

**POLLINATION ECOLOGY OF THE SPECIES
MOLLUGO CERVIANA (L.) SER. (MOLLUGINACEAE)**

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ABSTRACT

Mollugo cerviana is an annual herb which usually grows throughout the year in open dry sandy and sandy-loamy soils, but also occurs in moist habitats, especially in cultivated lands. *Haplothrips* uses the flowers for breeding and feeding; the feeding activity affects pollination. The flowers have specialized floral structural and functional behaviours for self-induced and spontaneous autogamy while keeping the options open for insect pollination after anthesis; it is facultative autogamous which is reflected in pollen-ovule ratio and natural fruit and seed set rates. Seed dispersal modes include anemochory, ombrohydrochory and hydrochory.

ZUSAMMENFASSUNG: Bestäubungsökologie von *Mollugo cerviana* (L.) Ser. (Molluginaceae).

Mollugo cerviana ist ein einjähriges Kraut, das in der Regel das ganze Jahr über auf offenen trockenen, sandigen und sandig-lehmigen Böden wächst, aber auch in feuchten Lebensräumen, vor allem in Kulturlandschaften, vorkommt. *Haplothrips* verwendet die Blüten zur Aufzucht und Fütterung; die Nahrungsaufnahme beeinflusst die Bestäubung. Die Blüten haben sich auf ein floral strukturelles und funktionelles Verhalten selbstinduzierter und spontaner Autogamie spezialisiert, während die Möglichkeiten für Insektenbestäubung nach der Anthese offen bleiben; die Pflanze ist fakultativ autogam, was sich im Pollen-Samen-Verhältnis und den natürlichen Frucht- und Samensatzraten widerspiegelt. Ihre Samenausbreitungsmodi umfassen Anemochorie, Ombrohydrochorie und Hydrochorie.

REZUMAT: Ecologia polenizării la *Mollugo cerviana* (L.) Ser. (Molluginaceae).

Mollugo cerviana este o plantă anuală care crește în mod normal pe soluri uscate, nisipoase și nisipo-argiloase, pe tot parcursul anului, dar se dezvoltă și în habitate umede, în special în locuri cultivate. *Haplothrips* folosește florile pentru reproducere și hrănire; Aportul alimentar afectează polenizarea. Florile se specializează în comportamentul structural și funcțional floral pentru autogamia auto-indusă și spontană, în timp ce posibilitățile de polenizare a insectelor rămân deschise după anteză; este autogamă facultativă, ceea ce se reflectă în raportul dintre semințele de polen și rata naturală a ratelor de fructe și semințe. Modurile de propagare a semințelor includ anemochoria, ombrohydrochoria și hidrochoria.

INTRODUCTION

Pollination is an important part of plants' life (Solomon Raju, 1998), a key element for mangrove flora ecology and conservation (Aluri, 2013). It is a successful tool for maximizing the gene flux (Almeida-Soares et al. 2010). The genus *Mollugo* is native to tropical and a warm temperate part of North and South America, but it is also distributed in Europe, Africa and Asia. The name derives from the Latin word "mollis" meaning soft (Short, 2002). *M. cerviana* is native to India, Sri Lanka, Pakistan and Bangladesh (Parvathamma and Shanthamma, 2000). It is a C₄ species distributed in hot arid regions from pantropics to temperate regions (Christin et al., 2010). It is valuable in medicine for treating different diseases and ailments (Parvathamma and Shanthamma, 2000; Rajamanikandan et al., 2011; Sahu et al., 2012).

Scientists know little about the pollination ecology of Molluginaceae. In this family, 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 and Dallwitz, 1992; Kubitzki et al., 1993). Syrphid fly, *Mesogramma marginata* pollinates *Mollugo verticillata* (Robertson, 1928). The most widely spread, weedy species of *Mollugo verticillata*, *M. nudicaulis*, and *M. cerviana* are self- and insect-pollinated (Pax and Hoffmann, 1934; Bogle, 1970). In Taiwan, *M. pentaphylla* is a minor pollen source for *Apis mellifera* (Lin et al., 1993). In South India, honey bees use *Mollugo* species as a pollen source and reciprocate the plants with pollination (Ponnuchamy et al., 2014). This study was done to investigate how *M. cerviana* is able to reproduce in semi-dry and dry habitats with scarce pollinators. The objective of the present study is to know how various aspects pollination ecology contributes for the reproductive success through seed mode in dry habitats.

