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POLLINATION ECOLOGY OF THREE ECOLOGICALLY VALUABLE CARPETWEED HERBS, *MOLLUGO CERVIANA*, *M. NUDICAULIS* AND *M. PENTAPHYLLA* (MOLLUGINACEAE)

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Pollination ecology of three ecologically valuable carpetweed herbs, *Mollugo cerviana*, *M. nudicaulis* and *M. pentaphylla* (Molluginaceae)

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Abstract: *Mollugo cerviana*, *M. nudicaulis* and *M. pentaphylla* are annual herbs which usually grow in open dry sandy and sandy/loamy soils, and also occur in moist habitats, especially cultivated lands. The flowers possess five tepals, functional stamens and 3-carpelled ovary with several ovules and three stigmas. *M. nudicaulis* and *M. pentaphylla* are pollinated by insects. *Haplothrips* uses the flowers for breeding and feeding, which affects pollination. These species have specialized floral structural and functional behaviours for self-induced and spontaneous autogamy while keeping the options open for insect pollination after anthesis. They are facultative autogamous, which is reflected in pollen-ovule ratios and natural fruit and seed set rates. Seed dispersal modes include anemochory, ombrohydrochory and hydrochory. The seeds germinate immediately after their dispersal, and soil moisture is important in rupturing the seed coat. These species are best adapted to survive in open dry habitats as they take advantage of any sign of temporary humidity to complete their life cycle quickly.

Keywords: Anemochory, facultative autogamy, hydrochory, insect-pollination, ombrohydrochory, soil binder.

INTRODUCTION

Hutchinson (1926) recognized Molluginaceae as distinct from Aizoaceae. Molluginaceae genera previously included in the larger family Aizoaceae have been separated and treated under the Molluginaceae in subsequent classifications of the Angiosperm Phylogeny Group (APG) 1998, APG II of 2003, APG III of 2009 and APG IV of 2016. APG IV classification is the modern molecular-based system of plant taxonomy for flowering plants (angiosperms). The genus *Mollugo* is distributed in tropical to warm temperate parts of North and South America, Europe, Africa and Asia. The generic name is derived from the Latin word "*mollis*" meaning soft (Short 2002). *M. cerviana* is native to India, Sri Lanka, Pakistan and Bangladesh (Parvathamma & Shanthamma 2000). *M. nudicaulis* is distributed throughout tropical Africa and Asia (Burrows & Willis 2005). *M. cerviana* is a C_4 species, *M. nudicaulis* C_3-C_4 species and *M. pentaphylla* C_3 species; the first species is distributed in hot arid regions from pantropics to temperate regions while the other two species are distributed from pantropical and subtropical regions (Christin et al. 2010). These three species are valuable in traditional medicine for treating different diseases and ailments (Parvathamma & Shanthamma 2000; Rajamanikandan et al. 2011; Sahu et al. 2012).

Little is known about the pollination ecology of Molluginaceae, where nectar secreting tissue is present in almost all species. In several genera showy sepals or petals have evolved, both of which strongly suggest entomophily (Watson & Dallwitz 1992; Kubitzki et al. 1993). *Mollugo verticillata* is pollinated by the syrphid fly *Mesogramma marginata* (Robertson 1928). The most widely spread, weedy species of *Mollugo verticillata, M. nudicaulis* and *M. cerviana* are self- and insect-pollinated (Pax & Hoffmann 1934; Bogle 1970). In Taiwan, *M. pentaphylla* is a minor pollen source for *Apis mellifera* (Lin et al. 1993). In southern India, honey bees use *Mollugo* species as pollen source and reciprocate the plants with pollination (Ponnuchamy et al. 2014). The present study examines how *M. cerviana, M. nudicaulis* and *M. pentaphylla* are able to reproduce in semi-dry and dry habitats where pollinators are usually scarce. The principal objective of this study is to understand how floral biology, sexual and breeding systems, pollination mechanisms, fruiting ecology and seed dispersal collectively contribute to the success of sexual reproduction in these three species growing in dry habitats.

MATERIALS AND METHODS

Wild patches of *Mollugo cerviana, M. nudicaulis* and *M. pentaphylla* growing in open dry and semi-dry areas of Visakhapatnam and its surroundings (17.686°N & 83.218°E) were selected for study during March 2015–May 2017. Field trips were conducted to record phenological aspects. Ten inflorescences which have not initiated flowering on five plants were tagged and followed to record anthesis schedule and the timing of anther dehiscence. Twenty-five fresh flowers were used to record the floral morphological details. Nectar could not be measured and analyzed due to its secretion in minute quantity which was further depleted by thrips during mature bud and flower life. Twenty mature, but un-dehisced anthers, two anthers each per flower/plant from ten plants were collected and examined for pollen output as per the protocol described in Dafni et al. (2005). The calculation of pollen output per flower and pollen-ovule ratio was done as per the formulas described in Cruden (1977). Ten flowers each from five individuals were used to test stigma receptivity. It was tested with hydrogen peroxide from mature bud stage to flower closure/drop as per Dafni et al. (2005). Seventy inflorescences were tagged prior to the initiation of their flowering and followed for three weeks to record fruit and seed set rate in open-pollinations. The fruit and seed morphological characteristics were observed in detail to evaluate their adaptations for dispersal by different means. Fields visits were made during rainy season to note the aspects of seed germination and production of new plants. Based on the timings of maturation of anthers and receptivity of stigmas, the sexual system was defined and also elaborately explained its functionality to achieve self-induced autogamy, spontaneous autogamy, geitonogamy and xenogamy. The positions of stamens and stigmas during and after anthesis were observed to evaluate as to how they facilitate spontaneous autogamy during anthesis and flower closure. Further, observations were also made to evaluate as to how these positions preclude self-pollination when flowers stay open.

Insects foraging at the flowers were observed from morning to evening on four different days for their mode of approach, landing, probing behavior and contact with the floral sexual organs. Bees were identified from representative specimens available with the Department of Environmental Sciences, Andhra University, Visakhapatnam. Butterflies were identified by consulting the books of Kunte (2007) and Gunathilagaraj et al. (1998). The foraging visits of

insects were recorded using 1mx1m area of flowering patch for 10min at each hour for the entire day on four different days and the data were tabulated to record the foraging pattern and the percentage of visits made by different insect categories. The pollen/nectar collection behaviour of insects was carefully observed to assess their role in effecting pollination. Ten specimens of each insect species were captured during 0800–1100 h and brought to the laboratory. Each specimen was washed in ethyl alcohol, stained with aniline-blue on a glass slide and observed under microscope to count the number of pollen grains present. From this, the average number of pollen grains carried by each insect species was calculated to know the pollen carryover efficiency.

