Cypselas are non-dormant and germinate as soon as they fall on the ground from the mother plant. They germinate readily in well-drained open areas with adequate soil moisture (Fig. 1e). Within a year, this species produces several generations, if the soil is adequately wet. Otherwise, the plant produces two or three generations a year during rainy season.

Vernonia cinerea

Phenology: The plant is an erect annual herb, simple to many-branched. It grows primarily in sunny or slightly shaded wastelands, along roadsides and in cultivated lands with well-drained moist soils (Fig. 3a). Stems are ribbed and glabrous to densely hairy. Leaves are alternate, ovate-lanceolate, glabrescent above, pubescent below; upper leaves are shorter, with a short petiole. The plant appears during June/July with the onset of the rainy season and disappears with the onset of the winter season, but it extends its growth, flowering and fruiting almost throughout the year, if the soil is adequately wet. Irrespective of the soil moisture status, the plant shows peak flowering in August–November. Individual plants produce capitula with purple florets or white florets, but not both. Based on the floret colour, the capitula were noted as dichromatic. The plants with purple-floret capitula are common (Fig. 4a), while those with white-floret capitula are very uncommon. The plant, flower, fruit and seed characters are alike in both categories of the capitula. Each plant produces 21–45 corymbose heads consisting of pedunculate flat-topped capitula terminally. A capitulum is 7.6 ± 0.7 mm long, 5.2 ± 1.2 mm wide, borne on leafless peduncle, tomentose outside, and consists of 25 ± 3 disc florets, while ray florets are totally absent. The florets open acropetally within two days (Fig. 3b). Of the total florets produced by



Fig. 3. *Vernonia cinerea*: a. Habit, b. Anthesing capitula, c. Anthesis in individual capitula, d. & e. Cypsela dispersal.

the capitulum, 81 % of them open on the first day and 19 % on the second day (Table 1).

Flower morphology: The capitulum produces only disc florets. The florets are small, tubate (7.1 ± 0.9 mm long, 1.3 ± 0.4 mm wide), purplish or white, odourless, actinomorphic, bisexual and nectariferous. The calyx is reduced to bristles and represented by white soft hair-like structures. The corolla is tubular (3.3 ± 0.4 mm long, 1 mm wide), tipped with five glabrous lobes (1.7 ± 0.6 mm long, 1.1 ± 0.3 mm wide). Stamens are five (1.6 ± 0.4 mm long, 1 mm wide), white, epipetalous and display syngenesious condition (Fig. 4h,i, 5g,h); the anthers are 1.4 ± 0.5 mm long, 1 mm wide, creamy-white, ditheous and with appendiculate apex. 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 (1.8 ± 0.3 mm long, 1 mm wide), hairy, bicarpellary, unilocular, with a single ovule on basal placentation (Fig. 4k,l, 5k,l). The style is 4.2 ± 0.6 mm long and terminates into two pubescent stylar arms. A nectariferous disc is present at the base of style inside the corolla tube. The style with its aligned stylar arms extends beyond the height of anthers; the stylar lobes diverge and curve inwards exposing the inner stigmatic surfaces and finally over-arching the florets.

Floral biology: The disc florets open early in the morning 08:00–13:00 h on clear sunny days (Table 1). The flowers open completely on sunny days, while they are partially open on rainy days. Individual disc florets take about three hours to open from the mature bud phase (Fig. 3c, 4b-f, 5a-f). The anthers dehiscence by

