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REPRODUCTIVE ECOLOGY OF SOME CARPET WEED SPECIES OF MOLLUGINACEAE

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ABSTRACT

Reproductive ecology of five carpet weed species *Glinus lotoides* L., *G. oppositifolius* (L.) Aug. DC., *Mollugo cerviana* (L.) Ser., *M. nudicaulis* Lam. and *M. pentaphylla* L. (Molluginaceae) was studied. *Glinus* species are prostrate, spreading, annual herbs that carpet the ground in open sandy soils and agricultural lands. They have a perianth of five or rarely six tepals in quincuncial arrangement, functional stamens, petaloid staminodes and numerous ovules. The flowers are weakly protandrous, herkogamous and facultively autogamous. Bees, thrips, ants and lycaenid butterflies pollinate the flowers. In both the species, the fruit is a dehiscent capsule and disperses scrotiform strophioled-seeds. Seed dispersal modes include anemochory, ombrohydrochory and hydrochory.

Mollugo species are annual herbs which usually grow throughout the year in open dry sandy and sandy and loamy soils but also occur in moist habitats, especially in cultivated lands. The flowers have a perianth consisting of five tepals in quincuncial aestivation, functional stamens and several ovules. The ovary has three carpels and three stigmas. In all, the flowers are facultative autogamous. *M. cerviana* is never visited by any insect species while *M. nudicaulis* and *M. pentaphylla* are pollinated by insects. Certain percentage of *in situ* pollen germination and the occurrence of pollen tubes on the stigma during the process of anthesis facilitates self-induced autogamy. Spontaneous autogamy occurs due to close proximity of dehisced anthers of all five anthers to the stigmas in *M. cerviana* and due to close proximity of 1-3 dehisced anthers to the stigmas in *M. nudicaulis* and *M. pentaphylla* during flower closure.

Seed dispersal modes include anemochory, ombrohydrochory and hydrochory.

Keywords: *Glinus lotoides*, *G. oppositifolius*, *Mollugo cerviana*, *M. nudicaulis*, *M. pentaphylla,* facultative autogamy, entomophily, polychory.

INTRODUCTION

In general, weeds are mostly annuals or biennials and rarely perennials. Weeds are abundantly available, usually grow fast, and reproduce quickly and easily. Some species of weeds, called pioneer species, not only grow fast, but produce carbon quickly as well. This carbon, when they die, lasts a long time in the soil, helps build structure, and helps retain water. They have certain nutrients that they absorb from the soil, bring to the top, and release when they die. The weeds quickly colonize disturbed habitats created by man and also grow in areas far removed from their native ranges. They are genetically labile and phenotypically flexible, such characters enable them to pass through successfully the process of survival of the fittest under vagaries of nature such as adverse weather conditions, soils equipped with little water and nutrient content, presence of herbivores, predators, parasitoids, parasites and pathogens, and build up their populations very rapidly in many geographic regions (Mulligan and Kevan 1973; Andrewartha and Birch 1984). The weeds are excellent subjects for understanding mechanisms of breeding systems, life-history evolution and adaptation (Baker 1965; Stebbins 1989). The importance of understanding the biological requirements and peculiarities of herbs has been emphasized by many writers (Harlan 1965; King 1966; Chancellor 1968; Hammerton 1968).

Naidu (2012) explained the negative and positive effects of weeds. Weeds are undesired plants in agricultural systems as they deplete the nutrients, water and space allotted for the intended crop, and finally cause huge reduction in crop yield. Weeds in crop fields reduce input efficiency, interfere with agricultural operations, impair quality and act as alternate hosts for several insect pests and diseases. Some weeds release toxic substances which affect the crop growth. The obvious effect of these traits is the hike in cost of cultivation by several folds. Along with this, weeds affect and interfere in the management of all the terrestrial and aquatic resources. They endanger the native biodiversity by choking and deliberate takeover of the native plants. The animals which depend on this native biodiversity for their survival are also affected. As part of the primary producers within farming systems, weeds are also considered as important components of the agro-ecosystem. Reductions in abundances of weeds which act as hosts may affect associated insects and other taxa which are beneficial. Thus, weeds have a role within agro-ecosystems in supporting biodiversity more generally. Weed biology relates to the plant attributes such as morphology, seed dormancy and germination, physiology of growth, competitive ability and reproductive biology. Knowledge of weed biology is essential for the development of both economically and environmentally acceptable weed management systems. It is also essential to understand and predict how weed species, their populations and biotypes evolve in response to the selection pressures and play their role in soil conservation and eco-restoration. Vaidya *et al.* (1978) documented that weeds are generally classified based on their habitat. Weeds of cultivated crop fields (agricultural land) are called agrestals and those of non-agricultural land i.e. fallow land, harvested fields, along rail tracks, road–sides, hedges, waste places, on

old walls and roof tops etc. are called ruderals. There are some weeds which are not specific to any particular habitat i.e. they act as both agrestals and ruderals. Weeds show wide ecological amplitude by means of which they can resist the extreme conditions of environment.

The database of Plants For A Future (PFAF) indicates that there is limited information on wind-pollination and this information shows that wind-pollination is not a significant life history trait in flowering plants. Grasses are wind-pollinated, this bias may cause an under-estimate of wind pollination in weeds. Baker (1965) predicted that wind-pollination is ideal for the reproductive success of weeds, but at the same he stated that generalized pollination is important over specialized pollination to enable weeds to spread and invade different niches. PFAF database does not distinguish between generalist insect pollination and specialist insect pollination. Weeds and non-weeds show significant differences in their pollination modes (Kartesz and Christopher 1999).

Invertebrate pollinators play important roles in the reproductive success of invasive indigenous and non-indigenous plant species, some or several of which threaten the native communities (Pascarella *et al.* 2001). Breeding system, flower morphology, pollinator traits, biomass allocated to vegetative versus reproductive tissues, all correlate with life history such as growth form, pattern of development, time to first breeding, number of reproduction events and offspring characteristics (Damagaard and Abbott 1995).

Molluginaceae is a small family in Caryophyllales order of flowering plants. It has 10 genera with 80 known species distributed in tropical, sub-tropical and even warm temperate regions of the world (Bogle 1970; Endress and Bittrich 1993). This family is coded as polymorphic and consists of taxa with uniseriate, undifferentiated perianth and taxa with differentiated perianth (Ronse De Craene 2008). Certain important characters in this family include quincuncial aestivation, dual role of perianth, petaloid staminodes, variation in stamen number, carpels and stigmas, closing of flowers and reniform seeds (Hofmann 1994). This family is of little economic value. Many species have a "weedy" nature and frequently invade disturbed places. Some species are important as forage plants while a few species are edible and used as potherbs (Kirk 1975). In *Glinus* and *Mollugo* genera, several species are weedy, and some species are used as vegetables and in traditional medicine (Bogle 1970; Endress and Bittrich 1993). The weedy *Glinus* and *Mollugo* species commonly known as carpet weeds are important in carpeting the soil in dry environments by their profuse prostrate growth and producing several batches of offspring in a year. But, there is no information on the reproductive ecology of these weedy species which is required to know how they are able to grow, thrive and carpet the soil.

The present study was contemplated to provide the details of reproductive ecology of five carpet weed species, *Glinus lotoides* L., *G. oppositifolius* (L.) Aug. DC., *Mollugo cerviana* (L.) Ser., *M. nudicaulis* Lam. and *M. pentaphylla* L. belonging to Molluginaceae family.

The following objectives were investigated: flowering phenology, floral structural and functional morphology, anthesis and anther dehiscence schedules, pollination mechanism, pollination, pollinators, sexual system, flower closing mechanism, fruiting ecology and seed dispersal. This information is important to understand the efficiency of sexual reproduction which enables them to be agrestals and ruderals as they occur both in natural and agricultural habitats, especially in dry environments. This study is useful to evaluate the abilities of these weeds to use local insect fauna as pollinators to achieve genetic variation through which they acquire adaptations to grow in different ecological niches and expand their distribution range, especially in open, dry soils which are devoid of any vegetative cover.

REVIEW OF LITERATURE

The Caryophyllales is a group long recognized by its distinctive placentation and embryology, and is a major order of angiosperms representing about 5% of core eudicot diversity. This order exhibits wide variation in perianth structure and morphology (Takhtajan 1991). The perianth varies from an undifferentiated to differentiated structure with the concomitant evolution of petals from either bracts or stamens, in varying positions in the flower. More recently, molecular phylogenetics has improved the understanding of intra-ordinal relationships within the Caryophyllales (Cuenoud *et al.* 2002). In this order, the clade core eudicots characterized by tricolpate pollen grains included Aizoaceae as a large family in which the present **Molluginaceae** genera are included. In Aizoaceae, members of the early-diverging subfamilies Sesuvioideae and Aizooideae possess a quincuncial uniseriate perianth; it is petaloid on the adaxial surface while it is sepaloid on the abaxial side. In the derived subfamilies Mesembryanthemoideae and Ruschioideae commonly referred to as mesembs, the petaloid staminodes are possibly stamen-derived as they possess a singular vascular trace and a narrow point of insertion. Both petals and stamens develop from primordia initiating in a centrifugal direction. Stamens and petals are linked by intermediates, as floral organs developing closest to the fertile stamens are increasingly filamentous while the outermost organs are increasingly petaloid (Hofmann 1994; Thiede *et al.* 2011). Concomitantly, the outer quincuncial uniseriate perianth loses all petaloid characters and resembles only a calyx (Brockington 2009).

Ronse De Craene (2012) reported that eudicots consist of a basal grade and a large (core eudicot) clade, which comprises the majority of species. Eudicots are a highly successful group of plants, occupying almost all habitats on earth. In core eudicots, the evolution of flowers is highly diverse and is driven by repeated diversifications of pollination mechanisms. Flowers of eudicots are mostly with parts in five and with differentiated perianth of sepals and petals. Specific pollination mechanisms have led to groups with specialized animal-pollinated zygomorphic flowers (Leguminosae and Lamiales) or wind-pollinated apetalous flowers (Fagales and Caryophyllales). Likewise, dispersal mechanisms of eudicots are also highly diverse.

Glover (2011) reported that flowering plants produce three classes of chemicals, the flavonoids, the betalains and the carotenoids. The flavonoids are the major floral pigments. They give rise to ivory and cream colours through flavonols and flavones, yellow and orange colours through aurones and chalcones and the red, purple and blue through anthocyanins. The betalains are not major floral pigments but when produced give red colour to flowers. The carotenoids are more widespread in plants but less significant as floral pigments than the flavonoids; they give yellow and orange colour to flowers. Rausher (2006) reported that anthocyanins color petals to attract pollinators while Gould (2004) noted that they provide protection to vegetative tissues against ultraviolet, herbivores, and pathogens. Hatlestad and Lloyd (2015) mentioned that plants also produce betalain pigments to attract pollinators to flowers. Stafford (1994) stated that a given plant species produces either anthocyanins or betalains but not both. Clement and Mabry (1996) stated that it is expensive for plants to produce both groups of pigments and perhaps the production of one group of pigments is cheaper under some environmental conditions or preferable if their metabolic precursors are limiting for some reason. Clement *et al.* (1994) and Stafford (1994) reported that in Caryophyllales order, anthocyanins are found only in two families, Caryophyllaceae and Molluginaceae while this pigmentation has been replaced by betalains in the rest of the Caryophyllales. Glover (2011) mentioned that the betalains are found exclusively in Caryophyllales, and nowhere else in the plant kingdom.

Floral evolution often modifies the androecium, resulting in either stamen loss or transformation of stamen function from pollen production and presentation to alternate functions. With the loss of their defining function as producers of viable male gametophytes, stamens become staminodes. Commonly implicated staminode roles include pollinator attraction through visual conspicuousness and/or provision of attractants and rewards, avoidance of self-pollination, and facilitation of pollen removal and receipt through various trigger-mechanisms. Direct evolution from stamen to functional staminode likely occurs when stamens initially serve purposes such as pollinator attraction in addition to pollen production and presentation. In this situation, functional constraints favor "division of labor," which converts some stamens into staminodes specialized for the ancillary function and allows specialization of the remaining stamens on their primary role. With indirect evolution, the nonfunctional phase preceding adoption of a new function allows staminodes to assume novel functions not expected of stamens. Therefore, the taxonomic distribution of staminodes reflect functional evolution and the variety of functions served by staminodes reveal the course of that evolution (Weberling 1989; Ronse De Craene and Smets 1993, 1995).

In animal-pollinated plants, reduction of entire stamen whorls usually involves actinomorphic flowers pollinated by diverse small insects with more than one whorl of fertile stamens (Stebbins 1974; Ronse De Craene and Smets 1993, 1995). Reallocation of resources to more, smaller flowers and/or adaptations that increase efficiency of pollen dispersal likely prompt reduced pollen production per flower through stamen loss. These adaptations include pollen packaging and pollen-dispensing mechanisms that limit pollen

removal by individual pollinators but maximize pollen dispersal, and more precise contact between pollinators and fertile anthers or pollinators and stigmas. Both adaptations increase the proportions of pollen grains delivered to stigmas (Harder and Thomson 1989).