RESULTS

Phenology

Mollugo cerviana is a small, glabrous, slender annual herb. It is common in open dry sandy and semi-dry soils along roadsides, waste places, bare ground and dry river beds (Image 1a). Its presence is usually overlooked due to its very low ground habit, wiry reddish orange stems and thin linear leaves. The stems are numerous, upright, thin and stiff. Leaves are sessile, grey green and linear with acute apex; they arise in whorls on the stem but some are in a rosette at the base. *M. nudicaulis* is a small acaulescent annual herb with a rosette of prostrate leaves while *M. pentaphylla* is small much-branched annual herb with a thin tap root. *M. nudicaulis* (Image 2a,b) and *M. pentaphylla* (Image 4a) are common in open dry sandy and moist soils along roadsides, waste places, bare ground and cultivated lands. In *M. nudicaulis*, the leaves are sessile, succulent, glabrous, obovate to spathulate, margin entire and apex rounded. In *M. pentaphylla,* the stem is thin, angular, glabrous and tinged with brownish red when old. Leaves are petiolate, unequal, succulent, glabrous, obovate to spathulate, margin entire and apex mucronate. The basal leaves are 5 or more in rosette formwhile those upwards vary from 4 to 1. All three species appear simultaneously in vegetative, flowering and fruiting phases in different populations growing in different habitats throughout the year (Image 1b, 4b). Individual plants, however, have a short life cycle of 3 months from seed germination to seed dispersal. Although they appear throughout the year, they show robust vegetative growth and profuse flowering and fruiting during July–October when soil is damp due to occurrence of rains. In *M. cerviana*, the flowers are borne on 7–8 mm long pedicels in dichotomous and trichotomous umbellate cymes produced terminally or in leaf axils. The inflorescence arises from the rosette of basal leaves in *M. nudicaulis* and from leaf axils and terminally in *M. pentaphylla*. In *M. nudicaulis*, the dichasial or trichasial cymes are common during dry season while polychasial cymes are common during wet season. In *M. pentaphylla*, polychasial cymes are common during wet season while di- or tri-chasial cymes are common during dry season. Further, the cymes are of spreading type, pedunculate and produce pedicellate flowers; the peduncle is 7–8 mm long pedicel is 4mm long in the former while the corresponding measures for the latter are 5–8 mm and 2–4 mm, respectively. In both, the peduncle and pedicel are wiry and stiff. A polychasial cyme produces 7.5 ± 1.5 flowers in *M. nudicaulis* and 13.83 ± 4.9 in *M. pentaphylla*.

Flower morphology

In all three species, the flowers are small, odourless, actinomorphic and bisexual. They are 2.52 ± 0.4 mm long, 1.51 ± 0.5 mm wide, whitish green on adaxial side and green on abaxial side in *M. cerviana*; 3.51 ± 0.4 mm long, 4.03 ± 0.3 mm wide, creamy white on adaxial side and light green on abaxial side in *M. nudicaulis*; and 2.75 ± 0.4 mm long, 1.8 ± 0.4 mm wide, white on both adaxial and abaxial side in *M. pentaphylla*. In all, the sepals and petals are represented by a monochlamydeous perianth of 5 elliptic to oblong free tepals. They are 2.45 ± 0.4 mm long, 1.13 ± 0.2 mm wide with white margins in *M. cerviana*; 3.28 ± 0.41 mm long, 1.82 ± 0.33 mm wide, connate base and hooded apically in *M. nudicaulis*; and 2–3 mm long but connate at base in *M. pentaphylla*. The stamens are 5, anti-petalous and 1.22 ± 0.3 mm long in *M. cerviana*; 3–6 and 2.27 ± 0.17 mm long in *M. nudicaulis*; and 3-5 and 1.8 ± 0.17 mm long in *M. pentaphylla*. In all, the filaments are free, connate at base and tipped with dorsifixed dithecous anthers. In *M. pentaphylla*, the flowers with 3-stamens constituted 60%, those with 4-stamens 33% and those with 5-stamens 7%; these three types of flowers occur on the same plant. The flowers with 6-stamens are very rare. A single plant all with 5-stamened flowers was encountered during the study period and these flowers are prominently larger than other types of flowers. In 3-stamened flowers, one stamen is alterni-tepalous while the other two are anti-tepalous (Image 2e). In 4-stamened flowers, three stamens are alterni-tepalous while the other one is anti-tepalous. In 5-stamened flowers, two stamens are alterni-tepalous while the other three are anti-tepalous (Image 2f). In 6-stamened flowers, three stamens are alterni-tepalous while three
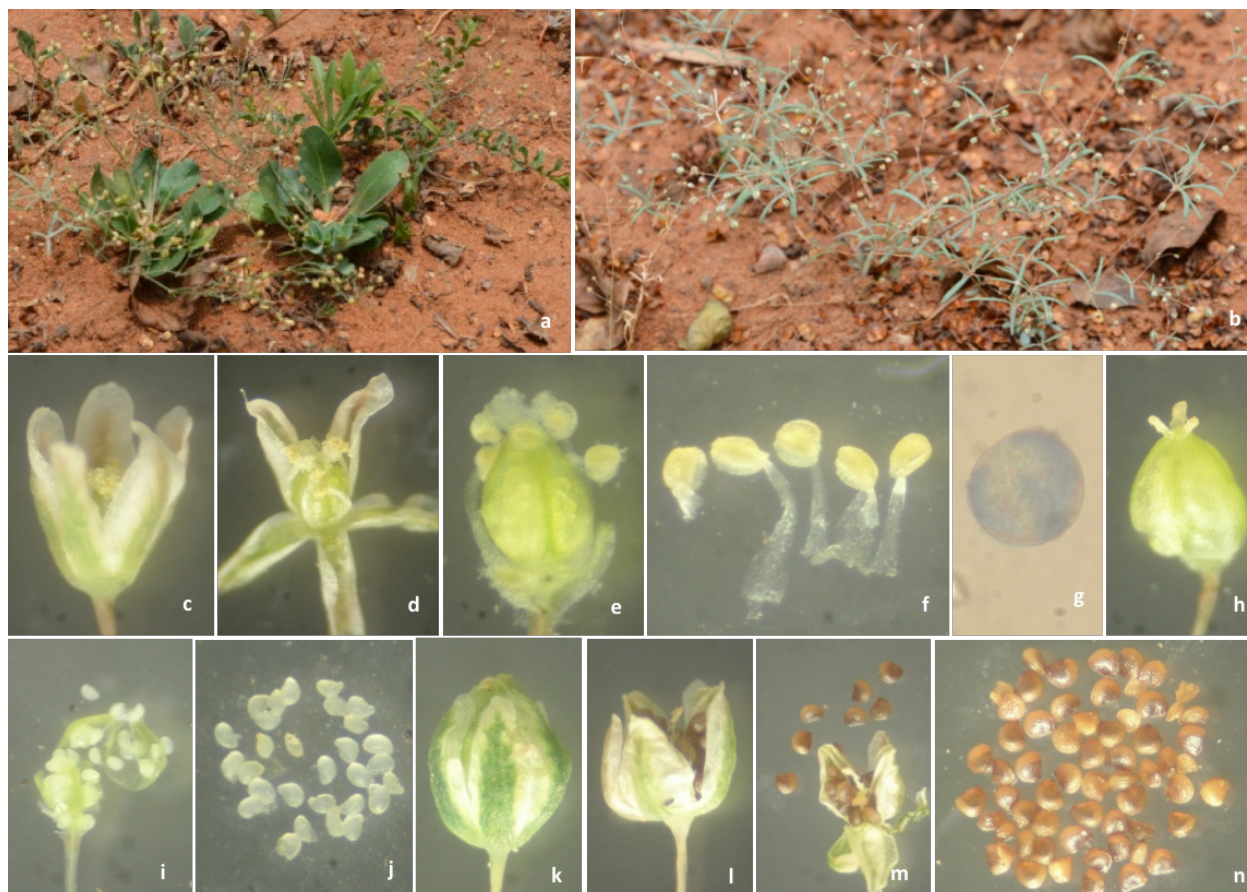
Image 1. *Mollugo cerviana*: a. Habitat with *M. nudicaulis*, b. flowering phase, c. & d. Flowering-opening phase, e. Position of stigmatic lobes and anthers at the same height contacting each other at anthesis, f. Dehisced anthers, g. Pollen grain, h. Ovary with three stigmas, i. & j. Multi-ovuled ovary, k. Maturing fruit, l. & m. Dehisced fruit capsule, n. Seeds. © A.J. Solomon Raju.