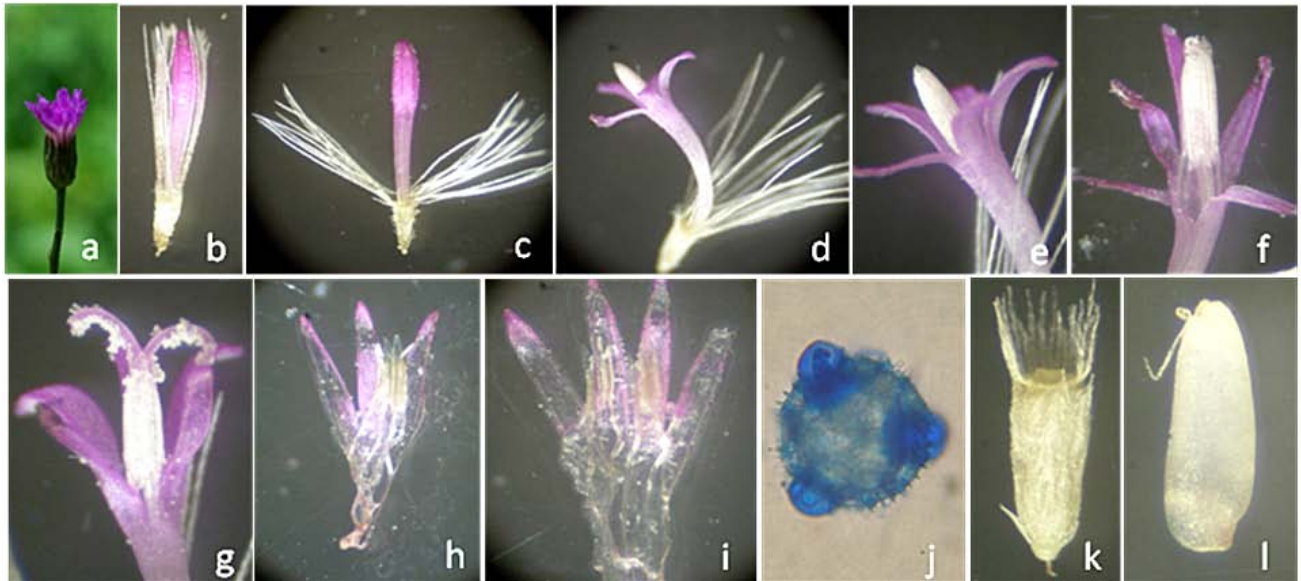


Fig. 4. *Vernonia cinerea* – Purple variety: **a.** Homogamous head inflorescence, **b-f.** Different stages of floret opening, **g.** Styler branches presenting pollen on the outer surface, **h. & i.** Syngeneous anthers, **j.** Pollen grain, **k.** Ovary, **l.** Ovule.

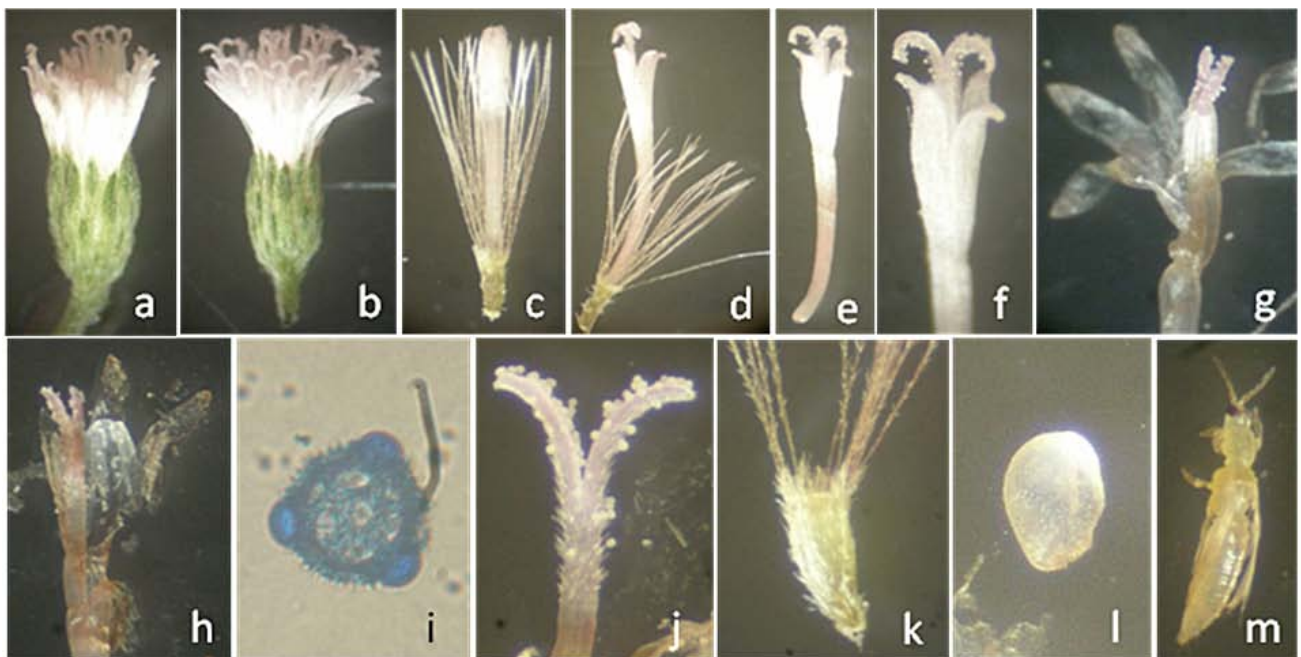


Fig. 5. *Vernonia cinerea* – White variety: **a. & b.** Different anthesis stages of capitulum, **c-f.** Different stages of anthesis of disc floret, **g. & h.** Syngeneous anthers, **i.** Pollen grain, **j.** Styler arms presenting pollen on the outer surface, **k.** Ovary, **l.** Ovule, **m.** Thrip.

longitudinal slits during the mature bud phase and, hence, the florets are protandrous. At the mature bud stage, the style with its aligned styler arms lies below the anthers. During and immediately after anthesis, the style grows, elongates and passes through the tube formed by the fused anthers, brushing the pollen with its external styler hairs (Fig. 4g, 5j). At this stage, the inner stigmatic surfaces are unreceptive and not exposed, functionally prevents autogamy. Such a form

of pollen presentation is referred to as "secondary pollen presentation mechanism", which ensures the pollen availability to insects visiting the capitula on daily basis. The style with its aligned branches gradually diverges in the early hours of the 2nd day; then the inner stigmatic surfaces attain receptivity and remain so until the end of that day. The styler arms curve inwards towards the center of the floret, completely exposing the receptive stigmatic surfaces. The pollen grains are