MATERIAL AND METHODS

Mollugo cerviana wild patches grow in open dry and semi-dry areas of Visakhapatnam and its surroundings (17°42'N latitude and 82°18'E longitude) 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 analysed 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 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. The flower buds were used by thrips for breeding and feeding and in this context their role in pollination was observed.

RESULTS

Phenology. The species is a small, glabrous, slender annual herb common in open dry sandy and semi-dry soils along roadsides, waste places, bare ground and dry river beds (Fig. 1a). Due to its very low ground habit, wiry reddish orange stems and thin linear leaves its presence is usually overlooked. 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. The plant appears simultaneously in vegetative, flowering and fruiting phases in different populations growing in different habitats throughout the year (Fig. 1b). An individual plant, however, has a short life cycle of three months from seed germination to seed dispersal. Although it appears throughout the year, it shows robust vegetative growth and profuse flowering and fruiting during July-October when the soil is damp due to the occurrence of rains. The flowers are borne on seven-eight mm long pedicels in dichotomous and trichotomous umbellate cymes produced terminally or in leaf axils.

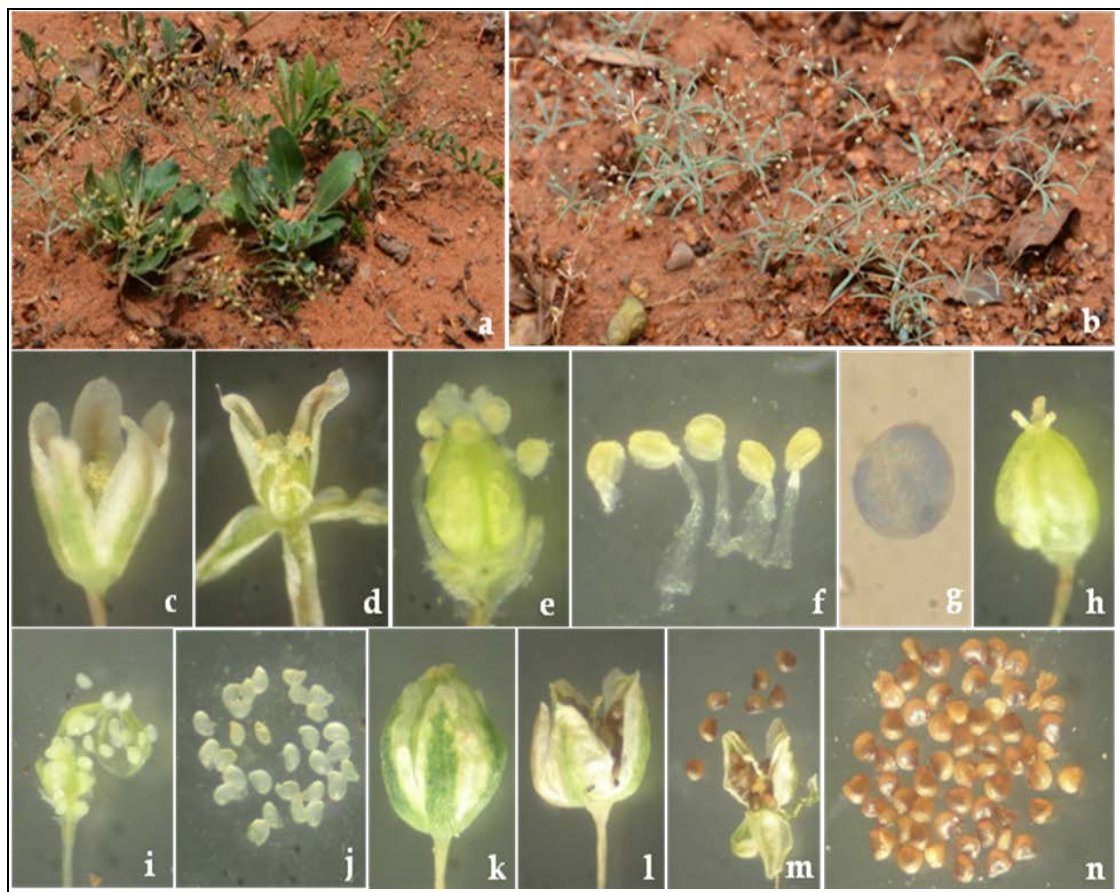


Figure 1a-n: *Mollugo cerviana*: a. Habitat with *Mollugo cerviana* and *M. nudicaulis*, b. *Mollugo cerviana* in flowering phase, c. and d. Flowering-opening phase, e. Position of stigmatic lobes and anthers at the same height contacting each other at anthesis, f. Dehisced anthers, g. Pollen grain, h. Ovary with three stigmas, i. and j. Multi-ovuled ovary, k. Maturing fruit, l. and m. Dehisced fruit capsule, n. Seeds.