others are anti-tepalous (Image 2g). In *M. pentaphylla*, the flowers with 3-stamens constituted 91%, those with 4-stamens 7% and those with 5-stamens 2%; all theree types of flowers occur on the same plant. In 3-stamened flowers, one stamen is alterni-tepalous while the other two are anti-tepalous. In 4-stamened flowers, three stamens are alterni-tepalous while the other one is anti-tepalous. In 5-stamened flowers, two stamens are alterni-tepalous while the other three are anti-tepalous. In all three species, the ovary is light green, tri-carpellary, tri-locular syncarpous with ovules arranged on axile placentation (Image 1i,j, 2k, 4i). The ovules are 58.2 ± 8.16 in *M. cerviana* but the ovule number varied with change in stamen number in the other two species. In *M. nudicaulis*, they are 17.45 ± 3.51 in 3-stamened flowers, 19.9 ± 2.88 in 4-stamened flowers and 23.1 ± 3.70 in 5-stamened flowers. In *M. pentaphylla*, they are 16.02 ± 4.0 in 3-stamened flowers, 18.44 ± 2.0 in 4-stamened flowers and 20.11 ± 2.6 in 5-stamened flowers. The ovules are D-shaped in *M. cerviana* and *M. nudicaulis*,

and reniform in *M. pentaphylla*. In all, the style is absent but the ovary is terminated with 3 free stigmas (Image 1h, 2j, 4h). The stigmas are minutely denticulate with membranous flaps in *M. cerviana* while they are densely papillose, shiny and spreading in the other two species.

Floral biology

In all three species, mature buds open during 0700-0800 h and extend until 0900h in *M. pentaphylla* (Image 2d). Individual buds take 5 to 10 minutes from partial to full opening (Image 1c,d; 4c–e). The flowers are homogamous as the anthers and stigmas attain maturity at the same time during anthesis; the former dehisce by longitudinal slits (Image 1f, 2h) while the latter continue receptivity until the noon of the second day. In *M. cerviana*, the pollen output is 159.7 ± 14.5 per anther and 798.5 ± 69.5 per flower. The pollen-ovule ratio is 14:1. In *M. nudicaulis*, the pollen output varied with change in stamen number. It varied from 209.6 ± 17.12 to 171.4 ± 13.44 per anther and from 628.8 ± 51.36 to

Image 2. *Mollugo nudicaulis:* a. Habit - flowering phase, b. Individual plant in flowering, c. New plants, d. Bud, e. 3-stamened flower, f. 5-stamened flower, g. 6-stamened flower, h. Dehisced anthers, i. Pollen grain, j. Ovary with three styles, k. Ovules, l. Maturing fruit, m. Dehisced fruit capsule, n. Dehisced fruit capsule with seeds intact, o. Seeds. © A.J. Solomon Raju.

Table 1. Pollen aspects in *Mollugo nudicaulis* and *Mollugo pentaphylla*

Flower type	Percentage of occurrence	Mean pollen output/ anther	Mean pollen output/ flower	Mean no. of ovules/ flower	Pollen: ovule ratio
Mollugo nudicaulis					
3-stamened	60	209.6 ± 17.12	628.8 ± 51.36	17.45 ± 3.51	36 : 1
4-stamened	33	184.4 ± 13.12	737.6 ± 52.48	19.90 ± 2.88	37 : 1
5-stamened	7	171.4 ± 13.44	857.0 ± 67.20	23.10 ± 3.70	37 : 1
Mollugo pentaphylla					
3-stamened	91	277.2 ± 13.4	831.6 ± 40.2	16.02 ± 4.0	52 : 1
4-stamened	7	242.6 ± 19.6	970.4 ± 78.4	18.44 ± 2.0	53 : 1
5-stamened	2	213.4 ± 12.9	1067 ± 64.5	20.11 ± 2.6	53 : 1

857 ± 67.2 per flower in 3- to 5-stamened flowers (Table 1). The pollen-ovule ratio is 36:1 in 3-stamened flowers while it is 37:1 in 4- and 5-stamened flowers. In *M. pentaphylla*, it varied from 277.2 ± 13.4 to 213.4 ± 12.9 per anther and from 831.6 ± 40.2 to 1067 ± 64.5 per flower in 3- to 5-stamened flowers (Table 1). The pollen-ovule ratio is 52:1 in 3-stamened flowers while it is 53:1 in 4- and 5-stamened flowers. In both *M. nudicaulis* and

M. pentaphylla, the pollen production trend showed that pollen output rate gradually increased with a gradual decrease in the number of stamens produced per flower. The pollen grains are pale yellow, spheroidal, tri-colpate, tri-zonoaperturate, granulated, tectum scabrate, 21.9 ± 4.12 µm (Image 1g; 2i, 4g). In all three species, the nectar is secreted in traces during mature bud stage. The tepals together with the stamens and stigmas close

back by 1000–1100 h but this event extends until 1200h in *M. nudicaulis*.

Pollination mechanism and Pollinators

In all three species, dehisced anthers collected during anthesis showed some percentage of pollen formed tubes indicating *in situ* germination. It varied from 20% to 25% in *M. cerviana*, from 11% to 21% in *M. nudicaulis* and from 18% to 26% in *M. pentaphylla*. In all, the pollen tubes were also found on the stigma. The pollen germination and formation of tubes both within the dehisced anthers and on the stigma indicate that the presence of self-induced autogamy. In *M. cerviana*, during and after anthesis, the dehisced anthers and receptive stigmas contact with each other due to their close proximity and their position at the same height due to which autogamy occurs (Image 1e). In the other two species, during anthesis, one anther in 3-stamened flowers and 2–3 anthers in 4- and 5-stamened flowers contact the stigmas due to their close proximity and their position at the same height (Image 4f). With this situation, the anthers brush against the stigmas causing autogamy. After anthesis, all anthers move away from the stigmas but both the sex organs are situated at the same height facilitating vector-mediated self- or cross-pollination. In all the three species, during the closing of the flower, the stamens and stigmas contact each other very closely assuring autogamy if it did not occur during open state of the flower.