creamy-white, slightly triangular, radially symmetrical, lophate, tricolporate, echinate and $36.36 \pm 4.13 \mu\text{m}$ in size (Fig. 4j, 5i). The pollen grain output per anther is 111 ± 15.44 and per flower 555. The pollen-ovule ratio is 555:1. A disc floret yields $1.4 \mu\text{l}$ of nectar, which rises up as it accumulates in the floret due to the narrow corolla tube. The sugar types present in the nectar include sucrose, glucose and fructose; they are present in that order of dominance. The nectar contains four essential amino acids, which include arginine, threonine, histidine, and lysine; the last two amino acids are dominant. The non-essential amino acids present in the nectar include aspartic acid, cysteine, glutamic acid, glycine, hydroxyproline, alanine and serine; the last two are dominant. 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 dehisce inwardly and discharge pollen grains into the anther tube during mature bud stage. At this stage, the style lies below the basal part of the anthers. During and immediately after anthesis, the style with its aligned stylar arms elongates within the anther tube and brushes the pollen out of the anther tube predominantly by the external stylar hairs called "sweeping hairs" presenting the pollen only on the outside of the style and stylar arms. Such a pollen presentation pattern is indicative of secondary pollen presentation functional through brush mechanism. Since the stylar arms are in closed state and the inside stigmatic surfaces are unreceptive, the occurrence of autogamy is impossible. In the early hours of the 2nd day, the stigmatic surfaces attain receptivity, gradually diverge and curve downwards totally exposing the inner stigmatic surfaces within three hours; the stigmatic surfaces remain receptive until the end of that day. The secondary pollen presentation mechanism represented by brush mechanism and the staminate phase on the first day and pistillate phase on the second day appear to have evolved to prevent autogamy and promote cross-pollination. However, the anthesis of disc florets for two consecutive days in the same and different capitula on the same plant facilitates the occurrence of vector-mediated self-pollination. Therefore, the secondary pollen presentation mechanism and the sexual system functional in this species do not insulate completely from the occurrence of self-pollination and, hence, the flowers set fruit and seed through self- as well as cross-pollination.

Foraging activity: The capitulum is the unit of attraction for insects. The disc florets presented by capitula were foraged by bees for pollen and nectar, and by flies and butterflies for nectar (Table 4). The bees were *Trigona iridipennis* (Fig. 6a), *Ceratina* sp. (Fig. 6b) and *Anthophora bicincta* (Fig. 6c). The fly was *Musca* sp. (Fig. 6d). The butterflies represented three families: Pieridae, Nymphalidae and Lycaenidae. Pierid butterflies included *Eurema hecabe* (Fig. 6e) and *Leptosia nina* (Fig. 6f). Nymphalid butterflies were *Junonia lemonias*, *Precis iphita* (Fig. 6g), *Danaus chrysippus* (Fig. 6h), and *Euploea core*. Lycaenid butterflies were *Castalius rosimon*, *Zizula hylax* (Fig. 6i), *Zizeeria karsandra*, *Chilades laius* (Fig. 6j,k), *C. pandava* (Fig. 6l), and *Euchrysops cnejus*. Of these insects, bees accounted for 28 %, flies for 4 % and butterflies for 68 % of all foraging visits (Fig. 12). All insects approached the flowers in upright position, landed on the flat-topped capitulum and then probed individual florets for nectar. The foraging activity pattern of insects showed a definite foraging schedule. They foraged the flowers during 08:00–16:00 h, with peak foraging during 10:00–12:00 h coinciding well with the standing crop

Table 4. List of insect foragers on *Vernonia cinerea*.

Order	Family	Genus	Species	Common Name	Forage sought
Hymenoptera	Apidae	<i>Trigona</i>	<i>iridipennis</i> Smith	Stingless Bee	Pollen+Nectar
		<i>Ceratina</i>	sp.	Small Carpenter Bee	Pollen+Nectar
	Anthophoridae	<i>Anthophora</i>	<i>bicincta</i> F.	Blue Banded Bee	Pollen+Nectar
	Muscidae	<i>Musca</i>	sp.	House Fly	Nectar
Lepidoptera	Pieridae	<i>Eurema</i>	<i>hecabe</i> L.	Common Grass Yellow	Nectar
		<i>Leptosia</i>	<i>nina</i> L.	Psyche	Nectar
	Nymphalidae	<i>Junonia</i>	<i>lemonias</i> L.	Lemon Pansy	Nectar
		<i>Precis</i>	<i>iphita</i> Cramer	Chocolate Pansy	Nectar
		<i>Danaus</i>	<i>chrysippus</i> L.	Plain Tiger	Nectar
	Lycaenidae	<i>Euploea</i>	<i>core</i> Cramer	Common Indian Crow	Nectar
		<i>Castalius</i>	<i>rosimon</i> F.	Common Pierrot	Nectar
		<i>Zizula</i>	<i>hylax</i> F.	Tiny Grass Blue	Nectar
		<i>Zizeeria</i>	<i>karsandra</i> Moore	Dark Grass Blue	Nectar
		<i>Chilades</i>	<i>laius</i> Stoll	Lime Blue	Nectar
	<i>Chilades</i>	<i>pandava</i> Horsfield	Plains Cupid	Nectar	
	<i>Euchrysops</i>	<i>cnejus</i> F.	Gram Blue	Nectar	