Ehrendorfer (1976) proposed that ancestral taxa in Caryophyllales occupied "open, warm, dry and windy habitats with mineral soils". Because, many of the families in Caryophyllales currently inhabit xeric, marginal environments. In this open, pollinator-deprived environment, wind pollination may have prevailed, and anthocyanin pigmentation was lost as there was no need to attract pollinators. Subsequently, following the radiation of pollinator lineages and the colonization of less marginal habitats, reversion to zoophily engendered a return to pigmentation in the form of betalains rather than anthocyanins. Clement and Mabry (1996) also argued that anemophily was the ancestral condition in Caryophyllales because the ancestral species in this order have evolved in open, dry, marginal environments at a time when pollinators were scarce. Strauss and Whittall (2006) noted that it is unreasonable to explain the evolutionary changes in pigmentation as a result of the absence or presence of pollinators alone because anthocyanins and betalains accumulate and function in both vegetative and reproductive tissues. Friedman and Barrett (2008) reported that there is a strong correlation between the occurrence of open habitat and anemophily. These authors also noted that this correlation may not necessarily be due to pollinator scarcity but rather to the selective advantage of anemophily in an open environment.

Hutchinson (1926) recognized Molluginaceae as distinct from Aizoaceae. Molluginaceae genera previously included in the larger family Aizoaceae have been separated and treated them under Molluginaceae family in subsequent classifications of 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). In this classification, 10 genera and 80 known species have been assigned to Molluginaceae. The genera include *Adenogramma* Rchb., *Coelanthum* E. Mey. ex Fenzl, *Glinus* L., *Glischrothamnus* Pilg., *Hypertelis* E. Mey. ex Fenzl., *Mollugo* L., *Pharnaceum* L., *Polpoda* C. Presl., *Psammotropha* Eckl. & Zeyh. and *Suessenguthiella* Friedrich (Christenhusz and Byng 2016). The genus *Glinus* has been assigned 11 species, *G. bainesii* (Oliv.) Pax, *G. herniarioides* (Gagnep.) Tardieu, *G. lotoides* L., *G. microphyllus* Hauman, *G. oppositifolius* (L.) Aug. DC., *G. orygioides* F. Muell., *G. pauli-wilhelmi* Hochst., *G. radiatus* (Ruiz & Pav.) Rohrb., *G. runkewitzii* Tackh. & Boulos, *G. sessiliflorus* P.S. Short and *G. setiflorus* Forssk; all these have been accepted to species level in this genus except *G. pauli-wilhelmi* which is yet to be resolved. The genus *Mollugo* has been assigned 93 species out of which only 18 have been accepted while others have been considered to be either synonyms or un-assessed. The accepted species include *M. angustifolia* M.G. Gilbert & Thulin, *M. caespitosa* Scott-Elliot, *M. cerviana* (L.) Ser., *M. crockeri* Howell, *M. decandra* Scott-Elliot, *M. flavescens* Andersson, *M. floriana* (B.L. Rob.) Howell, *M. fragilis* Wawra, *M. namaquensis* Bolus, *M. nudicaulis* Lam., *M. pentaphylla* L., *M. pinosia* Urb., *M. pusilla* Adamson, *M. snodgrassii* B.L. Rob., *M.*

stricta L., *M. tenella* Bolus, *M. verticillata* L. and *M. walteri* Friedr. Cuenoud *et al.* (2002) reported that Molluginaceae is polyphyletic and hence have different lines of evolution.

Hofmann (1994) documented that in Caryophyllaceae, the terms sepaloid "tepal' and petaloid 'tepal' are applied to the quincuncial perianth parts that are present in the core Caryophyllales while petaloid staminodes refer to perianth parts that are clearly androecium-derived. In Aizoaceae, androecial development proceeds centrifugally, and the basipetal members become progressively more sterile and petaloid with intermediates conceptually linking the outermost petals to the inner fertile stamens. This situation has been described in *Glinus* of Molluginaceae. Ronse De Craene (2008) coded Molluginaceae as polymorphic since this family exhibits taxa with uniseriate, undifferentiated perianth and taxa with differentiated perianth. Hofmann (1994) noted that *Glinus* possesses putatively staminodial petals while Ronse De Craene (2008) interpreted them as differentiated staminodial structures.

The genera *Glinus* and *Mollugo* are commonly called carpet weeds and their separation from each other is primarily based on seed characters, the former having appendaged seeds while the latter having non-appendaged seeds. Literature records concerning these weeds are limited to provide information on them. The genus *Glinus* is distributed in tropical and subtropical regions of the world. It originated from the Greek word "*glinos*" meaning a plant with sweet sap or juice. They are squat annual herbs with fuzzy to hairy green herbage. The fruit is a capsule containing many kidney-shaped seeds with a filiform appendaged aril and stellate hairs (Ronse De Craene 2013). *G. lotoides* is widely spread throughout the tropics and subtropics, especially in Africa, Asia, Australia and South Europe. It is native to Eurasia and Africa and has become widespread in tropical, subtropical, and warm-temperate areas worldwide. The species name "*lotoides*" means resembling the genus *Lotus*. It is a spreading annual herb distributed throughout India. The tender shoots and young leaves are used as green vegetable and in the indigenous system of medicine as antiseptic, anthelmintic, against diarrhoea, bilious attacks and as a purgative for curing boils, wounds and pains (Bhavani 2015; Hamed *et al.* 1996; Sastri 2002). Seeds are used for the treatment of tapeworm infections throughout Ethiopia, mainly among rural populations. In Ethiopia and Tanzania, it is currently given threatened status due to its regular harvest for medicinal purpose (Teshome and Feyissa 2015). *G. oppositifolius* is widely distributed in the Americas, tropical Asia, tropical Africa and Australia. The species name "*oppositifolius"* is derived from the Latin word "*oppositus*" meaning standing against or opposed and "*folium*" meaning a leaf, referring to the leaves arranged opposite each other (Huang and Wu 1998; Sahu *et al.* 2001). This species is widely used as a vegetable and in traditional medicine to treat skin diseases, join pains, inflammation, diarrhoea, intestinal parasites, fever and malaria (Dutta *et al.* 2012).

Glinus species are generally characterized by herb life form with flowers in axillary whorls or fascicles, indumentum of stellate hairs, presence of staminodes and by the filiform-

appendaged aril on the seeds (Short 2002). Among different species of *Glinus*, the stamen number is unstable ranging from five to several series of stamens including outer staminodes (Hoffman 1994). In this genus, the sepals are five and display quincuncial aestivation (Ronse De Craene 2010). The stamen loss is variable in different species. The gynoecium and the sepals advancing centripetally act as two separate forces on the intervening androecium to cause stamen loss. The stamen loss is linked with a reduction of carpels from five to three or two. A strong correlation exists between the numbers of stamens in the upper tier and numbers of carpels. Upper stamens always alternate with carpels and an increase or decrease in the upper tier of stamens invariably affects the upper stamen whorl. In flowers with three carpels, the alternisepalous stamens tend to converge in pairs against the flanks of the carpels and are protected to an extent from pressure by the sepals but they leave less space for the initiation of the antesepalous stamens. The outer stamens are replaced by petaloid structures and the petaloid number fluctuates enormously and these structures are either antesepalous by replacing a fertile stamen or alternisepalous as an appendage of upper stamen (Brockington *et al.* 2013). In *Glinus*, a white aril of funicular origin develops into elongate, filiform strophiole (Bittrich 1990). In *G. lotoides*, the androecium is extremely variable and only the alternisepalous whorl is complete with staminodes and odd stamen is opposite to sepals (Ronse De Craene 2010). But, Sharma (1963) stated that this species shows rarely more than five stamens. Bittrich (1990) noted that *G. lotoides* fruit is a capsule and opens when moistened with the aid of expanding keels. Sharma (1963) reported that in *G. oppositifolius*, the stamens vary from 10 to 13 arranged in three whorls indicative of a tendency for reduction with the loss of the outer stamen whorl.

Erdtman (1986) stated that Molluginaceae is a stenopalynous family because the pollen morphology is uniform among species indicating that the pollen type is characteristic and constant. Perveen and Qaiser (2000) provided the details of pollen grains of this family. The pollen grains are radially symmetrical, isopolar, oblate-spheroidal to prolate-spheroidal or sub-prolate, tricolpate, and the colpal membrane is finely-coarsely granulate. Sexine is slightly thicker than nexine. Tectum is scabrate-spinulose. Ronse De Craene (2010) reported that in Molluginaceae, the ovary is isomerous with antesepalous carpels or is reduced to three or two with ovules arranged on axile placentation with narrow partitions and styles are carinal. The fruit is a capsule with many seeds enclosed within persistent calyx. It is loculicidally dehiscent. Bittrich (1990) reported that in *M. verticillata*, the fruit capsule opens when moistened with the aid of expanding keels. Narayana (1962) and Hofmann (1973) noted that *Mollugo* species have a primordium-like swelling on the funiculus and it is considered to be a vestigial aril. Bittrich and Ihlendfeldt (1984) mentioned that *Mollugo* seeds germinate by means of an operculum.

The genus *Mollugo* is native to tropical to warm temperate parts of North and South America but it is distributed in Europe, Africa and Asia. The generic name is derived from the Latin word "*mollis*" meaning soft. *Mollugo* differs from other members of Molluginaceae by the presence of a combination of leaves in false whorls without stipules,

flowers borne in cymes or panicles and produce seeds lacking a caruncle or having a very small caruncle lacking an appendage (Short 2002). *M. verticillata* occasionally introduced in Europe, Africa and Asia. *M. disticha* is restricted to India and Sri Lanka. *M. brevipes, M. cubensis* and *M. pinosia* all are endemic to Cuba (Thulin *et al.* 2016). *M. cerviana* is native to India, Sri Lanka, Pakistan and Bangladesh. The species name is derived from the Latin word which means deer or fawn coloured. It is an ancient medicinal plant known as thread stem carpetweed. In India, it is widely used as a pot herb. It is also used in Ayurveda as an alternative treatment for various ailments such as skin diseases, rheumatism, piles, fever and snake bite (Parvathamma and Shanthamma 2000). Further, the extract of the plant has been reported to be a good inhibitor for the corrosion of mild steel (Arockiasamy *et al.* 2014). *M. pentaphylla* is distributed throughout India, Ceylon, Malacca, China, Japan and Fiji (Maharana *et al.* 2012). The species name refers to palmately compound leaf with five leaflets. It is used in traditional medicine as stomachic, antiseptic and to treat sore legs and promote menstrual discharge in women (Sahu *et al.* 2012). *M. nudicaulis* is distributed throughout tropical Africa and Asia (Burrows and Willis 2005). The species name is derived from the Latin word "*nudicaulis*" meaning naked or leafless stem. It is used in Indian phytotherapy for the treatment of inflammation, jaundice, urinary and kidney disorders, wounds, cold, cough, fever and body pain (Rajamanikandan *et al.* 2011).

Ronse De Craene (2010) reported that in *Mollugo*, the number of stamens ranges from five (*M. cerviana*) to three (*M. nudicaulis*). Perveen and Qaiser (2000) reported that *M. cerviana* and *M. pentaphylla* show a little variation in the exine pattern of pollen; the pollen grain is covered with a scabrate tectum in the former and with spinulose tectum in the latter.

Aizoaceae is closely associated with Molluginaceae in several leaf, flower and fruit characters. The flowers in these families are usually small or medium-sized and show adaptations to different categories of insects for pollination. In this connection, the literature available on pollination ecology of these two families has been reviewed and key aspects of pollination and pollinators have been presented.

Little information is available on the pollination biology or related aspects of Aizoaceae subfamilies Mesembryanthemoideae and Ruschoideae, commonly referred to as mesembs (Hartmann 1991; Chesselet *et al.* 1995; Juergens 2004; Peter *et al.* 2004; Thiede *et al.* 2011). The predominance of bright, showy petals and the presence of functional nectaries in the flowers of this family suggest insects as primary pollen vectors (Hartmann 1991; Ihlendfeldt 1994). In a detailed study, Chesselet *et al.* (1995) explained the importance of floral nectar as an attractant to insects in Aizoaceae species. Further, these authors also stated that the abundant pollen produced by many species is an important reward for many insects and insect pollination appears to be common in this family. On the contrary, Bittrich (1987) suggested that abundant pollen might be an adaptation for wind pollination. Ihlenfeldt (1994) noted that many flowers within the Aizoaceae attract a wide spectrum of floral

visitors and that most species are protandrous and self-sterile. Struck (1994) reported that the mesemb flowers are pollinated by masarid wasps in South Africa. Hartmann (1991) reported that the presence of prominent bright shiny petals and the open pollen presentation functional in diurnal flowering species of this family suggest insect pollination. He also stated that the flowers opening during the day are protandrous, with a very distinctive early male phase, followed by a later female phase. The flowers open repeatedly by basal growth of the androecial elements. In melittophilous flowers, the stigmas are at first shorter than the stamens. During the female phase, the stamens wither and collapse and the elongated stigmas become prominent in the middle of the flower. At this stage the stigmas spread and start to produce a copiously papillate surface, which is more intensively coloured than in the un-receptive stage. Such a sexual function in the flowers facilitate and promote cross-pollination by bees. Hammer (1995) reported that Aizoaceae members show synchrony in flowering time within populations. The period of flowering usually short and the repeated opening of flowers is usually restricted to a certain period of the day. Groen and Van Der Maesen (1999) reported that the populations of *Bergeranthus, Faucaria* and *Orthopterum* flower simultaneously. These authors considered this situation of flower synchrony in different species collectively promotes floral attraction to pollinator insects. Peter *et al*. (2004) speculated that *Bergeranthus* flowers stay closed at low ambient temperature and vapour pressure as a mechanism to protect the pollen from moisture because pollen fertility gets affected if it contacts with water. The flower closure mechanism probably evolved to protect pollen from water on cool humid days and from dew at night. Zietsman (2013) reported that *Stomatium bolusiae* flowers are hermaphroditic. In some flowers there is almost complete overlap of pollen presentation and stigma receptivity. In others, this time lapse is not more than a few minutes and in some others, there is complete overlap of male and female functions. The floral sexual function is indicative of facultative xenogamy.