Thrips pollination

Haplothrips sp. (Thysanoptera: Thripidae) used the flower buds of all three species for breeding and flowers for feeding. The larvae emerged from the eggs in synchrony with anthesis and nectar production in flowers. The larvae and adults foraged for pollen and nectar. Individual thrips were dusted with pollen during their movements within the flowers. They carried pollen on their body setae, wings and legs. The pollen carried by them varied from 87 to 176 pollen grains in *M. cerviana*, from 69 to 158 in *M. nudicaulis* and 89 to 217 in *M. pentaphylla*. The thrips dispersed the pollen on free denticulate and membranous stigmas of *M. cerviana* and on free densely papillose spreading stigmas of *M. nudicaulis* and *M. pentaphylla* due to their active movement, rubbing of abdomen against the stigmatic surface, cleansing of their body parts with their hind legs and also by their wing combing mechanism. In all, the homogamous flowers were found to facilitate self-pollination in the same or different flowers of the same plant. As the plant occurs as small or large populations, thrips could fly to migrate to the flowers of other closely spaced plants and effect cross-pollination by feeding on the forage.

Insect pollination

The flowers of *M. cerviana* were never visited by any insects. The flowers of *M. nudicaulis* were foraged by bees, flies and butterflies while those of *M. pentaphylla* by bees and butterflies. Bees and flies foraged for pollen and nectar while butterflies for nectar only during 0800–1100 h with concentrated foraging activity during 0900–1000 h (Figs. 1–4). The bees, *Apis cerana* (Image 3a, 5a), *A. florea* (Image 3b, 5b), *Trigona iridipennis* (Image 3c, 5c), *Ceratina* sp. (Image 3d, 5d) visited the flowers of both *M. nudicaulis* and *M. pentaphylla*; the former was
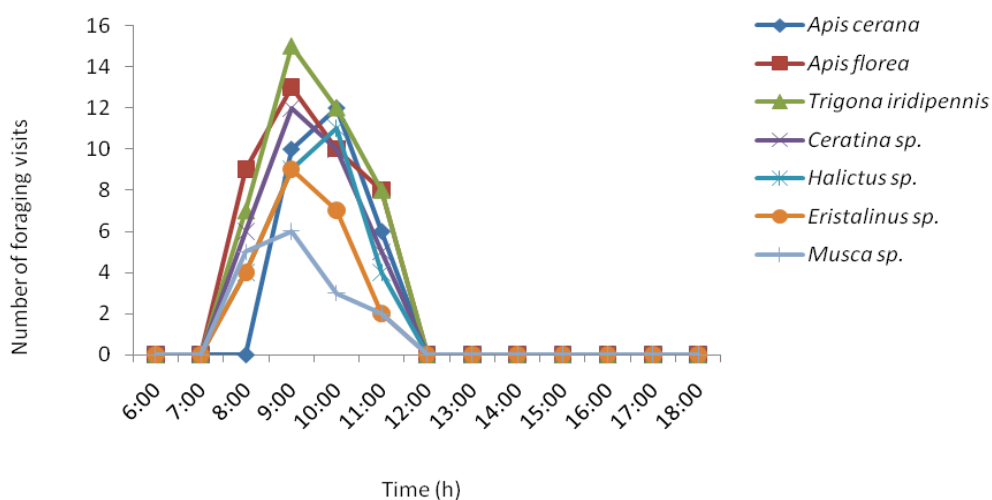

Figure 1. Hourly foraging visits of bees and flies on *Mollugo nudicaulis*
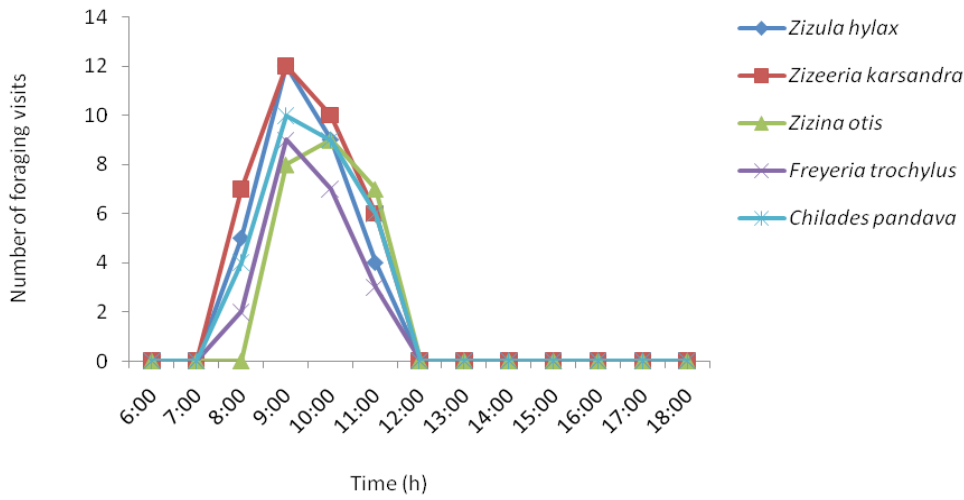
Figure 2. Hourly foraging activity of lycaenid butterflies on *Mollugo nudicaulis*
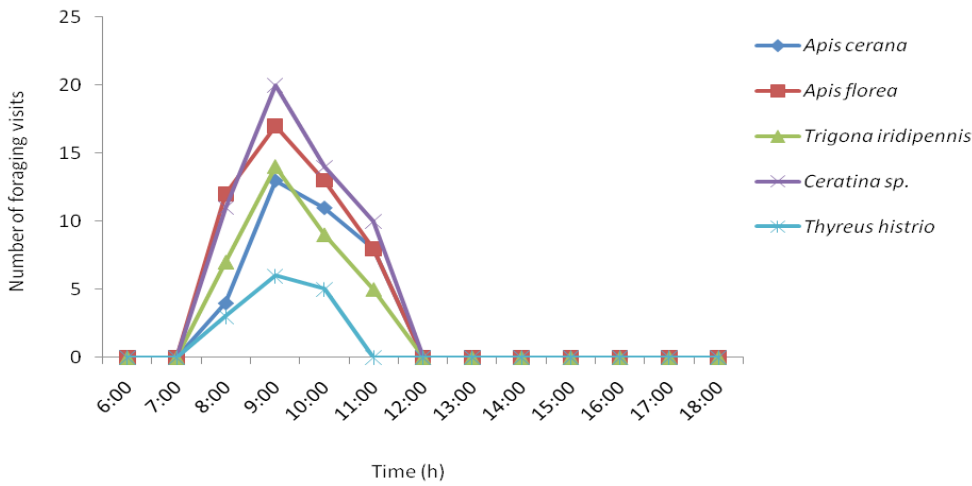