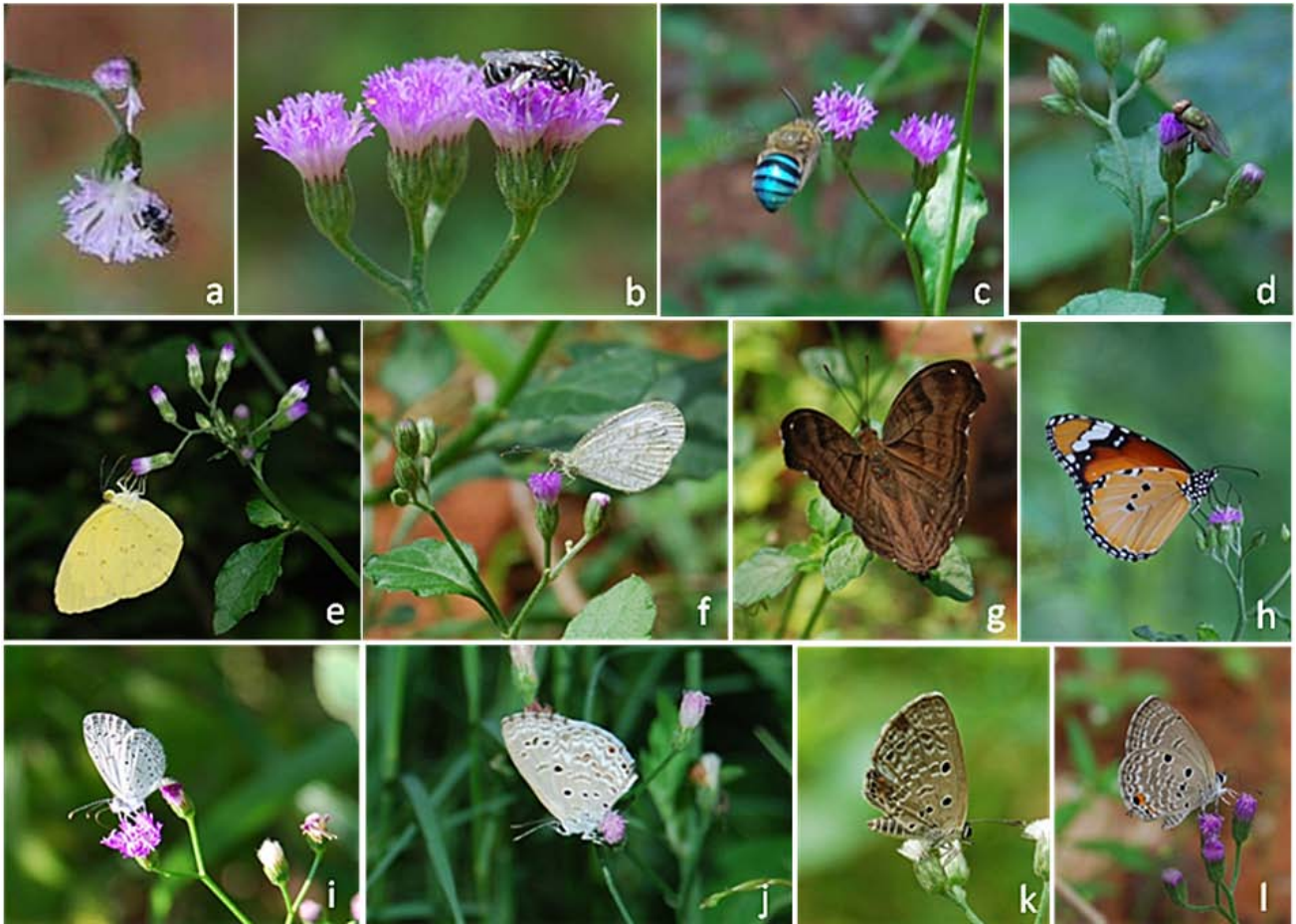


Fig. 6. *Vernonia cinerea* – Purple variety: **a.** *Trigona iridipennis* collecting pollen, **b.** *Ceratina* sp. collecting pollen, **c.** *Anthophora bicincta* collecting nectar, **d.** *Musca* sp. collecting pollen, **e-f.** Pierids – **e.** *Eurema hecabe*, **f.** *Leptosia nina*, **g-h.** Nymphalids – **g.** *Precis iphita*, **h.** *Danaus chrysippus*, **i-l.** Lycaenids – **i.** *Zizula hylax*, **j.** *Chilades laius* on purple variety, **k.** *Chilades laius* on white variety, **l.** *Chilades pandava*.

of nectar by that time (Fig. 10,11). They 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 the capitula of different closely and distantly spaced plants. Such a foraging behavior was considered to be promoting to a great extent both self- as well as cross-pollination. The body washings of insects collected from the flowers during the peak foraging period