In Molluginaceae, 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). *Glinus lotoides* is an important source of pollen for honey bees in Radom area, South Darfur State, Sudan (Aldeen 2014). Hesperiid butterfly, *Carcharodus alceae* during its larval stage avoids *G. lotoides* if the latter is present in the habitat (Benyamini 2005). *Zizeeria karsandra* uses *G. lotoides* and *G. oppositifolius* as larval host plant in south Australia (Grund 1998). *Mollugo verticillata* is pollinated by syrphid fly, *Mesogramma marginata* (Robertson 1928). It is the larval host plant for the Pierid butterfly, *Nathalis iole* in Alabama, USA (Keener *et al.* 2017). 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 pollen source and reciprocate the plants with pollination (Ponnuchamy *et al.* 2014). In South Africa, Andrenidae bees, *Meliturgula flavida* and *Meliturgula haematospila* use *Mollugo* species as pollen and nectar sources; the former

exhibits oligolecty by concentrating on *Mollugo* for forage collection while the latter exhibits polylecty by foraging on *Mollugo* and also on other forage plants growing simultaneously in the habitat.

Glinus lotoides and *G. oppositifolius* are C_3 species (Rama Das and Raghavendra 1973; Christin *et al.* 2010). The genus *Mollugo* contains C3, C4 species and species with C3 and C4 intermediate characteristics (Edwards and Walker 1983). In *Mollugo, 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). *M. nudicaulis* is a successful cosmopolitan weed of disturbed areas in warm climates (Vincent 2003). It produces some leaves with C_3 characteristics and some other leaves with C_4 characteristics according to their position on the stem. The leaves progress from C_3 to C_4 as they age. This photosynthetic variation in a single plant, correlated to the age of the leaf, indicates that C_4 phenotype is controlled by more than just Mendelian genetics (Raghavendra *et al.* 1978). The C_3-C_4 photosynthesis is believed to be a relatively rare condition in plants, with only a few dozen identified species, many of which belong to *Flaveria* (Sage *et al.* 1999). Of all C3-C4 intermediates, *M. nudicaulis* and *M. verticillata* are the most widespread and abundant. Both are found in hot, ruderal habitats where competition is low and the potential for photorespiration is high. Their ability to survive on such sites is likely due to their C_3-C_4 pathway, which improves carbon gain in the reduced atmospheric CO_2 levels. The ecological success of these C_3-C_4 *Mollugo* species 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 (Vogan *et al.* 2007). *M. cerviana* is the only known C_4 species in the Molluginaceae (Brockington *et al.* 2009). C_4 plants possess a characteristic Kranz type of leaf anatomy which involves the occurrence of a chlorenchymatous bundle sheath in the leaves. These plants also consistently exhibit low carbon dioxide compensation point, while the C_3 plants usually compensate at higher levels of carbon dioxide (Rama Das and Raghavendra 1973). The general pattern of abundance of C_4 species in warm environments indicates that C_4 pathway is physiologically advantageous for them to survive and broaden their niche (Lundgren *et al.* 2015).

Lundgren and Christin (2017) reported that C_3-C_4 taxa are remarkably widespread across geographical and environmental space, maintaining the ability to exist in both typical C_3 and C_4 niches. Their physiology does not strongly restrict the migration of species geographically or into new environments. These authors stated that C_3-C_4 lineages converged toward warm habitats, which may have facilitated the transition to C_4 photosynthesis, effectively bridging the ecological gap between C_3 and C_4 plants. The intermediates retained some precipitation aspects of the habitats of their C_3 ancestors, and likely transmitted them to their C_4 descendants, contributing to the diversity among C_4 lineages.

MATERIALS AND METHODS

Five plant species, namely, *Glinus lotoides, G. oppositifolius, Mollugo cerviana, M. nudicaulis* and *M. pentaphylla* were selected for study during March 2014-May 2017. *Glinus* species were studied at Paravada area while *Mollugo* species were studied in the Andhra University Campus and also at Paravada area. These species are very small prostrate annuals and grow throughout the year if the soil has little moisture. They are called "carpet weeds" as they form huge populations carpeting the soil due to their very low prostrate habit. Of these plant species, *M. cerviana* with its wiry stems and linear-lanceolate leaves is not prominent and usually goes unnoticed or overlooked while all other plant species are prominent and can be easily noticed despite their low prostrate habit.

Field visits were made regularly to record the flowering season in the selected plant species. The inflorescence type, the number of flowers produced per inflorescence and per plant were noted. Twenty five fresh flowers were used for each plant species to record the floral details such as flower shape, colour, odour, sex, symmetry, floral mechanism, perianth, stamens, staminodes and style and stigma, etc. The floral configuration and floral rewards presentation aspects were examined in relation to the forage collection activity of insects and the attendant pollination effect.

Anthesis was initially recorded by observing marked mature buds in the field. Later, the observations were repeated 3 to 4 times on different days in order to record accurate anthesis schedule for each plant species. The same buds were followed for recording the time of anther dehiscence. The pollen presentation pattern was also investigated by recording how anthers dehisced, whether all anthers in a flower dehisce simultaneously or not and the same was confirmed by observing the anthers under a 10x hand lens.

In all five plant species, the flowers close back. The time of flower closure was recorded for each plant species. Field observations were also made to record whether the stamens and stigmas stay inside or not after the flower closure.

Nectar secretion was observed from mature bud stage to the time of flower closure. In all five plant species, the nectar traces appeared in mature bud stage itself and there is no further secretion during flower life. Since nectar is not produced in measurable quantity, it was not analyzed for its sugar concentration and chemical constituents such as sugar types, amino acids and proteins. As the nectar was secreted around the ovary base and enclosed by connate staminal filaments, it was considered to be producing sucrose-rich nectar because the nectar concealed in the flowers is usually sucrose-rich.

Pollen output was determined by taking 25 un-dehisced anthers from ten individuals for each plant species. The anthers collected from the sample of flowers were placed in a Petri dish. Later, each time a single anther was taken out and placed on a clean microscope slide (75 x 25 mm) and dabbed with a needle in a drop of lactophenol-aniline blue. The anther tissue was then observed under the microscope for pollen. The pollen mass was

drawn into a band, and the total number of pollen grains was counted under a compound microscope (40x objective, 10x eye piece). This procedure was followed for counting the number of pollen grains in each anther collected. Based on these counts, the mean number of pollen produced per anther was determined. The mean pollen output per anther was multiplied by the number of anthers in the flower for obtaining the mean number of pollen grains per flower. Another set of dehisced anthers was collected in a Petri dish for each plant species and the pollen removed from these anthers was examined under microscope for recording the pollen grain features. The pollen-ovule ratio was determined by dividing the average number of pollen grains per flower by the average number of ovules per flower. The value thus obtained was taken as pollen-ovule ratio (Cruden 1977). The pollen-ovule ratios were calculated separately for 8 to 12-stamened flowers in *Glinus lotoides*, 4 to 6-stamened flowers in *G. oppositifolius*, 3 to 5-stamened flowers in *M. nudicaulis* and *M. pentaphylla*. The pollen-ovule ratio was constant in *M. cerviana* as it produces a fixed number of 5 stamens in all flowers. *In vitro* pollen germination was examined for the pollen of *G. oppositifolius* and *M. pentaphylla*. The pollen was collected from the anthers soon after anther dehiscence and transferred to Petri dish for storage. The pollen thus collected was placed in the cavity of slides, added modified Brewbaker and Kwack's medium and observed after one hour under microscope for germination. This was repeated at each hour from 1100 h to 1900 h to record the percentage of pollen germination in order to record the duration of pollen viability.

Ten flowers each from five individuals for each plant species were used to test stigma receptivity. It was tested with hydrogen peroxide from mature bud stage to flower closure and beyond as per Dafni *et al.* (2005). Hydrogen peroxide when applied to stigma does not stain but produces bubbles as a result of catalase (peroxidase) presence. This test is widely followed although it does not indicate the exact location of the receptive area. The period of release of bubbles from the surface of stigma following application of hydrogen peroxide was taken as the length of stigma receptivity period during flower life and also during closed state of flowers. Further, the receptivity was also observed visually whether the stigmas are shiny, wet or withering.

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 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.

After making preliminary observations on the foraging activities of insects on the plant species selected for study, a thorough knowledge of the local insect species was obtained by observing the representative species available with the Department of Environmental Sciences, Andhra University, Visakhapatnam. All butterflies were identified

to species level by consulting the books of Kunte (2007) and Gunathilagaraj *et al.* (1998) while other insects, some to species level while a few others to genus level only. The efforts to get the specimens identified to species level for the species which were identified up to genus level by Zoological Survey of India, Government of India were not successful during the study period. The insect species were observed with the naked eye and by using binoculars; the insect species that could not be identified on spot were captured and later identified with the help of the identified specimens available in the Department. The foraging activities of insects were recorded for 10 min at each hour during the open state of flowers on 4 occasions and the data was tabulated to use the same for further analysis, especially to understand the foraging activity rate. For each species, approximately fifty inflorescences were selected to record the foraging visits of insects. The data thus obtained was used to calculate the percentage of foraging visits made by each category of insects per day to evaluate their association and pollination role in the studied plant species. The insects feeding on nectar and/or pollen were carefully observed to assess their role in effecting pollination. They were observed on a number of occasions on each plant species for their foraging behaviour such as mode of approach, landing, probing behaviour, contact with essential organs to result in pollination, inter-plant foraging activity in terms of cross-pollination. Based on this data, the association between floral rewards of the studied plant species and insects was assessed.

All five plant species were used by thrips for breeding and feeding. They were collected from the flowers and identified using the key provided by Bhatti (1980) for Indian thrips. Field observations were made as to their mobility and foraging activity on flowers to assess their role in pollination. Further, their body washings were made to count the number of pollen grains in order to confirm whether they have any role in pollination or not.

Ten individuals of each insect species were captured while collecting pollen and/or nectar from the flowers of all the studied plant species; the collection was done during their peak foraging activity period. The captured specimens of insects were brought to the laboratory. They were washed first in ethyl alcohol and the contents stained with aniline-blue on a glass slide and observed under microscope to count the number of pollen grains present and evaluate their relative pollen carryover efficiency and pollination role.

Ten inflorescences each on ten individuals of each plant species were tagged prior to anthesis and followed for fruit and seed set for two weeks. The resulting fruit and seed output were pooled up for calculating fruit and seed set rates. Fruit and seed set rates were recorded separately for 8 to 12-stamened flowers in *Glinus lotoides*, 4 to 6-stamened flowers in *G. oppositifolius*, and 3 to 5-stamened flowers in *M. nudicaulis* and *M. pentaphylla*. Fruit and seed set rates were constant in *M. cerviana* as it produces a fixed number of stamens and ovules per flower.

Fruit and seed dispersal was carefully observed to draw practical inferences regarding their success as weeds. The role of wind and rain water in fruit and seed dispersal was

examined in the studied plant species. The fruit and seed morphological characteristics were observed in detail as to their adaptations for dispersal by different means in order to invade, colonize and establish populations in different areas. Seed is the only mode of propagation in all these plant species. Observations on seed germination were made in the field to know whether seeds germinate immediately after their dispersal or not, and if so, whether they form new plants or populations continuously or not.

RESULTS

GLINUS LOTOIDES L.

Phenology: It is a low-growing prostrate, spreading, annual herb that grows in open sandy soils, cultivated fields and open waste lands (Plate 2a,b). In soils with enough moisture, it produces well developed tap root and survives throughout the year producing flowers and fruits simultaneously or alternately. The stem is soft, succulent, pubescent and much-branched carpeting the soil with its foliage. Leaves are simple, basal ones borne in a rosette form while the upper ones in verticillate form or rarely arranged opposite, and densely stellate tomentose. The flowering is profuse when soil is very damp which occurs during July-October due to monsoonal rains. Flowers are borne on 1.5 mm long stalks in axillary cymes and each cyme consists of 4.72 ± 1.3 flowers and each plant produces 82.5 ± 33.65 flowers (Plate 2c,d).

Plate 1. Study area- a. Author (extreme left) surveying for the study species, b. Author examining study material under microscope.