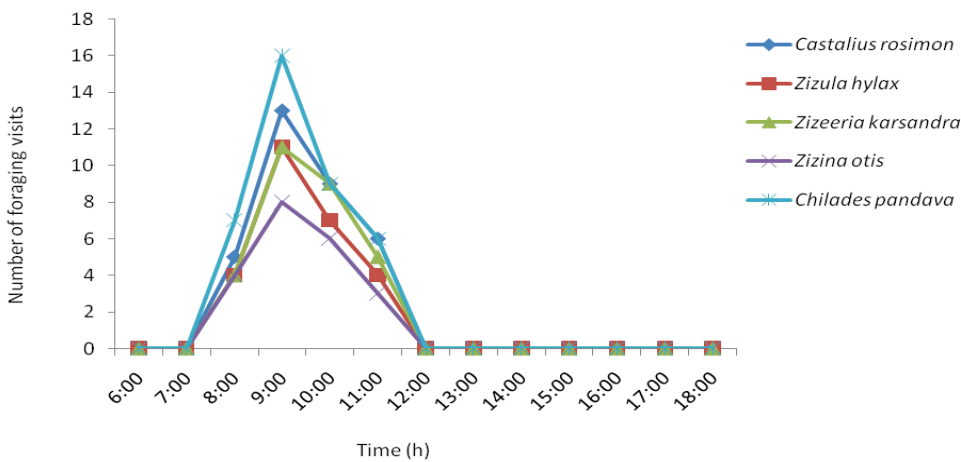**Figure 3. Hourly foraging activity of bees on *Mollugo pentaphylla***

Figure 4. Hourly foraging activity of lycaenid butterflies on *Mollugo pentaphylla*

Image 3. *Mollugo nudicaulis:* a. *Apis cerana*, b. *Apis florea*, c. *Trigona iridipennis*, d. *Ceratina* sp., e. *Halictus* sp., f. *Eristalinus* sp., g. *Musca* sp., h–j. Lycaenids - h. *Zizeeria karsandra*, i. *Zizina otis*, j. *Chilades pandava*. © A.J. Solomon Raju.

also visited by *Halictus* sp. (Image 3e) and the latter also by *Thyreus histrio* (Image 5e). The flies recorded on *M. nudicaulis* were *Eristalinus* sp. (Image 3f) and *Musca* sp. (Image 3g). The butterflies represented only lycaenids - *Zizula hylax* (Image 5g)*, Zizeeria karsandra* (Image 3h, 5h)*, Zizina otis* (Image 3i) and *Chilades pandava* (Image 3j) (Table 2) foraged on the flowers of both plant species. *M. nudicaulis* was also visited by *Freyeria trochylus* and *M. pentaphylla* also by *Castalius rosimon* (Image 5f). All these insects approached the flowers in upright position, landed on the tepals and then probed for forage collection. Bees first accessed anthers to collect pollen and then moved to the flower base to collect nectar, if available in the same and/or different visits. Flies and butterflies stretched out their proboscis and inserted into the flower base to collect nectar. All insect species collected forage from several flowers of different cymes of the same or different plants to collect the forage. The bees during pollen collection brushed against the stigmas with their ventral surface effecting sternotribic pollination. Further, these insects during nectar collection brushed against anthers and stigmas with their dorsal surface effecting nototribic pollination. The flies and butterflies during nectar collection contacted the stamens and stigmas with their proboscis and occasionally front side of head and ventral surface of thorax and abdomen effecting sternotribic pollination. The butterfly wings never contacted the stamens and stigma during nectar collection as they kept them in vertical position. In *M. nudicaulis*, bees made 49%, flies

Table 2. List of insect foragers on *Mollugo nudicaulis* and *Mollugo pentaphylla*

Order/Family	Insect species	*Mollugo nudicaulis*	*Mollugo pentaphylla*
Hymenoptera			
Apidae	*Apis cerana* F.	+	+
	Apis florea F.	+	+
	Trigona iridipennis Smith	+	+
	Ceratina smaragdula F.	-	-
	Ceratina sp.	+	+
	Thyreus histrio	-	+
Halictidae	*Halictus* sp.	+	-
Megachilidae	*Megachile* sp.	-	-
Formicidae	*Camponotus* sp.	-	-
	Crematogaster sp.	-	-
Diptera			
Syrphidae	*Eristalinus* sp.	+	-
Muscidae	*Musca* sp.	+	-
Lepidoptera			
Lycaenidae	*Castalius rosimon* F.	-	+
	Zizula hylax F.	+	+
	Zizeeria karsandra Moore	+	+
	Zizina otis F.	+	+
	Freyeria trochylus Freyer	+	-
	Chilades laius Stoll	-	-
	Chilades pandava Horsfield	+	+

Table 3. Pollen recorded in the body washings of insects on *Mollugo nudicaulis* and *Mollugo pentaphylla*

Insect species	Sample size (N)	*Mollugo nudicaulis*			*Mollugo pentaphylla*		
		Number of pollen grains			Number of pollen grains		
		Range	Mean	S.D.	Range	Mean	S.D.
Apis cerana	10	73–204	133.5	37.5	82–246	159.2	51.8
Apis florea	10	61–183	126.1	33.31	68–217	145.1	43.56
Trigona iridipennis	10	37–95	63.4	14.4	31–86	62.1	13.5
Ceratina sp.	10	34–62	47.8	8.27	24–51	38.2	9.07
Halictus sp.	10	41–87	69.8	12.2	---	---	---
Thyreus histrio		---	---	---	19–43	30.6	7.60
Eristalinus sp.	10	26–50	38.2	7.26	---	---	---
Musca sp.	10	11–38	27.9	7.5	---	---	---
Castalius rosimon	10	---	---	---	15–41	29.5	6.38
Zizula hylax	10		21.3	5.47	9–30	20.6	5.27
Zizeeria karsandra	10	13–32	23.8	5.57	13–45	27.8	9.49
Zizina otis	10	16–40	28.1	6.48	10–36	23.7	6.63
Freyeria trochylus	10	8–31	24.4	7.19	---	---	---
Chilades pandava	10	15–36	28.5	6.27	8-43	30.7	8.8

11% and lycaenids 40% of total foraging visits. In *M. pentaphylla*, bees made 56% and lycaenids 44% of total foraging visits. The body washings of insects collected from the flowers during peak foraging period revealed that all insects carry pollen but bees carry the highest number of pollen grains. Further, the mean number of pollen grains varied with each insect species (Table 3). The nectar secretion in traces and its depletion by thrips during and after anthesis appeared to be driving the insects to visit as many flowering cymes as possible to quench their thirst for nectar. Such a foraging behavior was considered to be facilitating the promotion of cross-pollination.