Flower morphology. The flowers are small (2.52 ± 0.4 mm long, 1.51 ± 0.5 mm wide), whitish green on adaxial side and green on abaxial side, odourless, actinomorphic and bisexual. A monochlamydeous perianth of five herbaceous scarious, elliptic to oblong, 2.45 ± 0.4 mm long, 1.13 ± 0.2 mm wide long free tepals with white margins represent sepals and petals. The stamens are five, anti-tepalous, free but connate at base, white, 1.22 ± 0.3 mm long with dorsifixed, golden yellow, less than one mm long and dithecous anthers. The ovary is light green, tri-carpellary, tri-locular syncarpous with 58.2 ± 8.16 D-shaped ovules arranged on axile placentation (Figs. 1i-j). The style is absent but the ovary is terminated with three free stigmas (Fig. 1h). The stigmas are minutely denticulate with membranous flaps.

Floral biology. Mature buds open during 07,00-08,00 h. Individual buds take five to 10 minutes from partial to a full opening (Figs. 1c-d). The flowers are homogamous as the anthers and stigmas attain maturity at the same time during anthesis; the former dehisce by longitudinal slits (Fig. 1f), and the latter continue receptivity until the noon of the 2nd day. The pollen output is 159.7 ± 14.5 per anther and 798.5 ± 69.5 per flower. The pollen-ovule ratio is 14:1. The pollen grains are pale yellow, spheroidal, tri-colpate, tri-zonoaperturate, granulated, tectum scabrate, and 21.9 ± 4.12 μM (Fig. 1g). The nectar secretes in traces during mature bud stage. The tepals with the stamens and stigmas close back by 10,00-11,00 h.

Pollination mechanism and pollinators. 20-35% of pollen grains found in dehisced anthers collected during anthesis possess pollen tubes indicating *in situ* germination. Further, the pollen tubes are also present on the stigma. The pollen germination and formation of tubes both within the dehisced anthers and on the stigma indicate the presence of self-induced autogamy. 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 (Fig. 1e). Further, the stamens and stigmas contact each other very closely during the closing of the flower assuring autogamy if it did not occur during the open state of the flower. Any insects never visited the flowers. *Haplothrips* sp. (Thysanoptera: Thripidae) used flower buds 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. Pollen dusts individual thrips during their movements within the flowers. They carried 87 to 176 pollen grains on their body setae, wings and legs. The thrips dispersed the pollen on free denticulate and membranous stigmas 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. 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 foliage.

Fruiting ecology and seed dispersal. Fruits mature within 8-10 days. 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 (Fig. 1k). Natural fruit set is 91.27% and seed set is 61.94%. Fruit is a loculicidal three-valved broadly-ellipsoid capsule, stalked, membranous, and densely pubescent, 2.35 ± 0.36 mm and 1.85 ± 0.23 mm wide. The seeds are arranged in two rows in each locule. They are tiny, brown, shiny, D-shaped and faintly striate dorsally (Fig. 1n). The seed coat is studded with minute granular excrescences with reticulate ornamentation. Dry capsules break open when fruit pericarp and tepals are dry and expose the seeds (Figs. 1l-m). But the seeds remain 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. Further, water acts as an efficient

dispersal agent for the dispersal of seeds fallen on the soil during rainy season. Seeds do not have adaptations for wind dispersal. But, wind disperses the dry cymes together with dry dehisced capsules to short distances and subsequently the seeds fall to the ground from capsules. Therefore, 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.

DISCUSSION

This study finds that *Mollugo cerviana* with its low ground habit populates the soil and for this reason is often called carpetweed. The plant grows throughout the year displaying vegetative, flowering and fruiting phases in different populations. However, the wet season confines its robust growth, profuse flowering and fruiting individual plants complete their life cycle within three months from seed germination to seed dispersal. Similarly, Owens and Lund (2009) reported that *M. cerviana* is a herbaceous ephemeral species and completes its life cycle in a very short time. This study finds that the inflorescence is a dichotomous or trichotomous umbellate cyme in *M. cerviana* suggesting that the soil moisture and nutrient environment regulate the branching of inflorescences and the production rate of flowers.