Flower morphology: The flowers are small (6.1 ± 1.28 mm long, 7.42 ± 1.25 mm wide), odourless, actinomorphic and bisexual. The calyx and corolla are represented by perianth with 5 or rarely 6 tepals. The tepals are succulent, free (6.02 ± 0.19 mm long, 4.05 ± 0.2 mm wide), arranged in quincuncial aestivation, whitish green adaxially and green abaxially, ovate-oblong and covered with stellate hairs. The stamens are 8 to 12, free, white and arranged in two whorls. The stamens of inner whorl close to ovary base are long and form a short tube at the base around the ovary while those of the outer whorl are short. The stamens of both

Plate 2. *Glinus lotoides*: a. Mixed populations of *G. lotoides* (plants with silver colour leaves) and *Glinus oppositifolius* (plants with bright green leaves), b. Habitat with extensive population of *G. lotoides*, c. & d. Close-up view of flowering inflorescences.

whorls are usually anti-tepalous and occasionally alterni-tepalous. The flowers with 8-stamens constitute 14.28%, those with 9-stamens 21.42%, those with 10-stamens 42.85%, 11-stamens 19.04% and 12-stamens 2.38%. Anthers are H-shaped, white, dithecous and versatile. Staminodes are 5-7, petaloid, white, bifid and usually alterni-tepalous but occasionally in between short stamens; they extend beyond the height of long stamens (Plate 3c-e). The ovary (5 ± 0.23 mm long and 2.03 ± 0.17 mm wide) is green, pentacarpellary and pentalocular syncarpous with variable number of ovules arranged in two rows in each locule on axile placentation. The ovule number varied from 181.9 ± 35.28 to 242.4 ± 35.14 in 8- and 12-stamened flowers (Plate 3g). The ovule production trend showed that the number of ovules produced gradually increased with a gradual increase in the number of stamens per anther and pollen out per flower but the variation is not significant. The style is absent and stigmas are five, greenish white, free, spreading, papillate, wet and shiny (Plate 3c,d,f).

Floral biology: Mature buds open during 1400-1500 h. Individual buds take 30 to 40 minutes from partial to full opening (Plate 3a,b, 4a-c). The anthers dehisce by longitudinal slits during anthesis (Table 1). The pollen output per anther varied from 1,193.85 ± 70.25 to 1,371.85 ± 65.76 and from 10,974.85 ± 526.08 to 14,326.28 ± 843.03 per flower in 8- to 12-stamened flowers (Table 2). The pollen production trend showed that the pollen output rate

gradually increased with a gradual decrease in the number of stamens produced per flower but the variation is not significant. The pollen-ovule ratio varied from 58: 1 to 61:1 in 8- to 12-stamened flowers. The pollen grains are white, spheroidal, tricolporate, tri-zonoaperturate, colpal membrane densely granulated, 32.52 ± 4.28 µm in size and tectum with scabrate ornamentation. The stigma attains receptivity after anthesis and continuous up to 2nd day noon time (Table 1). The nectar is secreted in traces during mature bud stage. The tepals together with the staminodes, stamens and stigma close back by 1700-1800 h on the same day and remain in place in fertilized flowers until fruit dispersal (Table 1). The un-fertilized flowers fall off after 7-10 days.

Plate 3. *Glinus lotoides*: a. Bud, b. Flower, c. & d. Relative positions of stamens and stigma, e. Stamens, f. Pistil, g. Ovules, h. Fruit capsule with stamens and stigma intact in withered state, i. & j. Fruit capsule with mature seeds.

Table1. Anthesis schedules in the studied plant species

Plant species	Anthesis time (h)	Anther dehiscence	Period ofstigma receptivity	Flower closing time (h)
Glinus lotoides	1400-1500	During anthesis	Starts after anthesis and continuous up to 2nd day noon	1700-1800
Glinus oppositifolius	1200-1400	During anthesis	Starts after anthesis and continuous up to 2nd day noon	1600-1800

Mollugo cerviana	0700-0800	During anthesis	Starts during anthesis and continuous up to 2nd day noon	1000-1100
Mollugo nudicaulis	0700-0900	During anthesis	Starts during anthesis and continuous up to 2nd day noon	1000-1200
Mollugo pentaphylla	0700-0800	During anthesis	Starts during anthesis and continuous up to 2nd day noon	1000-1100

Table 2. Pollen aspects in *Glinus lotoides*

Flower type	Percentage of occurrence	Mean pollen output/anther	Mean pollen output/flower	Mean no. of ovules/flower	Pollen: ovule ratio
8-stamened	14.20	1371.85 ± 65.76	10974.85 ± 526.08	181.9 ± 35.28	60 : 1
9-stamened	21.42	1331.85 ± 91.46	11986.71 ± 823.21	196.7 ± 35.78	61 : 1
10-stamened	42.85	1304.57 ± 62.65	13045.71 ± 626.57	221.8 ± 40.67	59 : 1
11-stamened	19.04	1221.85 ± 61.36	13440.42 ± 674.99	230.2 ± 34.23	58 : 1
12-stamened	2.38	1193.85 ± 70.25	14326.28 ± 843.03	242.4 ± 35.14	59 : 1

Pollination mechanism: The fully open flowers show different positions of the stamens and the stigmas. The stigmas are situated beyond the height of short stamens but below the height of long stamens. Further, both the sex organs are spatially separated and precludes spontaneous autogamy during open state of the flower. However, during the closure of the flower, the closely spaced dehisced anthers of long stamens contact the stigmas facilitating spontaneous autogamy but its occurrence is dependent on the availability of pollen in the anthers (Plate 4d).

Thrips breeding, feeding and pollination: Thrips species, *Haplothrips* sp. (Thysanoptera: Thripidae) ovi-posited during early stage of floral bud (Plate 4e). 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. The pollen morphological characters facilitated the thrips to carry 428 to 635 pollen grains on their body setae, wings and legs. The thrips dispersed the pollen on free spreading papillate stigmas due to their active movement, rubbing the abdomen against the stigmatic surface, cleansing of their body parts with their hind legs and also by their wing combing mechanism. The near homogamous nature of the flowers facilitate self-pollination within the same flower or different flowers of the same plant by thrips. 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.

Plate 4. *Glinus lotoides*: a. Initiation of anthesis by mature bud, b. Half-open flower, c. Fully open flower, d. Flower closure at 1800 h, e. *Haplothrips* sp. feeding on nectar, f. *Apis cerana* collecting pollen, g. *Apis cerana* collecting nectar, h. *Camponotus* sp. collecting nectar, i. Lycaenid butterfly, *Zizeeria karsandra* collecting nectar.

Insect visitors and Pollination: The flowers were foraged by bees for pollen and nectar, ants and butterflies for only nectar during 1400-1700 h with concentrated foraging activity during 1500-1600 h (Figure 1,2). The bees were *Apis cerana* (Plate 4f), *A. florea* (Plate 4g), *Trigona iridipennis* and *Ceratina* sp. The ants included *Camponotus* sp. (Plate 4h) and *Crematogaster* sp. The butterflies included only lycaenids, namely, *Zizula hylax, Zizeeria karsandra* (Plate 4i)*, Zizina otis, Freyeria trochylus, Chilades laius* and *Chilades pandava* (Table 3). 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. Ants were resident foragers and continuously crawled all over the plant and accessed the floral base to collect nectar. Butterflies stretched 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, the bees and also ants during nectar collection brushed against anthers and stigmas with their dorsal surface effecting nototribic pollination. The butterflies during nectar collection contacted the stamens and stigmas with their proboscis and front side of head and ventral surface of thorax and abdomen effecting sternotribic pollination. Their wings never contacted the stamens and stigma during nectar collection as they kept them in vertical position. Bees made 47%, ants 9% and lycaenids 44% of total foraging visits (Figure 3). 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 4). 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.

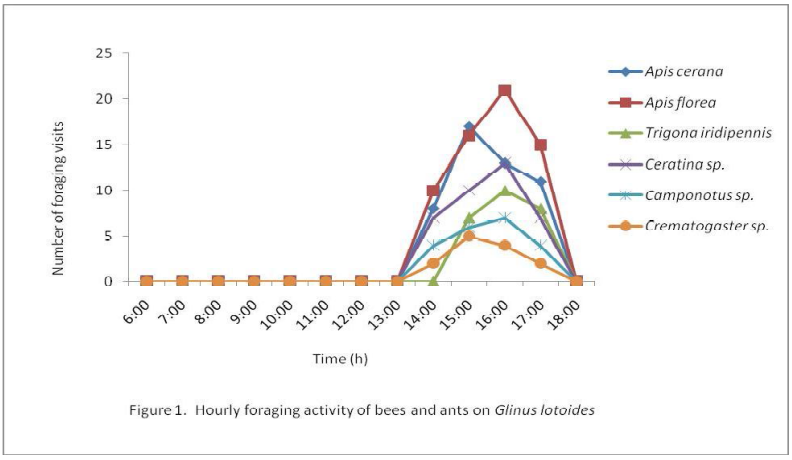

Figure 1. Hourly foraging activity of bees and ants on *Glinus lotoides*

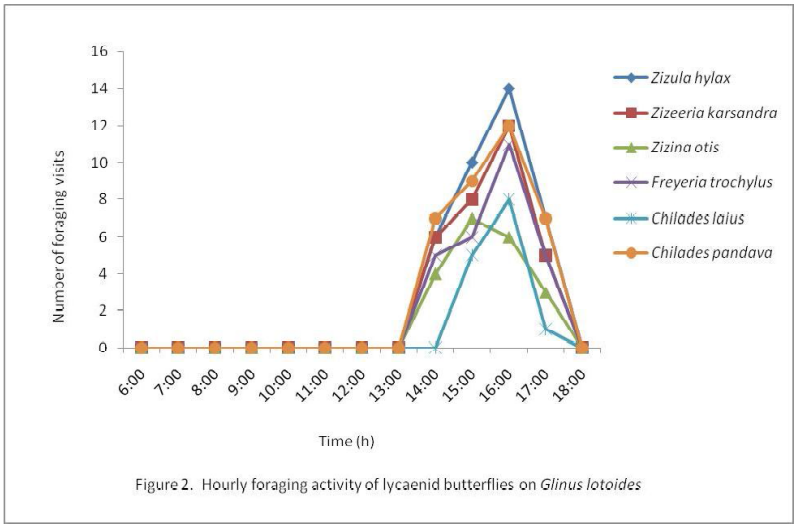

Figure 2. Hourly foraging activity of lycaenid butterflies on *Glinus lotoides*

Table 3. List of insect foragers on *Glinus lotoides*

Order	Family	Genus	Species	Common name	Forage sought
Hymenoptera	Apidae	*Apis*	*cerana* F.	Indian Honey Bee	Pollen + Nectar
		Apis	*florea* F.	Dwarf Honey Bee	Pollen + Nectar

		Trigona	*iridipennis* Smith	Stingless Honey Bee	Pollen + Nectar
		Ceratina	sp.	Small Carpenter Bee	Pollen + Nectar
	Formicidae	*Camponotus*	sp.	Carpenter Ant	Nectar
		Crematogaster	sp.	Cocktail Ant	Nectar
Lepidoptera	Lycaenidae	*Zizula*	*hylax* F.	Tiny Grass Blue	Nectar
		Zizeeria	*karsandra* Moore	Dark Grass Blue	Nectar
		Zizina	*otis* F.	Lesser Grass Blue	Nectar
		Freyeria	*trochylus* Freyer	Grass Jewel	Nectar
		Chilades	*laius* Stoll	Lime Blue	Nectar
		Chilades	*pandava* Horsfield	Plains Cupid	Nectar

Table 4. Pollen recorded in the body washings of insects on *Glinus lotoides*

Insect species	Sample size(N)	Number of pollen grains		
		Range	Mean	S.D
Apis cerana	10	92-307	208.2	55.45
Apis florea	10	78-252	167.1	56.83
Trigona iridipennis	10	43-214	129.2	46.26
Ceratina sp.	10	35-94	64.1	17.44
Camponotus sp.	10	27-58	39.4	8.59
Crematogaster sp.	10	23-46	34.5	6.43
Zizula hylax	10	8-31	21.4	6.29
Zizeeria karsandra	10	15-40	27.8	7.40
Zizina otis	10	11-29	20.8	5.24
Freyeria trochylus	10	10-38	25.4	7.4
Chilades laius	10	12-34	23.3	6.37
Chilades pandava	10	10-42	28.4	8.27

Fruiting ecology and seed dispersal: The pollinated and fertilized flowers grow continually and produce fruits within 8-12 days. The stamens and stigmas are persistent and remain inside due to the closure of the flower (Plate 3h). The tepals bulge gradually and protect the bulging ovary in which the seeds form and mature (Plate 3i,j). Natural fruit set rate varied from 88% to 92% while seed set rate varied from 85% to 93% in 8- to 12-stamened flowers

(Table 5). Fruit is a loculicidal 5-valved capsule, stalked, membranous, densely pubescent, 6.05 ± 0.75 mm long and 4.1 ± 0.64 mm wide. The seeds are small, reniform, smooth, 0.7 mm long and 0.5 mm wide, initially red and finally dark brown and have a white aril of funicular origin developed into elongate filiform strophiole. They are arranged in two rows in each locule. Dry capsules break open when tepals are wet and expose the seeds. But the seeds remain so and gradually separate and fall to the ground on their own due to their smooth and slippery nature on clear sunny days. In dry season, when the capsules are ripe, the plant dies, dries out and becomes brittle. In this state, the base of the stem breaks off and it is more so when high winds prevail. Then, the plant parts roll readily and fruit and seeds disperse to other areas. On rainy days, drops of water falling on the distal opening after the locules are filled with rain water result in an explosive expulsion of water droplets and seeds. Further, water acts as an efficient dispersal agent for the dispersal of seeds fallen on the soil during rainy season. Therefore, seed dispersal is characteristically anemochorous, ombrohydrochory and hydrochory.