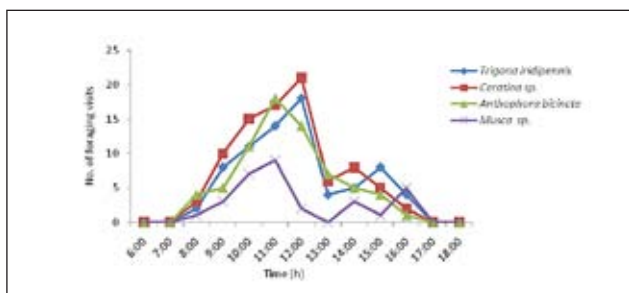


Fig. 10. Hourly foraging activity of bees and flies on *Vernonia cinerea*.

revealed that they carry pollen grains ranging from 7 to 87. Individual species showed variation in the number of pollen grains carried by them. The mean number of pollen grains recorded varied from 39 to 55 in the case of bees, 22 in the case of flies, and 17–37 in the case of butterflies (Table 5). Among these insects, bees and butterflies were consistent foragers, especially during the peak flowering season, while the fly was

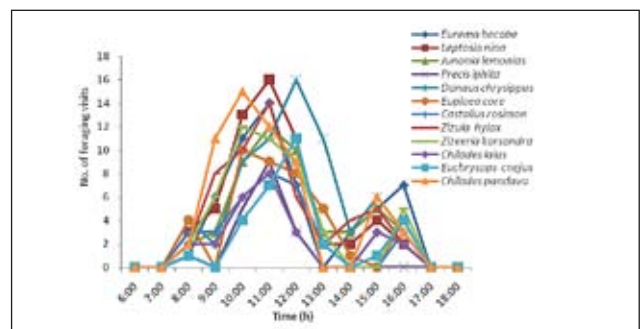


Fig. 11. Hourly foraging activity of butterflies on *Vernonia cinerea*.

an occasional forager. Therefore, bees and butterflies were considered to be the principal pollinators.

Apart from all these insects, thrips were found in the mature buds and emerged during anthesis (Fig. 5m). 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 the first day and pistillate on the second day, their foraging activity within the capitulum does not contribute to self-pollination within or between florets of the same capitulum. However, self-pollination is possible, if viable pollen is self-deposited on the stigmatic surfaces of disc florets of the same capitulum by thrips, while collecting forage during the post-anthesis period.

Fruiting ecology and cypselas dispersal: The fertilized flowers produce single-seeded cypselas within two weeks. Individual capitula produced 23 ± 4 cypselas and 19 ± 4 seeds. In open pollination, the fruit set accounted for 66.80%, of which the filled seed set claimed 80.06%. The cypselas is oblong, brownish, 2 mm long, densely adpressed, 5 hairy, indehiscent, angled, tipped with pappus of silky white hairs up to 3–5 mm long. The pappus aids in the dispersal of cypselas and cypselas dispersal occurs primarily by wind (Fig. 3d,e). Furthermore, the cypselas stick readily to hair and clothing and, hence, they are also dispersed by humans. Cypselas

Table 5. Pollen recorded in the body washings of insect foragers on *Vernonia cinerea*.

Bees and flies	Sample size (N)	Number of pollen grains		
		Range	Mean	S.D
Bees				
<i>Trigona iridipennis</i>	10	32–87	55.1	15.49
<i>Ceratina</i> sp.	10	16–54	35.8	9.73
<i>Anthophora bicincta</i>	10	23–67	39.8	12.79
Flies				
<i>Musca</i> sp.	10	8–31	22.4	6.73
Butterflies				
<i>Leptosia nina</i>	10	9–34	21.7	6.65
<i>Junonia lemonias</i>	10	20–57	37.4	11.42
<i>Precis iphita</i>	10	12–46	28.8	9.27
<i>Danaus chrysippus</i>	10	17–55	31.8	10.60
<i>Euploea core</i>	10	15–48	33.2	8.44
<i>Castalius rosimon</i>	10	11–43	25.3	9.48
<i>Zizula hylax</i>	10	7–28	18.8	5.32
<i>Zizeeria karsandra</i>	10	12–35	24.9	6.69
<i>Chilades laius</i>	10	8–24	17.7	4.29
<i>Euchrysops cnejus</i>	10	11–30	22.1	5.27
<i>Chilades pandava</i>	10	12–37	25.9	7.01

dispersal occurs principally on clear sunny days and during dry spells of the rainy season.

Cypselas are non-dormant and germinate as soon as they fall on the ground from the mother plant. They germinate readily in well-drained open areas with adequate soil moisture. Within a year, this species produces several generations, if the soil is adequately wet. Otherwise, the plant produces two or three generations a year during the rainy season.

The important phenological and reproductive aspects of both *V. albicans* and *V. cinerea* are provided in Table 6.

Table 6. Phenological and reproductive aspects of *Vernonia albicans* and *Vernonia cinerea*.