The floral descriptions of *Mollugo* species provided by different authors (Goncalves, 1978; Matthew, 1995; Pullaiah, 2000; Pullaiah and Mohammed, 2000; Bora and Kumar, 2003) are not accurate and/or complete. The present study provides details of the floral descriptions, especially of perianth, androecium and gynoecium in *M. cerviana* as these are important from the pollination of point view. In this species, perianth typically consists of five tepals which serve the function of calyx (sepals) and corolla (petals). 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 the display of two different colors on each surface. However, the perianth acting as both calyx and corolla is unable to attract any insect pollinators in pollinator-deprived or pollinator-available habitat. Such a situation explains that *M. cerviana* is not dependent on insect foragers for pollination. Ronse De Craene (2010) reported that in *Mollugo*, the androecium generally consists of five stamens alternating with the sepals. *M. cerviana* flowers produce a fixed number of five stamens, and all are opposite to tepals suggesting that there is no process evolving to produce flowers with three or four stamens. Further, the plant produces trimerous ovary with three stigmas; each carpel with a variation in ovule number. Despite the absence of vector-mediated pollination, the plant produces high fruit and seed set rates indicating that this plant is facultative autogamous.

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 *M. cerviana* is attributable to its predominance in open, dry habitats where herbaceous flora usually does not grow. The 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.

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, *M. cerviana* produces fruits within or slightly more than a week time. The fruit is an ellipsoid 3-valved capsule and it breaks open to disperse seeds during sunlight days. But, on rainy days, the fruits when filled with water expel seeds and water violently. Wind also disperses dry cymes along with dry dehisced capsules to short distance and then seeds find their way into the ground. The seeds disseminated through these modes further dispersed by rain water during rainfall. Therefore, *M. cerviana* species is anemochorous, ombrohydrochorous and hydrochorous.

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. *M. cerviana* produces tiny, brown, shiny, D-shaped seeds with a faintly striate dorsal surface. Minute granular excrescences with reticulate ornamentation stud the seed coat. 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. This study agrees with this report because *M. cerviana* lacks external structures to aid seed dispersal by animals and hence there is no possibility of seed dispersal by animals.

Bittrich and Ihlenfeldt (1984) reported that *Mollugo* seeds germinate by means of an operculum. *M. cerviana* propagates by seeds and reseeds itself, often forming colonies. It produces several batches of populations in a year, and the seeds germinate as soon as they disperse, but their germination is related to soil moisture which plays an important role in breaking the seed coat.

As a therophyte, this species it is best adapted to survive in open dry habitats as it takes advantage of any sign of temporary humidity that allows it to complete its life cycle quickly. Jurado et al. (1991) reported that *M. cerviana* does not form a dense cover that inhibits other vegetation and compete well in crowded conditions. The present study also indicates that *M. cerviana* does not grow in shaded habitats or form dense populations that inhibit other vegetation.

Brockington et al. (2009) reported that *Mollugo cerviana* is the only known C₄ species in Molluginaceae. Christin et al. (2010) reported that *M. cerviana* being a C₄ species is distributed in hot, arid regions of tropical and temperate latitudes. The present study also shows that *M. cerviana* with C₄ 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 C₄ species are usually abundant in warm but not cool environments and this photosynthetic pathway is physiologically advantageous for their niche broadening in warm environments. In *M. cerviana*, genetic variation achieved through thrips pollination is essential to expand and invade dry habitats.

CONCLUSIONS

Mollugo cerviana as an annual facultative autogamous therophyte grows throughout the year in open dry sandy and sandy-loamy soils, and also in moist habitats. The flowers have specialized floral structural and functional behaviors for self-induced and spontaneous autogamy while keeping the options open for insect pollination after anthesis but the insects never visited the flowers. Seed dispersal is polychorous involving anemochory, ombrohydrochory and hydrochory. The seeds germinate immediately after dispersal, but soil moisture is required to rupture the seed coat. The plant is best adapted to survive in open dry habitats as it takes advantage of any sign of temporary humidity to complete its life cycle quickly and acts as a soil binder and also moisture accumulator in the root zone.

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