Table 5. Natural fruit and seed set rate in *Glinus lotoides*

Flower type	Number of flowers sampled	Number of flowers set fruit	Fruit set (%)	Seed set (%)
8-stamened	50	45	90	85
9-stamened	60	53	88	87
10-stamened	110	98	89	90
11-stamened	45	41	91	92
12-stamened	25	23	92	93

GLINUS OPPOSITIFOLIUS (L.) AUG. DC.

Phenology: It is a low-growing prostrate, spreading, annual herb that grows in open sandy soils, cultivated fields and open waste lands (Plate 5a). In soils with enough moisture, it produces well developed tap root and survives throughout the year producing flowers and fruits simultaneously or alternately (Plate 5b-d). The stem is soft, succulent, sub-glabrous and much-branched covers the soil with its foliage. Leaves are petiolate, simple, arranged in pseudo-whorls of 3-6 or opposite to each other. Leaf blade is spatulate-oblanceolate. Its margins are covered with sparse teeth. The flowering is profuse when soil is very damp which occurs during July-October due to monsoonal rains. Flowers are borne on 3-7 mm long pedicels in axillary fascicles and each fascicle consists of 7.5 ± 1.5 flowers and each plant produces 64.52 ± 41.28 flowers.

Flower morphology: The flowers are small (3.51 ± 0.5 mm long, 8.57 ± 0.7 mm wide), odourless, actinomorphic and bisexual. The calyx and corolla are represented by a perianth with 5 or rarely 6 tepals . The tepals are succulent, free (4.01 ± 0.2 mm long, 2.03 ± 0.2 mm

wide), arranged in quincuncial aestivation, creamy white adaxially and brownish orange abaxially, ovate-oblong and pubescent. The stamen are 4 to 6, free but connate at the base, and alterni-tepalous. The flowers with 4-stamens constitute 5%, those with 5-stamens 80% and those with 6-stamens 15%. Anthers are H-shaped, white, dithecous and versatile. Staminodes are 5 or 6, petaloid, white, bifid and anti-tepalous. The ovary (4.07 ± 0.16 mm long and 2 mm wide) is green, tri-carpellary and tri-locular syncarpous with variable number of ovules arranged in two rows in each locule on axile placentation. The ovule number varied from 115.5 ± 7.1 to 137.7 ± 9.9 in 4- and 6-stamened flowers. The ovule production trend showed that the number of ovules produced gradually increased with a gradual increase in the number of stamens per anther and pollen out per flower but the variation is not significant. The style is absent and stigmas are three, creamy white, free, spreading, papillate, wet and shiny (Plate 6d).

Floral biology: Mature buds open during 1200-1400 h (Plate 6a). Individual buds take 10 to 15 minutes from partial to full opening. The anthers dehisce by longitudinal slits during anthesis (Table 1, Plate 6b). The pollen output per anther varied from 1,151 ± 67.22 to 957.33 ± 49.1 and from 4,604 ± 268.9 to 5,744 ± 295.1 per flower in 4- to 6-stamened flowers (Table 6). The pollen production trend showed that the pollen output rate gradually increased with a gradual decrease in the number of stamens produced per flower but the variation is not significant. The pollen-ovule ratio is constant despite variation in the number of stamens and ovules; it is 40:1. The pollen grains are white, spheroidal, tricolporate, tri-zonoaperturate, colpal membrane densely granulated, 29.34 ± 4.26 µm in size and tectum with scabrate ornamentation (Plate 6c). *In vitro* pollen viability test indicated that the pollen grains are viable during the open state of flowers only (Table 7). The pollen is available from anthesis onwards and remain so until the closure of the flower; it is the highest immediately after anthesis and gradually decreases towards the time of closing of the flower. The stigma attains receptivity after anthesis and continuous up to 2nd day noon time (Table 1). The nectar is secreted in traces during mature bud stage. The tepals together with the staminodes, stamens and stigma close back by 1600-1800 h on the same day and remain in place until fruit dispersal in fertilized flowers (Table 1). The un-fertilized flowers fall off after 6-8 days.

Pollination mechanism: The fully open flowers show different positions of the stamens and the stigmas. The stamens, staminodes and stigmas are situated at the same height. But, both the sex organs are spatially separated and precludes spontaneous autogamy during open state of the flower. However, during the closure of the flower, the anthers contact the stigmas facilitating spontaneous autogamy but its occurrence is dependent on the availability of pollen in the anthers.

Thrips breeding, feeding and pollination: Thrips species, *Haplothrips sp.* (Thysanoptera: Thripidae) ovi-posited during early stage of floral bud. The larval emergence from the eggs was in synchrony with anthesis and nectar production in flowers. Both larvae

and adults foraged for pollen and nectar. Individual thrips were dusted with pollen during their movements within the flowers. The pollen morphology facilitated the thrips to carry 157 to 253 pollen grains on their body setae, wings and legs. The thrips dispersed the pollen on free papillate spreading stigmas due to their active movement, rubbing of the abdomen against the stigmatic surface, cleansing of their body parts with their hind legs and also by their wing combing mechanism. The near homogamous nature of the flowers facilitate self-pollination within the same flower or different flowers of the same plant by thrips. 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.

Plate 5. *Glinus oppositifolius*: a. Habit, b. & c. Bud stage, d. Flowering phase.

Insect visitors and Pollination: The flowers were foraged by bees for pollen and nectar, ants and butterflies for only nectar during 1300-1700 h with concentrated foraging activity during 1500-1600 h (Figure 4,5). The bees were *Apis cerana*, *A. florea* (Plate 6g,h), *Ceratina* sp. (Plate 6i,j), *Ceratina smaragdula* (Plate 6k), *Halictus* sp. and *Megachile* sp. (Plate 6l). The ants included *Camponotus* sp. and *Crematogaster* sp. The butterflies included only lycaenids, namely, *Zizula hylax* (Plate 6m), *Zizeeria karsandra* (Plate 6n,o), *Zizina otis* (Plate 6p), *Freyeria trochylus, Chilades laius* and *Chilades pandava* (Table 8). 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. Ants were resident foragers and continuously crawled all over the plant and accessed the floral base to collect nectar. Butterflies stretched out their proboscis and inserted into the flower

base to collect nectar. All insect species collected forage from several flowers of different fascicles 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, the bees and also ants during nectar collection brushed against anthers and stigmas with their dorsal surface effecting nototribic pollination. The butterflies during nectar collection contacted the stamens and stigmas with their proboscis and front side of head and ventral surface of thorax and abdomen effecting sternotribic pollination. Their wings never contacted the stamens and stigma during nectar collection as they kept them in vertical position. Bees made 60%, ants 5% and lycaenids 35% of total foraging visits (Figure 6). 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 9). 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.

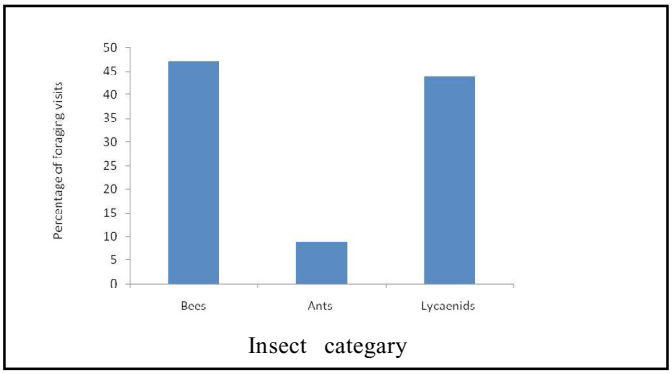

Figure 3. Percentage of foraging visits of bees, ants and lyaenid butterflies of *Glinus lotoides*

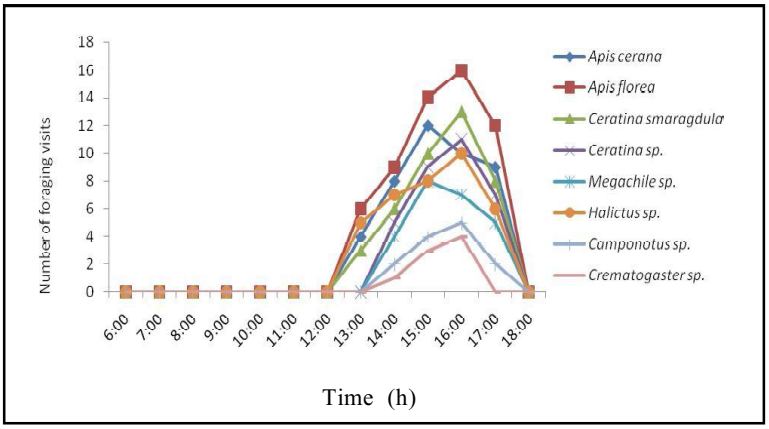

Figure 4. Hourly toraging activity of bees and ants on *Glinus oppositolius*

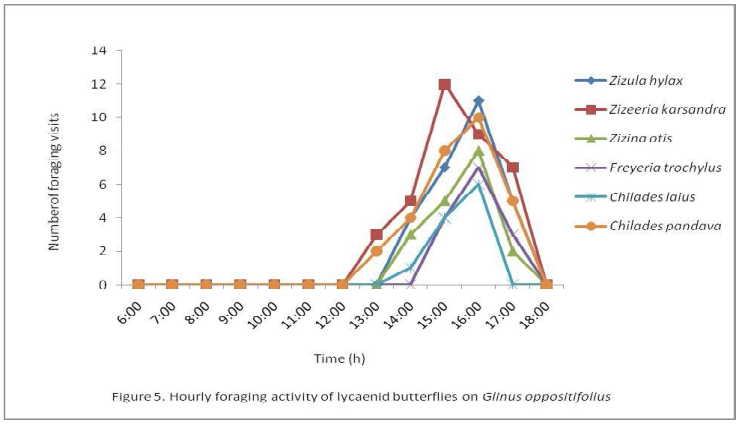

Figure 5. Hourly foraging activity of lycaenid butterflies on *Glinus oppositifolius*

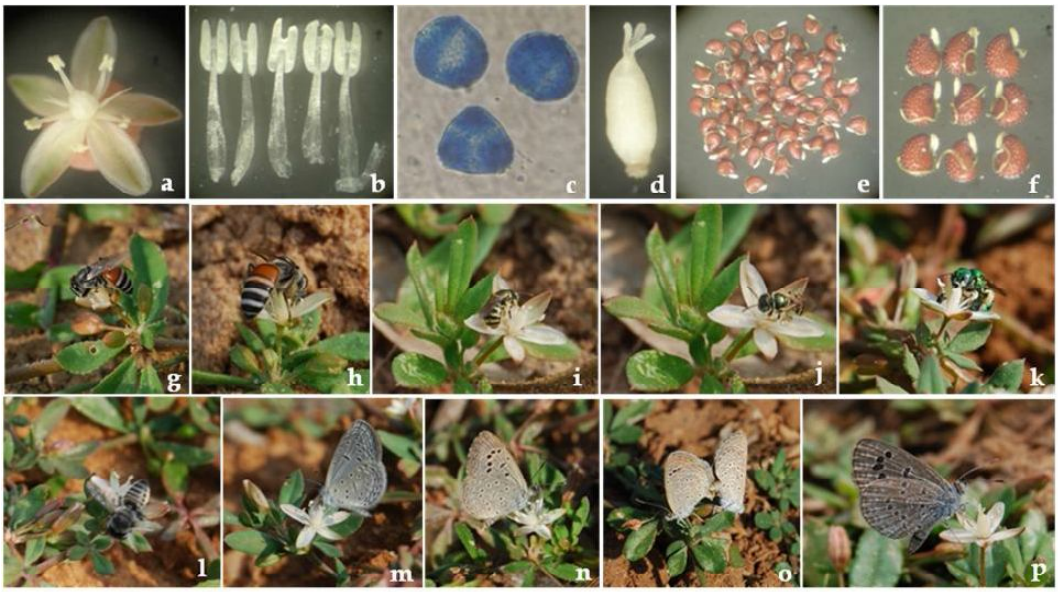

Plate 6. *Glinus oppositifolius*: a. Flower, b. Dehisced stamens, c. Pollen grain, d. Ovary with three stigmas, e. & f. Seeds, g-l. Pollen and nectar foragers – g. *Apis florea* collecting pollen, h. *Apis florea* collecting nectar, i. *Ceratina* sp. collecting pollen, j. *Ceratina* sp. collecting nectar, k. *Ceratina smaragdula* collecting nectar, l. *Megachile* sp. collecting nectar, m-p. Nectar foragers (Lycaenid butterflies) – m. *Zizula hylax*, n. *Zizeeria karsandra*, o. *Zizeeria karsandra* in mating state, p. *Zizina otis*.