Fruiting ecology and seed dispsersal

In all three species, fruits mature within 8–12 days (Image 6a). The stamens and stigmas are persistent and remain inside due to the closure of the flower. The tepals bulge gradually and protect the bulging ovary in which the seeds form and mature (Image 1k, 6b). The natural fruit set is 91.27% in M. cerviana, 86–89 % in *M. nudicaulis*, and 83–88 % in *M. pentaphylla*. Seed set rate is 61.94% in *M. cerviana*, 88–92 % in *M. nudicaulis*, and 83–86 % in *M. pentaphylla* (Table 4). Fruit is a loculicidal 3-valved broadly-ellipsoid capsule, stalked and membranous and densely pubescent in all three species but it is densely pubescent in *M. cerviana* and *M. nudicaulis* while it is glabrous in *M. pentaphylla*. It is 2.35 ± 0.36 mm and 1.85 ± 0.23 mm wide in *M. cerviana*, 3.4

± 0.4 mm long and 2.33 ± 0.39 mm wide in *M. nudicaulis*, and 2.67 ± 0.4 mm long and 1.97 ± 1.4 mm wide in *M. pentaphylla*. In all three species, the seeds are arranged in two rows in each locule. In *M. cerviana*, the seeds are tiny, brown, shiny, D-shaped and faintly striate dorsally (Image 1n). The seed coat is studded with minute granular excrescences with reticulate ornamentation. In *M. nudicaulis* and *M. pentaphylla*, the seeds are tiny, black, slightly shiny, reniform and concentrically ridged (Image 2o, 6e). The seed coat is closely packed with uniformly distributed, pebble-like, lyrate and chipped areoles. Dry capsules break open when fruit pericarp and tepals are dry and expose the seeds (Image 1l,m; 2l,n; 6c). But the seeds remain so and gradually separate and fall to the ground on their own on clear sunny days. On rainy days, the water droplets falling on the dehisced capsules washout seeds to the ground. Water also acts as an efficient dispersal agent for seeds that fall during the rainy season. Seeds do not have adaptations for wind dispersal, but wind disperses dry cymes and dehisced capsules short distances and subsequently fall to the ground from capsules. Thus, seed dispersal modes include ombrohydrochory, hydrochory and anemochory. The seeds produced from plants growing in cultivated lands have the potential to be dispersed as a cereal grain contaminant and in effect agricultural produce movement contributes to seed dispersal and expansion of its distribution (Image 2c; 6f,g).

Image 4. *Mollugo pentaphylla:* a. Habit, b. Flowering phase, c–e. Different stages of anthesis, f. Position of anthers and stigmas at the same height, g. Pollen grain, h. Ovary with three stigmas, i. Ovules. © A.J. Solomon Raju.

Table 4. Natural fruit and seed set rate in *Mollugo nudicaulis* and *M. pentaphylla*

Flower type	Number of flowers sampled	Number of flowers set fruit	Fruit set (%)	Seed set (%)
Mollugo nudicaulis				
3-stamened	320	286	89	88
4-stamened	85	73	86	91
5-stamened	40	35	88	92
Mollugo pentaphylla				
3-stamened	250	220	88	83
4-stamened	150	130	87	84
5-stamened	75	62	83	86

DISCUSSION

Mollugo species are annual herbs which usually grow in open dry sandy and sandy and loamy soils but also occur in moist habitats, especially in cultivated lands. In this study, it is found that *M. cerviana*, *M. nudicaulis* and *M. pentaphylla* with their low ground habit populate the soil and for this reason, they are often called as carpet weeds. Of these, *M. cerviana* does not cover the soil extensively due to its wiry stems and thin, linear leaves. *M. nudicaulis* without any stem covers the soil with a rosette of prostrate leaves. *M. pentaphylla* with branched stems carpets the soil with its basal rosette form of leaves and upper spathulate leaves. All the three plant species grow throughout the year displaying vegetative, flowering and fruiting phases in different populations. Their robust growth, profuse flowering and fruiting, however, is confined to the wet season.   Individual plants complete their life cycle within three months from seed germination to seed dispersal. Similarly, Owens & Lund (2009) reported that *M. cerviana* is a herbaceous ephemeral species and completes its life cycle in a very short time. In the present study, it is found that the inflorescence is a dichotomous or trichotomous umbellate cyme in *M. cerviana* while it is di- or tri- or poly-chasial cyme in *M. nudicaulis* and *M. pentaphylla*. In the last two species, di-/tri-chasial cymes are common during dry season while poly-chasial cymes are common during wet season, suggesting that the branching of inflorescences and the production rate of flowers is regulated by the soil moisture and nutrient environment. *M. cerviana* and *M. pentaphylla* produce inflorescences in leaf axils and terminally while *M. nudicaulis* produces inflorescences from the axils of rosette of leaves due to lack of stems.   Since all the three plant species usually grow as green carpets, the simultaneous display of several flowers from individual plants and from the entire population(s) enhances their attraction to insect pollinators.

Image 5. *Mollugo pentaphylla:* Foragers: a. *Apis cerana*, b. *Apis florea*, c. *Trigona iridipennis*, d. *Ceratina* sp., e. *Thyreus histrio,* f–h. Lycaenid butterflies – f. *Castalius rosimon*, g. *Zizula hylax*, h. *Zizeeria karsandra*. © A.J. Solomon Raju.

Image 6. *Mollugo pentaphylla:* a. Fruiting phase, b. Maturing fruits, c. Dehisced fruit capsule, d. Dehisced fruit capsule with seeds intact, e. Seeds, f. & g. New plants. © A.J. Solomon Raju.

The floral descriptions of *Mollugo* species provided by different authors are not accurate. The present study provides details of the floral descriptions, especially of perianth, androecium and gynoecium in *M. cerviana, M. nudicaulis* and *M. pentaphylla* as these are important from the pollination of point view. In these species, perianth typically consists of five tepals which serve the function of calyx (sepals) and corolla (petals). In *M. cerviana* and *M. nudicaulis*, the abaxial surface of the perianth serves the role of calyx while the adaxial surface of the perianth serves the role of corolla due to display two different colours on each surface. But, in *M. pentaphylla*, the perianth is white on both abaxial and adaxial surface. The study shows that *M. cerviana* with perianth acting as both calyx and corolla is unable to attract any insect pollinators in pollinator-deprived

habitat or pollinator-available habitat. Such a situation explains that *M. cerviana* is not dependent on insect foragers for pollination. *M. nudicaulis* with perianth displaying light green on its abaxial surface and creamy white on its adaxial surface, and *M. pentaphylla* with perianth displaying white colour on both adaxial and abaxial surface attract insect foragers. Eckardt (1974) and Stannard (1988) reported that the sister genera of *Mollugo, Corbichonia* and *Lophiocarpus* have only four stamens of which three alternate with sepals and one is opposite a sepal. Batenburg & Moeliono (1982) reported that the presence of one stamen opposite a sepal is unusual in these genera and indicate that this stamen is derived from an original condition with five alternisepalous stamens by a fusion of two stamens under the influence of a reduced tetramerous ovary which is similar to a process occurring in *Mollugo*.

Ronse-De-Craene (2010) reported that in Molluginaceae including *Mollugo*, the androecium consists of generally of five stamens alternating with the sepals. In *Mollugo*, the number of stamens ranges from five in *M. cerviana* to three in *M. nudicaulis*. The present study shows that *M. cerviana* flowers produce a fixed number of 5 stamens and all are opposite to tepals suggesting that there is no process evolving to produce flowers with 3 or 4 stamens. *M. nudicaulis* produces flowers with 3-6 stamens while *M. pentaphylla* produces flowers with 3-5 stamens on the same plant. In these species, 3-stamened flowers have one stamen between two tepals and two stamens opposite to tepals, the 4-stamened flowers have three stamens alternate to tepals and one stamen opposite to a tepal, and the 5-stamened flowers have two stamens alternate to tepals and three stamens opposite to tepals. In *M. nudicaulis*, the 6-stamened flowers have three stamens alternate to tepals and three stamens opposite to tepals. The study indicates that all the three plant species produce trimerous ovary with three stigmas irrespective of the number of stamens produced in the flowers. In *M. nudicaulis* and *M. pentaphylla*, the production of 5-stamened flowers appears to be a residual trait still functional because these flowers are occasionally or rarely produced. In *M. nudicaulis*, the rarity of 6-stamened flowers may be a trait of polyploidy. In *M. nudicaulis* and *M. pentaphylla*, the two stamens opposite to tepals in 3-stamened flowers appear to be derived from the pair-wise fusion of four stamens (Ronse-De-Craene 2010) and the stamen opposite a tepal in 4-stamened flowers appear to be derived from the fusion of two stamens as in *Corbichonia* and *Lophiocarpus, sensu* Batenburg & Moeliono (1982).