Aspect	<i>Vernonia albicans</i>	<i>Vernonia cinerea</i>
Flowering	Year-long	Year-long
No. of panicles/plant	35–40	21–45
No. of disc florets/capitulum	27 ± 3	25 ± 3
Duration of anthesis of capitulum	2 days	2 days
Time of anthesis (h)	0800–1300	0800–1300
Anther dehiscence	Mature bud stage	Mature bud stage
Pollen grain size (μm)	31.54 ± 5.61	36.36 ± 4.13
Pollen outpt/anther	49 ± 1.12	111 ± 15.44
Pollen-ovule ratio	245:1	555:1
Stigma receptivity	2 nd day of anthesis	2 nd day of anthesis
Nectar volume/disc floret (μl)	1.3	1.4
Sugar types present in nectar	Sucrose, glucose & fructose	Sucrose, glucose & fructose
Amino acids present in nectar		
Essential amino acids	arginine, histidine, lysine, leucine, threonine, tryptophan, isoleucine, methionine, phenylalanine, valine	arginine, threonine, histidine, lysine
Non-essential amino acids	alanine, amino-butyric acid, aspartic acid, cysteine, cystine, glutamic acid, glycine, hydroxyproline, proline, serine, tyrosine	aspartic acid, cysteine, glutamic acid, glycine, hydroxyproline, alanine, serine
Pollination mechanism	Brush type	Brush type
Insect pollinators	Butterflies, thrips	Bees, flies, butterflies, thrips
Foraging schedule (h)	0800–1700	0800–1600
Fruiting	Year-long	Year-long
Fruit set (%)	70.89	66.80
Seed set (%)	67.36	80.06
Seed dispersal	Anemochory, anthropochory	Anemochory, anthropochory

Discussion

Vernonia albicans is a very uncommon species that grows commonly as isolated erect plants, while *V. cinerea* is a common species that usually shows patchy distribution and additionally grows as isolated erect plants. Field studies indicated that *V. albicans* is naturally distributed on bare slopes, where sunlight strikes directly and in the sunlight striking areas of forest undergrowth. *V. cinerea* also grows primarily in open or slightly shaded areas, but it is found both in cultivated and uncultivated areas. The seeds of both species germinate and produce new plants during the rainy season. Within the rainy season, they normally produce two or three generations due to the non-dormant state of seeds. Furthermore, the study showed that the plants produce several generations in areas where the soil is sufficiently wet. Peak flowering occurs during September-December for *V. albicans* and August-November for *V. cinerea*, irrespective of the state of soil moisture. But, the plants of both species continue 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 of both *V. albicans* and *V. cinerea*.

Flowering phenology is a developmental process crucial for determining the plant's reproductive success (McNeilly & Antonovics 1968; Waser 1978). Morphological and phenological aspects of floral design and display primarily influence the quantity and quality of pollen dispersal during the pollination process. Several functional or adaptive floral traits, such as protandry, self-incompatibility, herkogamy, and secondary pollen presentation, have evolved to avoid or minimize the effects of self-interference and improve out-crossing rates (Shabir & al. 2013). Protandry, where anther dehiscence precedes stigma receptivity within a flower, is a mechanism prevalent in the *Asteraceae* (Funk & al. 2009). In self-incompatible *Asteraceae*, self-deposited pollen fails to germinate on stigmas of the same plant, but its deposition can cause pollen or stigma clogging (Barrett 2002) and reduce the access of cross-pollen to stigma surfaces and the likelihood of a floret to set seed. In contrast, in self-compatible species, self-deposited pollen is expected to germinate rapidly on the stigma in the same floret, or a neighbouring floret, and leads to rapid self-fertilization and prevention of out-crossing, although

this has never been investigated in detail in any self-compatible *Asteraceae* (Love & al. 2016). A large degree of asynchrony from floret to floret in a capitulum and capitulum to capitulum in a plant keep the pollen dispersed for a longer duration to attract the insects again and again to pollinate a number of florets (Shabir & al. 2013). In the genus *Vernonia*, the capitula produce only one type of florets, disc florets (Jones 1977; Tovang & Verpoorte 2013). Literature available on this genus indicates that the details of floral structural and functional aspects have not been studied so far. In this context, the present study on *V. albicans* and *V. cinerea* provides details helping to understand the sexual reproduction functional through the sexual system and breeding system, both of which are enabled in turn by pollinators. In both species, the inflorescence is a capitulum which produces approximately thirty disc florets presenting both pollen and nectar, and each plant produces several capitula. The aggregated arrangement of florets in a capitulum as individual units enables them to be more conspicuous and attractive to insect visitors. In case of *V. cinerea*, the dichromatic florets produced by capitula on different plants present more attraction to insect visitors. The capitulum forms a flat surface consisting of many protruding, reproductive organs. Such a flat surface 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. Since each capitulum presents several disc florets, the pollinator insects have the advantage of reducing flight time, search time and also each visit paid by them is energetically rewarding.