Table 6. Pollen aspects in *Glinus oppositifolius*

Flower type	Percentage of occurrence	Mean pollen output/anther	Mean pollen output/flower	Mean no. of ovules/flower	Pollen: ovule ratio
4-stamened	5	1151 ± 67.2	4604 ± 268.9	115.5 ± 7.1	40 : 1
5-stamened	80	1027 ± 55.5	5133 ± 277.5	128.6 ± 7.7	40 : 1
6-stamened	15	957 ± 49.1	5744 ± 295.1	137.7 ± 9.9	40 : 1

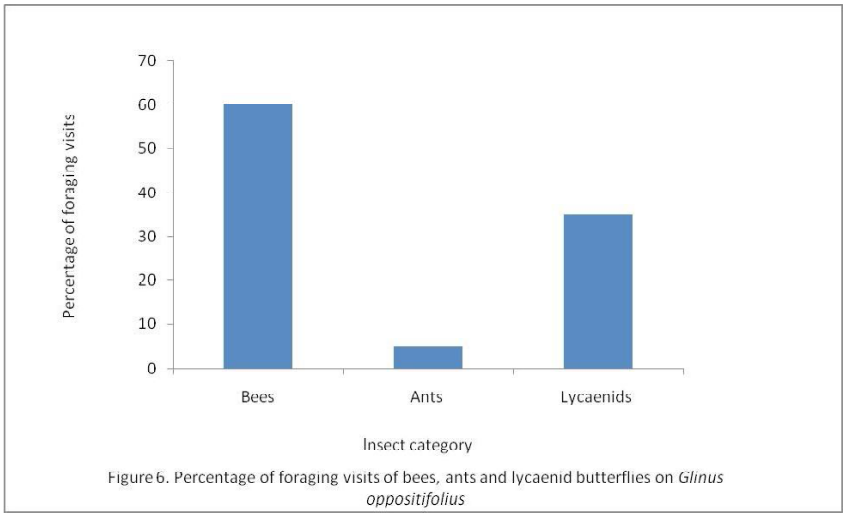

Figure 6. Percentage of foraging visits of bees, ants and lycaenid butterflies on *Glinus oppositifolius*

Table 7. *In vitro* pollen germination in *Glinus oppositifolius*

Time (h)	Pollen sample	No. of germinated pollen grains	Germination (%)
1100	—	—	—
1200	224	210	94
1300	367	307	84
1400	22	16	73
1500	233	118	51
1600	90	42	47
1700	45	8	18
1800	34	3	9
1900	—	—	—

Modified Brewbaker and Kwack's medium

Table 8. List of insect foragers on *Glinus oppositifolius*

Order	Family	Genus	Species	Common Name	Forage Sought
Hymenoptera	Apidae	*Apis*	*cerana* F.	Indian Honey Bee	Pollen + Nectar
		Apis	*florea* F.	Dwarf Honey Bee	Pollen + Nectar
		Ceratina	*smaragdula* F.	Small Carpenter Bee	Pollen + Nectar
		Ceratina	sp.	Small Carpenter Bee	Pollen + Nectar

	Halictidae	*Halictus*	sp.	Sweat Bee	Pollen + Nectar
	Megachilidae	*Megachile*	*sp.*	Leafcutter Bee	Pollen + Nectar
	Formicidae	*Camponotus*	sp.	Carpenter Ant	Nectar
		Crematogaster	sp.	Cocktail Ant	Nectar
Lepidoptera	Lycaenidae	*Zizula*	*hylax* F.	Tiny Grass Blue	Nectar
		Zizeeria	*karsandra* Moore	Dark Grass Blue	Nectar
		Zizina	*otis* F.	Lesser Grass Blue	Nectar
		Freyeria	*trochylus* Freyer	Grass jewel	Nectar
		Chilades	*laius* Stoll	Lime Blue	Nectar
		Chilades	*pandava* Horsfield	Plains Cupid	Nectar

Table 9. Pollen recorded in the body washings of insects on *Glinus oppositifolius*

Insect species	Sample size(N)	Number of pollen grains		
		Range	Mean	S.D
Apis cerana	10	87-236	161.5	46.6
Apis florea	10	66-214	140.5	42.9
Ceratina smaragdula	10	68-164	115.9	24.8
Ceratina sp.	10	41-117	84.2	21.6
Megachile sp.	10	43-102	74.8	16.1
Halictus sp.	10	27-63	44.1	9.1
Camponotus sp.	10	22-45	31.3	7.4
Crematogaster sp.	10	13-34	25.1	6.4
Zizula hylax	10	11-38	26.8	7.2
Zizeeria karsandra	10	9-46	28.8	9.2
Zizina otis	10	14-30	23.1	5.1
Freyeria trochylus	10	7-29	19.3	6.1
Chilades laius	10	10-35	24.8	7.0
Chilades pandava	10	12-41	28.1	7.2

Fruiting ecology and seed dispsersal: The pollinated and fertilized flowers grow continually and produce fruits within 7-10 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. Natural fruit set rate varied from 88% to 92% while seed set rate varied from 88% to 91% in 4- to 6-stamened flowers (Table 10).

Fruit is an ellipsoid loculicidal 3-valved capsule, short-stalked, membranous, densely pubescent, 5.5 ± 0.5 mm long and 2.1 ± 0.2 mm wide. The seeds are small, sub-reniform, granulose, 0.9 mm long and 0.7 mm wide, reddish-brown and have a white aril of funicular origin developed into extensively curved scrotiform strophiole (Plate 6e,f). They are arranged in two rows in each locule. Dry capsules break open when tepals are wet and expose the seeds. But the seeds remain so and gradually separate and fall to the ground on their own on clear sunny days. In dry season, when the capsules are ripe, the plant dies, dries out and becomes brittle. In this state, the base of the stem breaks off and it is more so when high winds prevail. Then, the plant parts roll readily and fruit and seeds disperse to other areas. On rainy days, drops of water falling on the distal opening after the locules are filled with rain water result in an explosive expulsion of water droplets and strophiolate seeds. Further, water acts as an efficient dispersal agent for the dispersal of seeds fallen on the soil during rainy season. Therefore, seed dispersal is characteristically anemochorous, ombrohydrochory and hydrochory.

Table 10. Natural fruit and seed set rate in *Glinus oppositifolius*

Flower type	Number of flowers sampled	Number of flowers set fruit	Fruit set (%)	Seed set (%)
4-stamened	61	54	88	88
5-stamened	225	206	91	90
6-stamened	105	97	92	91

MOLLUGO CERVIANA (L.) SER.

Phenology: It is 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 (Plate 7a). Its presence is easily 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. The plant appears simultaneously in vegetative, flowering and fruiting phases in different populations growing in different habitats throughout the year (Plate 7b). An individual plant, however, has a short life cycle of 3 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 soil is damp due to occurrence of rains. The flowers are borne on 7-8 mm long pedicels in dichotomous and trichotomous umbellate cymes produced terminally or in leaf axils.

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. The sepals and petals are represented by a monochlamydeous perianth of 5 herbaceous scarious, elliptic to oblong, 2.45 ± 0.4 mm long, 1.13 ± 0.2 mm wide long free tepals with

white margins. The stamens are 5, anti-tepalous, free but connate at base, white, 1.22 ± 0.3 mm long with dorsifixed, golden yellow, less than 1 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 (Plate 8g,h). The style is absent but the ovary is terminated with 3 free stigmas (Plate 8f). The stigmas are minutely denticulate with membranous flaps.

Plate 7. *Mollugo cerviana*: a. Habitat with *Mollugo cerviana* and *M. nudicaulis*. B. *Mollugo cerviana* in flowering phase.

Floral biology: Mature buds open during 0700-0800 h. Individual buds take 5 to 10 minutes from partial to full opening (Plate 8a,b). The flowers are homogamous as the anthers and stigmas attain maturity at the same time during anthesis; the former dehisce by longitudinal slits (Plate 8d) and the latter continue receptivity until the noon of the 2nd day (Table 1). 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, 21.9 ± 4.12 µm (Plate 8e). The nectar is secreted in traces during mature bud stage. The tepals together with the stamens and stigmas close back by 1000-1100 h (Table 1).

Pollination mechanism and Pollinators: In dehisced anthers collected during anthesis, 20-35% of pollen grains were found with pollen tubes indicating *in situ* germination. Further, 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. During and after anthesis, the dehisced anthers and receptive stigmas contact each other due to their close proximity and their position at the same height (Plate 8c). With this situation, the anthers brush against the stigmas causing autogamy. Further, the stamens and stigmas contact each other very closely during the closing of the flower assuring autogamy if it did not occur during open state of the flower.

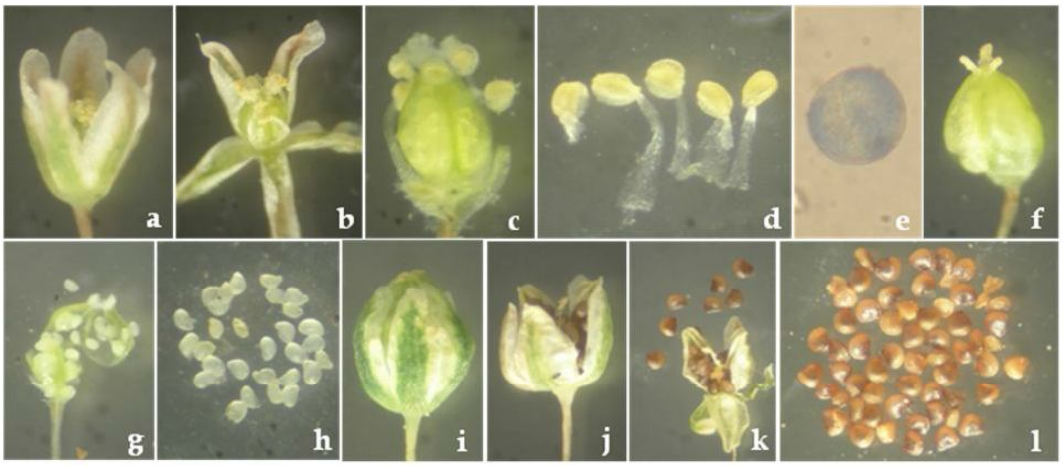

Plate 8. *Mollugo cerviana*: a. & b. Flowering-opening phase, c. Position of stigmatic lobes and anthers at the same height contacting each other at anthesis, d. Delisced anthers, e. Pollen grain, f. Ovary with three stigmas, g. & h. Multi-ovuled ovary, i. Maturing fruit, j. & k. Delisced fruit capsule, l. Seeds.

The floral characters such as radial symmetry, whitish green adaxial surface and minute amount of nectar are considered as adaptations for insect-pollination. But, insects never visited the flowers during the study period. In the habitats of *M. cerviana, M. nudicaulis* and *M. pentaphylla* also grow as pockets or as large carpet populations; here the insects visited the last two species for forage. In open habitats where *M. cerviana* alone occurred, insects were not found and hence this plant is obligately autogamous. However, thrips feeding activity contributed to self- and cross-pollination.

Thrips breeding, feeding and pollination: The thrips species, *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. Individual thrips were dusted with pollen 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 forage.

Fruiting ecology and seed dispersal: The pollinated and fertilized flowers grow continually and produce fruits 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 (Plate 8i). Natural fruit set is 91.27% and seed set is 61.94%. Fruit is a loculicidal 3-valved broadly-ellipsoid capsule, stalked, membranous, 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 (Plate 8l). 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 (Plate 8j,k). 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. 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.

Plate 9. *Mollugo nudicaulis*: a. Habit - flowering phase, b. Individual plant in flowering, c. & d. New plants.

MOLLUGO NUDICAULIS LAM.

Phenology: It is a small acaulescent annual herb with a rosette of prostrate leaves. It is

common in open dry sandy and moist soils along roadsides, waste places, bare ground and cultivated lands (Plate 9a,b). Leaves are sessile, succulent, glabrous, obovate to spathulate, margin entire and apex rounded. The plant appears simultaneously in vegetative, flowering and fruiting phases in different populations growing in different habitats throughout the year. An individual plant, however, has a short life cycle of 3 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 soil is damp due to occurrence of rains. The inflorescence is a polychasial cyme which arises from the rosette of basal leaves. The dichasial or trichasial cymes are common during dry season while polychasial cymes are common during wet season. It is spreading, pedunculate (7-8 mm long) and produces pedicellate (4 mm long) flowers. The peduncle and pedicel are wiry and stiff. A polychasial cyme produces 7.5 ± 1.5 flowers.

Flower morphology: The flowers are small (3.51 ± 0.4 mm long, 4.03 ± 0.3 mm wide), creamy white on adaxial side and light green on abaxial side, odourless, actinomorphic and bisexual. The sepals and petals are represented by a monochlamydeous perianth of 5 tepals. The tepals are free but connate at base, elliptic to oblong, 3.28 ± 0.41 mm long, 1.82 ± 0.33 mm wide and hooded. The stamens are 3 to 6, free, but connate at base, creamy white, 2.27 ± 0.17 mm long with dorsifixed, light yellow, dithecous anthers. The flowers with 3-stamens constituted 60%, those with 4-stamens 33% and those with 5-stamens 7%. All the three types of flowers were found 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 (Plate 10b). 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 (Plate 10c). In 6-stamened flowers, three stamens are alterni-tepalous while three others are anti-tepalous (Plate 10d). The ovary is light green, oblong, tri-carpellary, tri-locular syncarpous with D-shaped ovules arranged on axile placentation. The ovule number varied with change in stamen number (Plate 10h). It is 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. The style is absent but the ovary is terminated with 3 free densely papillose, shiny, spreading stigmas (Plate 10g).