In *M. nudicaulis* and *M. pentaphylla*, the variation in pollen output levels due to variation in stamen number in 3-5(6) stamened flowers make bees and/or flies to fly from flower to flower in quick succession to collect pollen from the same or different conspecific plants and effect both self- and cross-pollination.

Hammer (1995) reported that different populations of Aizoaceae growing in the same habitat exhibit synchrony in flowering time. The period of flowering is usually short and the flowers show repeated opening but this phenomenon is restricted to a certain period of the day. Groen & van der Maesen (1999) observed that the mixed populations of Aizoaceae genera, *Bergeranthus, Faucaria* and *Orthopterum* flower simultaneously. These authors suggested that such a synchrony in flowering in these genera in the same habitat collectively enable them to enhance their floral attraction to pollinators. In the present study, it is found that *Mollugo* species form mixed and distinct populations in the same and different habitats depending on soil moisture and nutrient conditions. These species exhibit synchrony in flowering by opening flowers during morning time. Further, the flowers are too small, lack corolla, tepals not vividly coloured and stay open for a brief period of three hours for visitation by insects. Therefore, the synchrony in anthesis schedule and massive floral display appear to be imperative for them to attract pollinators during the brief period of open state of flowers.

Peter et al. (2004) reported that the temperature and relative humidity are probably important cues determining flower opening in the afternoon. In the present study, the anthesis during morning time in *Mollugo* species is attributable to their predominance in open, dry habitats where herbaceous flora usually do not grow. With synchrony in anthesis schedule, these species provide sufficient forage but insect foragers collect forage only from *M. nudicaulis* and *M. pentaphylla*. Bees and lycaenid butterflies visit and pollinate both the plant species while flies additionally visit and pollinate *M. nudicaulis*. Bees and butterflies are generalists which visit a wide range of flowers and hence are polylectic. Since *Mollugo* species keep the flowers open only for a brief period, the polylectic foragers soon switch over to other plant species which provide forage in the nearby habitats. The morning anthesis in *Mollugo* species ensures insect pollination and reciprocates the insect pollinators with pollen and/or nectar. The total absence of insect foraging activity on *M. cerviana* could be attributable to its common occurrence in pollinator-excluded or deprived habitats and production of tiny flowers which can be overlooked or unnoticed by

foragers.

Watson & Dallwitz (1992) stated that Molluginaceae members are entomophilous. These authors considered nectar secreting tissue and showy tepals in several species as adaptations for entomophily. Robertson (1928) reported that *Mollugo verticillata* is pollinated by syrphid fly, *Mesogramma marginata*. Pax & Hoffmann (1934) and Bogle (1970) stated that the showy sepals or petals evolved in several genera of Molluginaceae suggest entomophily. *Mollugo verticillata, M. cerviana* and *M. nudicaulis* are the most widely spread, weedy species and adapted for self- and insect-pollination. In the present study, it is found that in *Mollugo* species, the floral characters such as the erect position of flowers above foliage, adaxial surface of the tepals and nectar secreting tissue between the ovary base and connate part of staminal filaments appear to be adaptations for insect pollination. In *M. nudicaulis*, the bees while collecting pollen, and flies and butterflies while collecting nectar effect sternotribic pollination. Further, the bees while collecting nectar effect nototribic pollination. In *M. pentaphylla*, the bees while collecting pollen effect nototribic pollination. The bees and also butterflies while collecting nectar effect sternotribic pollination. In *M. nudicaulis* and *M. pentaphylla*, the pollen output per anther varies with the number of stamens present in the flowers; it increases with a decrease in the stamen number. The pollen output per flower in *M. pentaphylla* is more than in *M. nudicaulis*. The variation in pollen production in these plant species is partly attributable to the number of stamens produced. The varying amount of pollen output in the flowers of the same and different inflorescences on the same plant drives the pollen collecting bees to visit the flowers across population(s) in search of more pollen and such a foraging activity contributes to both self- and cross-pollination. The nectar secreted in traces in both the species and nectar removal by thrips species, *Haplothrips* also drives the nectar collecting bees, flies and lycaenid butterflies to visit flowers across population(s) due to which both self- and cross-pollinations occur. *M. nudicaulis* and *M. pentaphylla* appear to be important sources of pollen for bees, especially for honey bees. Further, these plant species in the study area are important nectar sources for lycaenid butterflies. Among butterflies, lycaenids are the smallest, low-flying and appropriate pollinators for prostrate herbs, *M. nudicaulis* and *M. pentaphylla*.

Bhargava (1934) and Kshirsagar (1960) reported *in situ* pollen germination in *M. nudicaulis* and *M. pentaphylla*. Johri et al. (1992) noted that self-pollination seems to occur in these species as pollen tubes reached the ovules of ovaries in un-opened flowers and pollen grains with pollen tubes occur both inside the anther and on the stigma of the same flowers. But, these authors did not mention the time of the occurrence of these events in unopened flowers. In the present study, all three *Mollugo* species show certain percentage of pollen germination only in the dehisced anthers and also the pollen tube formation on the stigma during anthesis process which occurs in individual flowers over a period of five to ten minutes. Such *in situ* pollen germination and the occurrence of pollen tubes on the stigma during the process of anthesis facilitates self-induced autogamy to some extent. In *M. cerviana*, the close proximity of dehisced anthers of all five anthers to the stigmas facilitate the occurrence of spontaneous autogamy. In *M. nudicaulis* and *M. pentaphylla*, the close proximity of one dehisced anther in 3-stamened flowers and 2-3 dehisced anthers in 4- and 5-stamened flowers facilitate the occurrence of spontaneous autogamy. The minutely denticulate stigmas with membranous flaps in *M. cerviana* and densely papillose spreading stigmas in *M. nudicaulis* and *M. pentaphylla* capture pollen easily from the dehisced anthers to result in pollination. Further, in all the three *Mollugo* species, the thrips emerging from the floral buds during anthesis and their movements in the flowers after anthesis for pollen and nectar collection result in autogamy. They also bring about geitonogamy due to their migration to different inflorescences on the same plant for forage collection and xenogamy due to their migration to other conspecific plants for forage collection. In these plant species, the movement of tepals together with stamens towards the pistil during the flower closure facilitates contact between the sex organs and effects spontaneous autogamy if pollen is still available in the dehisced stamens. Further, the tiny thrips have the possibility to carry pollen from other flowers, enter the closed flowers from the apical portion and laterally, and deposit the same on the stigmas effecting either geitonogamy or xenogamy. Therefore, all the three *Mollugo* species have specialized floral structural and functional behaviours for self-induced and spontaneous pollination while keeping the options open for insect pollination after anthesis.