The secondary pollen presentation system is an important characteristic of the family *Asteraceae* (Howell & al. 1993). This form of pollen presentation is the result of functional and/or adaptive features of the flower. It enhances the placement of pollen onto the pollination vector (Inouye & al. 1994). In fact, it is a strategy to improve accuracy in pollen removal and deposition to result in the enhancement of the male and female fitness (Ladd 1994). This mechanism seems to occur in *Asteraceae* by means of stigmatic lobes curvature (Cerana 2004). Diverse methods have evolved for secondary pollen presentation, with pollen being presented onto the style (Nyman 1993), in specialized regions of the style or stigma (Westerkamp & Weber 1997), or even

over the stigmatic area (Imbert & Richards 1993), usually before flower opening. In the present study, the *Vernonia* species are protandrous and the pollen shed from the anthers is brushed by the sterile hairs (sweeping hairs) present from the tip down to the position below the branching of style in the bud stage, when the style branches are joined and inner stigmatic surfaces are not receptive. This type of pollen presentation by sweeping hairs is characteristic of the brush mechanism described in *Asteraceae* members by Torres & Galetto (2007). As the style grows out of the anther tube, the outer sweeping hairs of the style arms present pollen for pollination. The receptive papillate stigmatic surface is hidden between the two appressed style arms, preventing self-pollination. After the pollen presentation, during the functionally female phase of the floret, which occurs on the second day, the style arms separate partially exposing the receptive papillae for the receipt of pollen. The style arms serve as secondary pollen presenters in the staminate phase and expose receptive stigmatic surfaces for pollen during pistillate phase. This type of active pollen presentation is typical of the disc florets of *Asteraceae* (Ladd 1994). From day three onwards, the florets enter the senescence stage. The secondary pollen presentation system functional in *Vernonia* species has evolved to enhance the efficiency and accuracy of pollen exportation and/or pollen reception, thus increasing male and/or female fitness of the plant (Ladd 1994).

In *V. albicans* and *V. cinerea*, the capitulum inflorescence, narrow tubular corolla, production of nectar, pollen accessibility to foragers within and outside the corolla tube, and pollen characteristics such as slightly spheroidal shape, tri-porate apertures and echinate exine suggest that the plant is adapted for insect pollination. The echinate exine enables the pollen to stick to the body of the foraging insects. In *V. guineensis* also, the presence of similar pollen characters has been considered as structural adaptations for effective pollination by insects (Gimenes 1991; Edeoga & al. 1996; Mbagwu & Edeoga 2006). 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.

Duara & Kalita (2014) reported that pollination syndromes reflect convergent evolution towards forms (phenotypes) that limit the number of species

of pollinators visiting the plant. Benadi & al. (2013) reported that specialized pollinators are more flexible than generalized pollinators in the use of plant species as floral resources. There is no relationship between specialization and phenological synchrony of pollinators with particular plants. Faegri & van der Pijl (1979) provided a suite of floral characteristics that conform to butterfly pollination. They are white, pink, red, yellow, or blue, narrow, narrow tubate corolla, hidden nectar and nectar guides. Baker & Baker (1982; 1983) described two categories of flowers with reference to butterfly visits: true butterfly flowers which are characterized by deep, narrow corolla tubes with relatively copious sucrose-rich nectar, and “bee and butterfly flowers” which are characterized by short-tubed corolla with hexose-rich nectar. In the present study, the capitula of both *Vernonia* species characteristically produce only pink bisexual disc florets. The florets in a capitulum slightly vary in number, but the number stands approximately at 30. They produce a minute amount of sucrose-rich nectar which is hidden and positioned at the base of the narrow corolla tube. Furthermore, the nectar is a potential source of essential amino acids which include arginine, histidine, lysine, leucine, threonine, tryptophan, isoleucine, methionine, phenylalanine, and valine in case of *V. albicans*, and arginine, threonine, histidine, and lysine in case of *V. cinerea*. The nectar is also a source of non-essential amino acids such as alanine, aspartic acid, amino butyric acid, cysteine, cystine, glutamic acid, glycine, hydroxyproline, proline, serine and tyrosine in the case of *V. albicans*, and of aspartic acid, cysteine, glutamic acid, glycine, hydroxyproline, alanine, and serine in the case of *V. cinerea*. Therefore, the characteristics possessed by disc florets conform to butterfly pollination syndrome in both species of *Vernonia*.

In the present study, the capitula of *V. albicans* attract only butterflies, while those of *V. cinerea* attract butterflies, bees and flies. However, in both species, only butterflies are regular and consistent foragers. The butterflies visiting the florets in both species represent pierids, nymphalids and lycaenids, with the two latter categories as primary foragers suggesting mutualistic interaction between lycaenids and disc florets of these plants. As the florets are small, tubate and aggregated in capitula, the visiting small to medium-sized butterflies are appropriate pollinators. Since the disc florets possess a 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 stigmatic surfaces and sweeping hairs of the stylar arms dusted with the pollen grains and the dehisced anthers inside the corolla tube, as a result of which pollination occurs. 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 visiting butterflies, because the latter, being small to medium-bodied, do not require a huge quantity of nectar. In case of *V. cinerea* which has patchy distribution in certain areas, the butterflies frequent the capitula of flowering individuals hopping from capitulum to capitulum on the same or different plants and effect cross-pollination. But in areas where *V. cinerea* and *V. albicans* occur as isolated or scattered individuals, the butterflies do not visit them frequently. Their foraging schedule and the peak foraging activity period coincide well with the availability of standing crop of nectar. The consistent foraging activity of butterflies evidenced on both *V. albicans* and *V. cinerea* suggests that they use this plant as a major source of nectar and the relationship between the two partners conform to psychophily.