Floral biology: Mature buds open during 0700-0900 h (Plate 10a). Individual buds take 5 to 10 minutes from partial to full opening. The flowers are homogamous as the anthers and stigmas attain maturity at the same time during anthesis; the former dehisce by longitudinal slits (Plate 10e) and the latter continue receptivity until the noon of the 2nd day (Table 1). The pollen output is 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 857 ± 67.2 per flower in 3- to 5-stamened flowers (Table 11). The pollen production trend showed that pollen output rate gradually increased with a gradual decrease in the number of stamens produced per flower but the variation is slight significant. The pollen-ovule ratio is 36:1 in 3-stamened flowers

while it is 37:1 in 4- and 5-stamened flowers. The pollen grains are pale yellow, spheroidal, tri-colpate, tri-zonoaperturate, granulated, tectum scabrate, 25.3 ± 0.5 µm on polar axis. The nectar is secreted in traces during mature bud stage (Plate 10f). The tepals together with the stamens and stigmas close back by 1000-1200 h (Table 1).

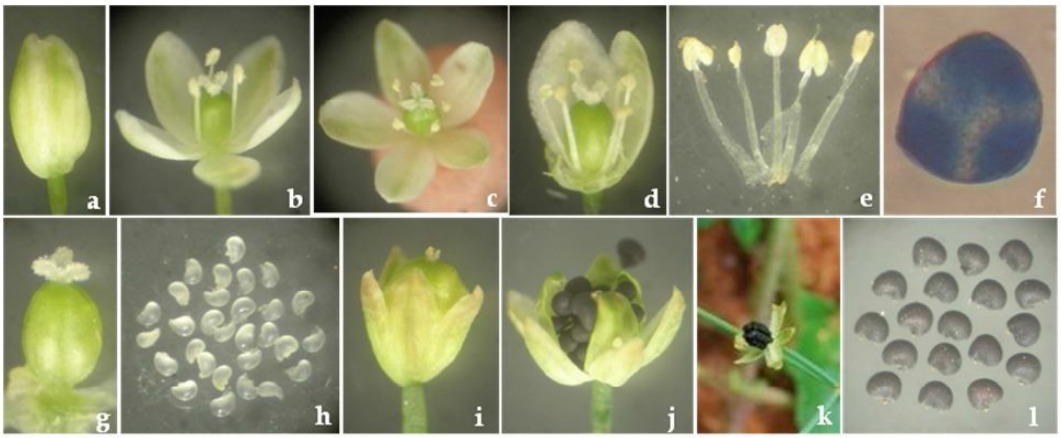

Plate 10. *Mollugo nudicaulis*: a. Bud, b. 3-stamened flower, c. 5-stamened flower, d. 6-stamened flower, e. Dehisced anthers, f. Pollen grain, g. Ovary with three styles, h. Ovules, i. Maturing fruit, j. Dehisced fruit capsule, k. Dehisced fruit capsule with seeds intact, l. Seeds.

Table 11. Pollen aspects in *Mollugo nudicaulis*

Flower type	Percentage of occurrence	Mean pollen output/anther	Mean pollen output/flower	Mean no. of ovules/flower	Pollen: ovule ratio
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

Pollination mechanism: In dehisced anthers collected during anthesis, 11-21% of pollen grains were found with pollen tubes indicating *in situ* germination. Further, 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. 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. 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. Further, the stamens and stigmas contact each other very closely during the closing of the flower assuring autogamy if it did not occur during open state of the flower.

Thrips breeding, feeding and pollination: The thrips species, *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. Individual thrips were dusted with pollen during their movements within the flowers. They carried 69 to 158 pollen grains on their body setae, wings and legs. The thrips dispersed the pollen on free densely papillose spreading 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 forage.

Insect visitors and Pollination: The flowers were foraged by bees and flies for pollen and nectar, and butterflies for only nectar during noon time from 0800-1100 h with concentrated foraging activity during 0900-1000 h (Figure 7,8). The bees were *Apis cerana* (Plate 11a), *A. florea* (Plate 11b), *Trigona iridipennis* (Plate 11c), *Ceratina* sp. (Plate 11d) and *Halictus* sp (Plate 11e). The flies included *Eristalinus* sp. (Plate 11f) and *Musca* sp. (Plate 11g). The butterflies included only lycaenids, namely, *Zizula hylax, Zizeeria karsandra* (Plate 11h), *Zizina otis* (Plate 11i), *Freyeria trochylus* and *Chilades pandava* (Plate 11j) (Table 12). 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. Their wings never contacted the stamens and stigma during nectar collection as they kept them in vertical position. Bees made 49%, flies 11% and lycaenids 40% of total foraging visits (Figure 9). 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 13). 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.

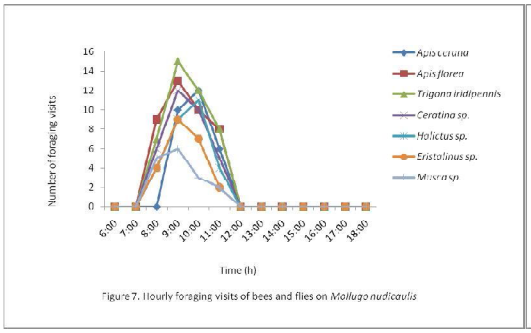

Figure 7. Hourly foraging visits of bees and flies on *Mollugo nudicaulis*

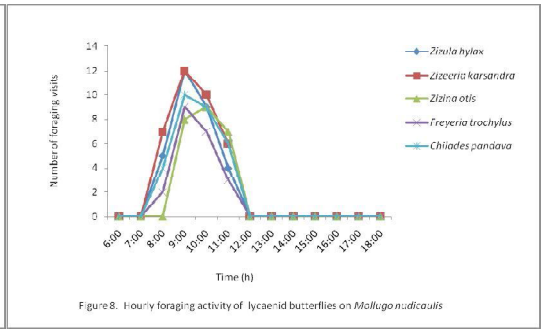

Figure 8. Hourly foraging activity of lycaenid butterflies on *Mollugo nudicaulis*

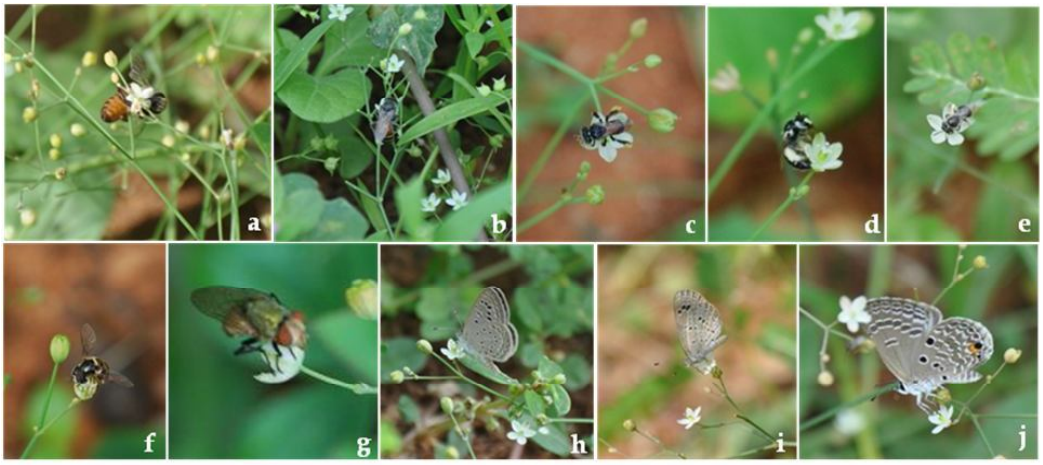

Plate 11. *Mollugo nudicaulis*: a. *Apis cerana*, b. *Apis florea*, c. *Trigona iridipennis*, d. *Ceratina* sp., e. *Halictus* sp., f. *Eristalinus* sp., g. *Musca* sp., h-j. Lycaenids – h. *Zizeeria karsandra*, i. *Zizina otis*, j. *Chilades pandava*.

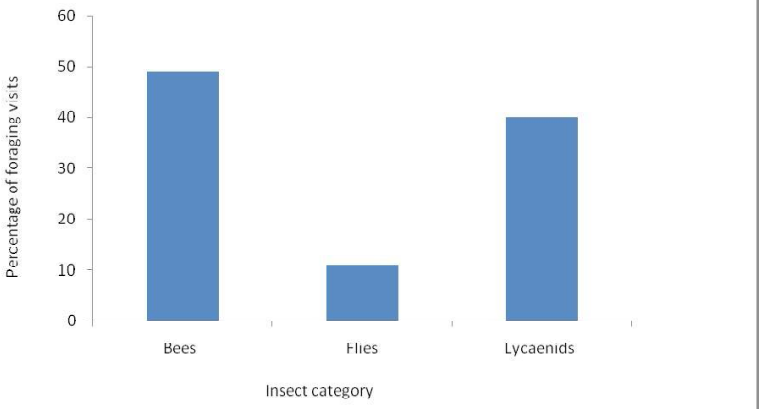

Figure 9. Percentage of foraging visits of bees, flies and lycaenid butterflies on *Mollugo nudicaulis*

Table 12. List of insect foragers on *Mollugo nudicaulis*

Order	Family	Genus	Species	Common Name	Forage Sought
Hymenoptera	Apidae	*Apis*	*cerana* F.	Indian Honey Bee	Pollen + Nectar
		Apis	*florea* F.	Dwarf Honey Bee	Pollen + Nectar
		Trigona	*iridipennis* Smith	Stingless honey Bee	Pollen + Nectar
		Ceratina	sp.	Small Carpenter Bee	Pollen + Nectar
	Halictidae	*Halictus*	sp.	Sweat Bee	Pollen + Nectar
	Syrphidae	*Eristalinus*	*Sp*	Hover fly	Nectar
	Muscidae	*Musca*	sp.	House Fly	Nectar
Lepidoptera	Lycaenidae	*Zizula*	*hylax* F.	Tiny Grass Blue	Nectar
		Zizeeria	*karsandra* Moore	Dark Grass Blue	Nectar
		Zizina	*otis* F.	Lesser Grass Blue	Nectar
		Freyeria	*trochylus* Freyer	Grass jewel	Nectar
		Chilades	*pandava* Horsfield	Plains Cupid	Nectar

Table 13. Pollen recorded in the body washings of insects on *Mollugo nudicaulis*

Insect species	Sample size(N)	Number of pollen grains		
		Range	Mean	S.D
Apis cerana	10	73-204	133.5	37.5
Apis florea	10	61-183	126.1	33.31
Trigona iridipennis	10	37-95	63.4	14.4
Ceratina sp.	10	34-62	47.8	8.27
Halictus sp.	10	41-87	69.8	12.2
Eristalinus sp.	10	26-50	38.2	7.26
Musca sp.	10	11-38	27.9	7.5
Zizula hylax	10	9-28	21.3	5.47
Zizeeria karsandra	10	13-32	23.8	5.57
Zizina otis	10	16-40	28.1	6.48
Freyeria trochylus	10	8-31	24.4	7.19
Chilades pandava	10	15-36	28.5	6.27

Fruiting ecology and seed dispsersal: The pollinated and fertilized flowers grow continually and produce fruits 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. Natural fruit set varied from 86 to 89% while seed set varied from 88 to 92% in 3-, 4- and 5-stamened flowers (Table 14). Fruit is a loculicidal 3-valved broadly-ellipsoid capsule, stalked, membranous, densely pubescent, 3.4 ± 0.4 mm long and 2.33 ± 0.39mm wide. The seeds are arranged in two rows in each locule. They are tiny, black, slightly shiny, reniform and concentrically ridged. 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 (Plate 10j,k). 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. 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 produce contaminant and in effect agricultural produce movement contributes to seed dispersal and expansion of its distribution (Plate 9c,d; Plate 10l).

Table 14. Natural fruit and seed set rate in *Mollugo nudicaulis*

Flower type	Number of flowers sampled	Number of flowers set fruit	Fruit set (%)	Seed set (%)
3-stamened	320	286	89	88
4-stamened	85	73	86	91
5-stamened	40	35	88	92

MOLLUGO PENTAPHYLLA L.

Phenology: It is a small much-branched annual herb with a thin tap root. It is common in open dry and moist sandy and sandy loamy soils along roadsides, waste places and cultivated lands (Plate 12a). 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 form while those upwards vary from 4 to 1. The plant appears simultaneously in vegetative, flowering and fruiting phases in different populations growing in different habitats throughout the year (Plate 12b). An individual plant, however, has a short life cycle of 3 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 soil is damp

due to occurrence of rains. The inflorescence is a polychasial cyme which arises from leaf axils and terminally during wet season while it is usually di- or tri-chasial cyme during dry season. It is spreading, pedunculate (5-8 mm long) and produces pedicellate (2-4 mm long) flowers. The peduncle and pedicel are wiry and stiff. An polychasial produces 13.83 ± 4.9 flowers.