In the present study, all three *Mollugo* species have three carpels with variation in ovule number per flower which is highest in *M. cerviana* and lowest in the other two *Mollugo* species. In *M. nudicaulis* and *M. pentaphylla*, the ovule number also varies depending on the number of stamens and pollen output per flower. This ovule production trend indicates that the pollen output increases with an increase in ovule number in

order to provide sufficient pollen to fertilize as many ovules as possible. This situation is reflected in the natural fruit and seed set rates in both the plant species. The highest fruit and seed set rates and also the lowest pollen-ovule ratios recorded in *Mollugo* species now studied indicate that they are facultatively autogamous.

Bittrich (1990) reported that in Molluginaceae, *Adenogramma* is the only genus which produces one-seeded nutlets. All other genera produce capsules with many seeds which become exposed by loculicidal dehiscence. Soerjani et al. (1987) reported that *Mollugo pentaphylla* is hydrochorous. In the present study, the *Mollugo* species produce fruits within a week or slightly more than a week. The fruit is a 3-valved broadly ellipsoid capsule which breaks open and exposes the seeds on clear sunny days; the seeds subsequently fall to the ground. On rainy days, water drops find their way into the fruits which are then filled with water. In effect, the fruits expel both water and seeds explosively. Further, wind disperses the dry cymes together with dry dehisced capsules to short distances and subsequently the seeds fall to the ground from the capsules. The seeds that reach the ground through these modes are further disseminated through surface water runoff during rain fall. Therefore, *Mollugo* species now studied exhibit anemochory, ombrohydrochory and hydrochory.

Narayana (1962) and Hofmann (1973) noted that *Mollugo* species produce seeds with a primordium-like swelling on the funiculus and this structure is considered to be a vestigial aril. In the present study, it is found that *M. cerviana* produces tiny, brown, shiny, D-shaped seeds with faintly striate dorsal surface. The seed coat is studded with minute granular excrescences with reticulate ornamentation. *M. nudicaulis* and *M. pentaphylla* produce tiny, black, slightly shiny, reniform and concentrically ridged seeds. The seed coat is closely packed with uniformly distributed, pebble-like, lyrate and chipped areoles. Since the seeds of these plant species lack any aril or strophiole-like structure that usually serves as food for ants, the possibility for myrmecochory is ruled out. Wagner et al. (1999) noted that *Mollugo* species produce fruit capsules and inside seeds that lack means of external attachment for dispersal by animals. The present study is also in agreement with this report as all the three *Mollugo* species now studied do not have external structures that aid in the dispersal of seeds by animals. Therefore, seed dispersal by animals is totally ruled out.

Bittrich & Ihlendfeldt (1984) reported that *Mollugo* seeds germinate by means of an operculum. *M. cerviana* and *M. pentaphylla* propagate by seeds and reseed

themselves, often forming colonies. The present study showed that *Mollugo* species produce several batches of populations in a year and their seeds germinate as soon as they are dispersed but their germination is related to soil moisture which plays an important role in breaking the seed coat. As therophytes, these species are best adapted to survive in open dry habitats as they take advantage of any sign of temporary humidity that allows them to complete their life cycle quickly. Jurado et al. (1991) reported that *M. cerviana* does not form dense cover that inhibits other vegetation and compete well in crowded conditions. The present study also indicates that all the three *Mollugo* species do not grow in shaded habitats or form dense populations that inhibit other vegetation but *M. nudicaulis* and *M. pentaphylla* share insect pollinators along with other simultaneously flowering herbaceous taxa in certain habitats.

Brockington et al. (2009) reported that *Mollugo cerviana* is the only known C_4 species in Molluginaceae. Edwards & Walker (1983) noted that the genus *Mollugo* contains C_3, C_4 and C_3-C_4 species. Christin et al. (2010) reported that *M. cerviana* being a C_4 species is distributed in hot arid regions of tropical and temperate latitudes. *M. nudicaulis* is a C_3-C_4 species while *M. pentaphylla* is a C_3 species but both are distributed in tropical and subtropical regions of the world. Raghavendra et al. (1978) reported that *M. nudicaulis* produces some leaves with C_3 characteristics and some other leaves with C_4 characteristics according to their position on the stem. Sage et al. (1999) documented that C_3-C_4 photosynthesis is believed to be a relatively rare condition in plants and only a few dozen species have been identified so far, many of which belong to *Flaveria* (Asteraceae). The present study shows that *M. pentaphylla* with C_3 photosynthesis usually occurs in dry habitats displaying the sparse growth of a few other prostrate or erect herbs and the presence of insect pollinators although they grow in cultivated lands that enable herbaceous flora, especially weeds and insect pollinators thrive well. Their occurrence in habitats with scanty or robust vegetation indicates that C_3 photosynthesis does not facilitate them to grow in habitats without any vegetation or insect pollinators. On the contrary, *M. cerviana* with C_4 photosynthesis grows only in dry habitats which are almost devoid of other vegetation and also devoid of pollinator fauna. This finding is in line with the statement by Lundgren et al. (2015) that C_4 species are usually abundant in warm but not in cool environments and this photosynthetic pathway is physiologically advantageous for their niche broadening in warm environments. *M. nudicaulis* with C_3-C_4 photosynthesis is versatile

to flourish well both in dry habitats and cultivated areas with scanty and robust vegetation comprising of herbaceous flora that support insect pollinators. The C_3-C_4 photosynthetic pathway enables this species to grow in warm and cool habitats which in turn enables it to be widespread and abundant. Vogan et al. (2007) reported that of all C_3-C_4 intermediates, *M. nudicaulis* and *M. verticillata* are the most widespread and also abundant. These species are found in hot, ruderal habitats where competition is low and the potential for photorespiration is high. Their ability to survive in such habitats is likely due to their C_3-C_4 pathway. Their ecological success demonstrates that C_3-C_4 intermediacy is a successful photosynthetic pathway in its own right and not merely a transitional phase to C_4 photosynthesis. Lundgren & Christin (2017) also reported that C_3-C_4 taxa are remarkably widespread across geographical and environmental space, maintaining their ability to exist in both typical C_3 and C_4 niches. Because, the physiology of C_3-C_4 species does not strongly restrict the migration of species geographically or into new environments and it is a lineage that converges towards warm habitats to facilitate the transition to C_4 photosynthesis, effectively bridging the ecological gap between C_3 and C_4 plants. *M. pentaphylla* with C_3 photosynthesis, *M. nudicaulis* with C_3-C_4 photosynthesis and *M. cerviana* with C_4 photosynthesis have developed different pollination mechanisms to maximize fruit and seed set rate. Genetic variation achieved through insect pollination in all these species, except *M. cerviana,* is essential to broaden their ecological niches since they grow both in dry and moist habitats. In *M. cerviana*, genetic variation achieved through thrips pollination is important to expand and invade dry habitats.

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