In *V. cinerea*, bees and flies use the florets opportunistically as pollen and/or nectar source. The foraging behavior of the bees indicated that they are successful as pollen collectors, mostly due to a slight mismatch between the length of their tongue and the length of the corolla tube to collect the deeply seated nectar. However, their foraging activity on the same or different conspecific plants brings about both geitonogamy and xenogamy; but their opportunistic foraging activity rates them as supplementary pollinators. Furthermore, thrips use both species of *Vernonia* 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 the case of *V. cinerea*, 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 butterflies are compelled to make multiple visits to the same or different plants in quest of nectar.

Thrips appear to be promoters of cross-pollination in both plant species by the actual pollinators by consuming the nectar. Therefore, both *V. albicans* and *V. cinerea* are entomophilous in general, but psychophilous in particular. Other researchers have also reported entomophily in *V. oligocephala* and *V. missurica*. Pooley (1998) noted that *V. oligocephala* attracts many insects, but is mainly pollinated by bees and butterflies. Robinson (1999) mentioned that *V. missurica* is mainly pollinated by different bees such as bumblebees, halictid bees and miner bees, as well as by butterflies and skippers.

Lane (1996) stated that the *Asteraceae* members studied so far display different sexual systems such as monoecy, dioecy, gynodioecy, andromonoecy, gymnomonoecy, and hermaphroditism. In the present study, both *Vernonia* species 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 a staminate phase on the day of anthesis and a pistillate phase on the following day. The display of alternate staminate and pistillate phases by the florets constitutes temporal dioecy, a sexual system evolved in this species to prevent autonomous selfing and to minimize vector-mediated selfing, especially 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 is also commensurate with the functional breeding systems in these species (Cruden 1977). Such a mixed breeding system enables *Vernonia* species to reproduce sexually, in order to thrive well seasonally and also throughout the year, if favourable soil conditions exist.

Marzinek & al. (2008) reported that cypselas are complex fruits which are dry, indehiscent, unilocular, with a single seed not adnate to the pericarp (linked only by the funicle) and originating from an inferior or epigynous ovaries, while achenes are simple fruits which are dry, indehiscent, unilocular, with a single seed linked to the pericarp only by the funicle, originating from superior ovaries. In *Asteraceae*, the ovary is inferior and produces complex fruit with the characters

mentioned by Marzinek & al. (2008) and, hence, the term 'cypsela' is used to explain fruit characteristics in this study. The fruit and seed set rates in *V. albicans* and *V. cinerea* indicate that they produce cypselas from both out-crossed and self-pollinated florets and most of the filled cypselas appear to be a result of the out-crossed florets and, hence, they may exhibit higher fitness than those resulting from selfed ones. Each cypsela appears to be the product of separate selection and fertilization by individual pollination. The pollination mechanism functional in these species ensures the necessary genetic variability to the numerous offspring produced in the same capitulum, and preserves the morphological stability of the genetically fixed characteristics.

Funk & al. (2005) reported that the plants that exhibit anemochory predominantly occur in open areas. Pooley (1998) mentioned that *Vernonia oligocephala* growing in open areas produces light seeds with hairy parachutes and disperses by wind. In the present study, *Vernonia* species are predominantly distributed in open sunny areas than in shaded ones. The cypselas consisting of seed crowned 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 *Vernonia* species, due to their predominant occurrence in open sunny areas. However, anemochory is effective in these species only on clear sunny days and long dry spells during the rainy season. Therefore, the rainy season is not ideal timing for the dispersal of seeds of these species. The ambient weather appears to be a limiting factor for the expansion and distribution of the species as a major weed. Field studies indicate that both *Vernonia* species are minor weeds and have limitations in producing huge populations, both in open and slightly shaded areas.

Vernonia albicans and *V. cinerea* have high medicinal value in several countries of their distribution (Venkata Ratnam & al. 2010; Bandyopadhyay & al. 2014; Shelar & al. 2014; Nwaogaranya & Mbaekwe 2015). The two species appear to have high potential for use in traditional medicine. Their seeds are non-dormant and germinate as soon as they fall on the ground, if the soil is well drained and sufficiently wet. Akobundu & Agyakwa (1998) also reported that flowering and fruiting occur throughout the year and seeds are the mode of propagation; the seeds do not have dormancy and germinate within a week in

V. cinerea. Both *V. albicans* and *V. cinerea* mainly support local small to medium-sized butterflies during their flowering season. Since these plant species are not invasive and minor weeds, they can be allowed to grow, in order to provide ecological services to flower foragers and the soils of open or slightly shaded habitats, which are mostly devoid of other plant species, because in such places, they serve as pioneer species, prevent erosion and regulate desertification. Perdue (1988) also noted that *V. galamensis* is important in preventing erosion and desertification. The study indicates that the studied and other species of *Vernonia* occur primarily in open habitats, add organic matter upon their death and decay, and, hence, play an important role in the restoration of habitats of low soil fertility with a scanty low-ground herbaceous flora.

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