Flower morphology: The flowers are small (2.75 ± 0.4 mm long, 1.8 ± 0.4 mm wide), white on adaxial and abaxial side, odourless, actinomorphic and bisexual. The sepals and petals are represented by a monochlamydeous perianth of 5 tepals. The tepals are free, 2-3 mm long, but connate at base, elliptic to oblong and hooded. The stamens are 3 to 5, free, but connate at base, white, 1.8 ± 0.17 mm long with broadly flat filaments but dilated at base and dorsifixed, white, dithecous anthers. The flowers with 3-stamens constituted 91%, those with 4-stamens 7% and those with 5-stamens 2%. All the three types of flowers were found 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. The ovary is white, ovoid, 1.16 ± 0.24 mm long, 1.5 mm broad, tri-carpellary, tri-locular syncarpous with reniform ovules arranged on axile placentation. The ovule number varied with change in stamen number. It is 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 (Plate 12i). The style is absent but the ovary is terminated with 3 free densely papillose, shiny, spreading stigmas (Plate 12h).

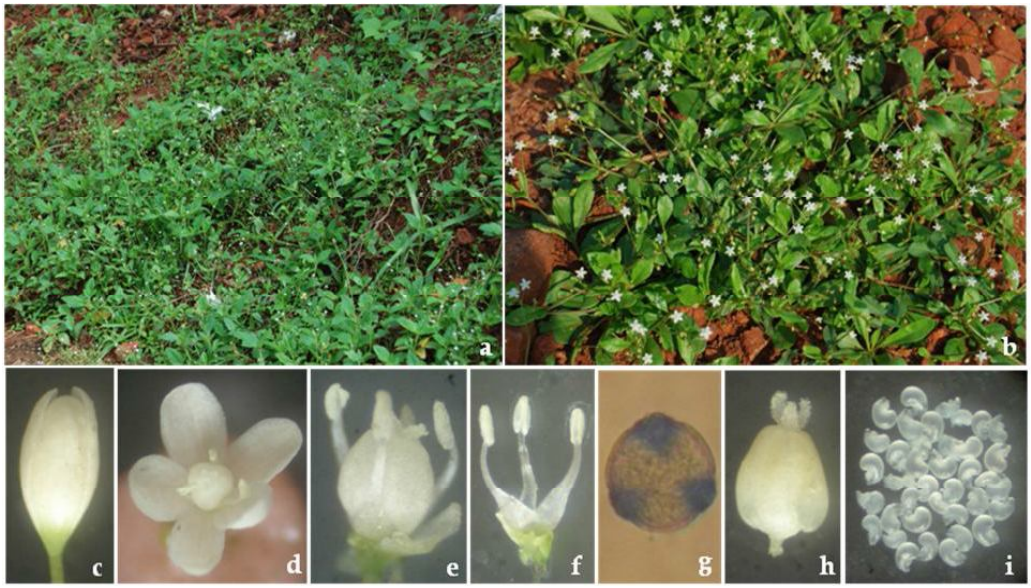

Plate 12. *Mollugo pentaphylla*: a. Habit, b. Flowering phase, c-e. Different stages of anthesis, f. Position of anthers and stigmas at the same height, g. Pollen grain, h. Ovary with three stigmas, i. Ovules.

Floral biology: Mature buds open during 0700-0800 h. Individual buds take 5 to 10 minutes from partial to full opening (Plate 12c-e). The flowers are homogamous as the anthers and stigmas attain maturity at the same time during anthesis; the former dehisce by longitudinal slits and the latter continue receptivity until the noon of the 2nd day (Table 1). The pollen output varied with change in stamen number. 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 15). The pollen production trend showed that pollen output rate gradually slightly increased with a gradual decrease in the number of stamens produced per flower. The pollen-ovule ratio is 52:1 in 3-stamened flowers while it is 53:1 in 4- and 5-stamened flowers. The pollen grains are pale yellow, spheroidal, tri-colpate, tri-zonoaperturate, granulated, tectum scabrate, 26.4 ± 0.5 µm (Plate 12g). *In vitro* pollen viability test indicated that the pollen grains are viable from anthesis onwards and remain so even after the closure of the flower (Table 16). The nectar is secreted in traces during mature bud stage. The tepals together with the stamens and stigmas close back by 1000-1100 h (Table 1).

Table 15. Pollen aspects in *Mollugo pentaphylla*

Flower type	Percentage of occurrence	Mean pollen output/anther	Mean pollen output/flower	Mean no. of ovules/flower	Pollen: ovule ratio
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

Table 16. *In vitro* pollen germination in *Mollugo pentaphylla*

Time (h)	Pollen sample	No. of germinated pollen grains	Germination (%)
0600	-	-	-
0700	50	26	52
0800	34	23	68
0900	39	28	72
1000	23	14	61
1100	15	9	60
1200	46	18	39
1300	15	4	27
1400	35	3	9
1500	-	-	-
1600	-	-	-

Modified Brewbaker and Kwack's medium

Pollination mechanism: In dehisced anthers collected during anthesis, 18-26% of pollen grains were found with pollen tubes indicating *in situ* germination. Further, 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. 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 (Plate 12f). 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. Further, the stamens and stigmas contact each other very closely during the closing of the flower assuring autogamy if it did not occur during open state of the flower.

Thrips breeding, feeding and pollination: The thrips species, *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. Individual thrips were dusted with pollen during their movements within the flowers. They carried 89 to 217 pollen grains on their body setae, wings and legs. The thrips dispersed the pollen on free densely papillose spreading 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 forage.

Insect visitors and Pollination: The flowers were foraged by bees for pollen and nectar while butterflies for only nectar during noon time from 0800-1100 h with concentrated foraging activity during 0900-1000 h (Figure 10,11). The bees were *Apis cerana* (Plate 13a), *A. florea* (Plate 13b), *Trigona iridipennis* (Plate 13c), *Ceratina* sp. and *Thyreus histrio* (Plate 13e). The butterflies included only lycaenids, namely, *Castalius rosimon* (Plate 13f), *Zizula hylax* (Plate 13g), *Zizeeria karsandra* (Plate 13h), *Zizina otis* and *Chilades pandava* (Table 17). 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. 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 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. Their wings

never contacted the stamens and stigma during nectar collection as they kept them in vertical position. Bees made 56% and lycaenids 44% of total foraging visits (Figure 12). 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 18). 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.

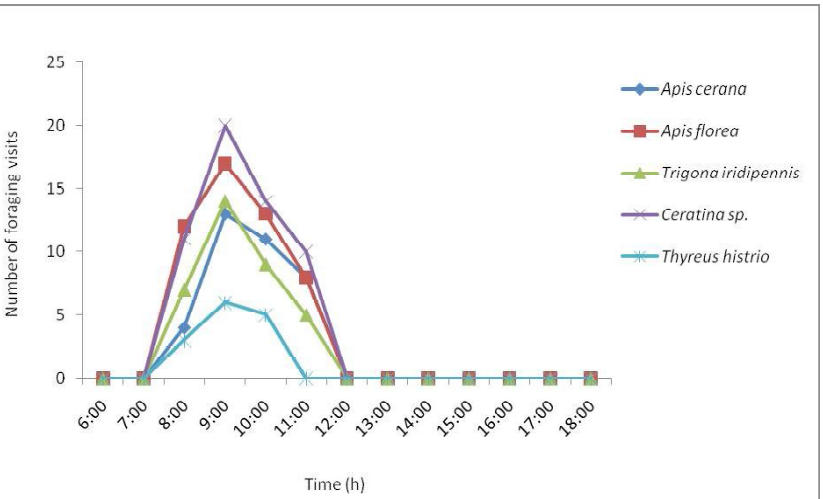

Figure 10. Hourly foraging activity of bees on *Mollugo pentaphylla*

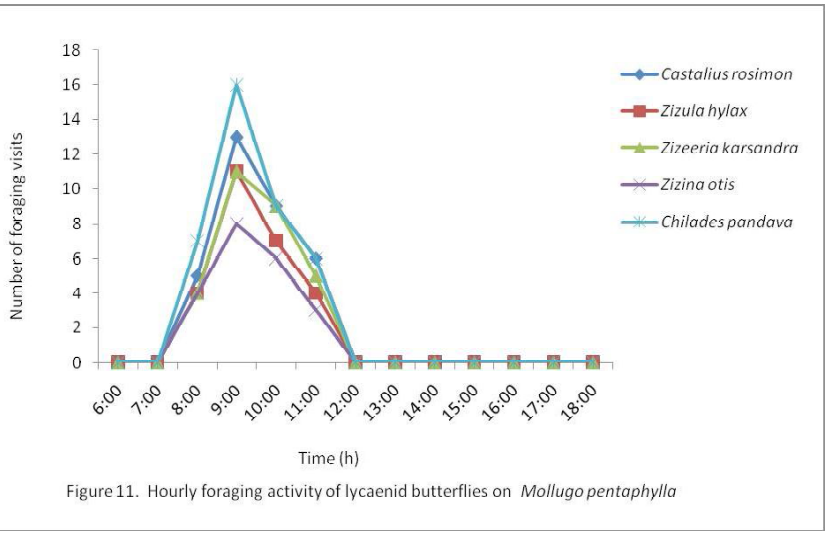

Figure 11. Hourly foraging activity of lycaenid butterflies on *Mollugo pentaphylla*

Plate 13. *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*.

Table 17. List of insect foragers on *Mollugo pentaphylla*

Order	Family	Genus	Species	Common name	Forage sought
Hymenoptera	Apidae	*Apis*	*cerana* F.	Indian Honey Bee	Pollen + Nectar
		Apis	*florea* F.	Dwarf Honey Bee	Pollen + Nectar
		Trigona	*iridipennis* Smith	Stingless Honey Bee	Pollen + Nectar
		Ceratina	sp.	Small Carpenter Bee	Pollen + Nectar
		Thyreus	*histrio* F.	Bee-fly	Pollen + Nectar
Lepidoptera	Lycaenidae	*Castalius*	*rosimon* F.	Common Pierrot	Nectar
		Zizula	*hylax* F.	Tiny Grass Blue	Nectar
		Zizeeria	*karsandra* Moore	Dark Grass Blue	Nectar
		Zizina	*otis* F.	Lesser Grass Blue	Nectar
		Chilades	*pandava* Horsfield	Plains Cupid	Nectar

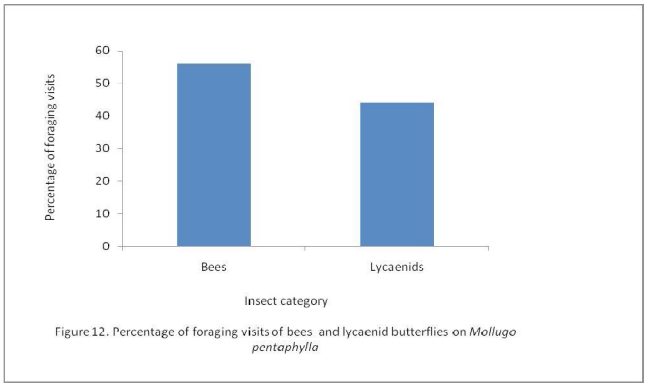

Figure 12. Percentage of foraging visits of bees and lycaenid butterflies on *Mollugo pentaphylla*

Table 18. Pollen recorded in the body washings of insects on *Mollugo pentaphylla*

Insect species	Sample size (N)	Number of pollen grains		
		Range	Mean	S.D
Apis cerana	10	82-246	159.2	51.8
Apis florea	10	68-217	145.1	43.56
Trigona iridipennis	10	31-86	62.1	13.5
Ceratina sp.	10	24-51	38.2	9.07
Thyreus histrio	10	19-43	30.6	7.60
Castalius rosimon	10	15-41	29.5	6.38
Zizula hylax	10	9-30	20.6	5.27
Zizeeria karsandra	10	13-45	27.8	9.49
Zizina otis	10	10-36	23.7	6.63
Chilades pandava	10	8-43	30.7	8.8

Fruiting ecology and seed dispersal: The pollinated and fertilized flowers grow continually and produce fruits within 8-12 days (Plate 14a). 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 (Plate 14b). Natural fruit set varied from 83 to 88% while seed set varied from 83 to 86% in 3-, 4- and 5-stamened flowers (Table 19). Fruit is a loculicidal 3-valved broadly-ellipsoid capsule, stalked, membranous, glabrous, 2.67 ± 0.4 mm long and 1.97 ± 1.4 mm wide. The seeds are arranged in two rows in each locule. They are tiny, black, slightly shiny, reniform and concentrically ridged (Plate 14e). 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 (Plate 14c). But the seeds remain so (Plate 14d) 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 produce contaminant and in effect agricultural produce movement contributes to seed dispersal and expansion of its distribution (Plate 14f,g).

The study shows that all five plant species studied display certain common characters such as homogamy, spontaneous autogamy, brief period of open state of flowers, flower closure and facultative autogamy. These species serve as breeding and feeding host plants

for *Haplothrips* species which in turn reciprocate pollination service. *M. cerviana* is never foraged by any insect species. The other four plant species are pollinated by bees and lycaenid butterflies. *G. oppositifolius* is also pollinated by ants while *M. nudicaulis* is also pollinated by flies (Table 20).

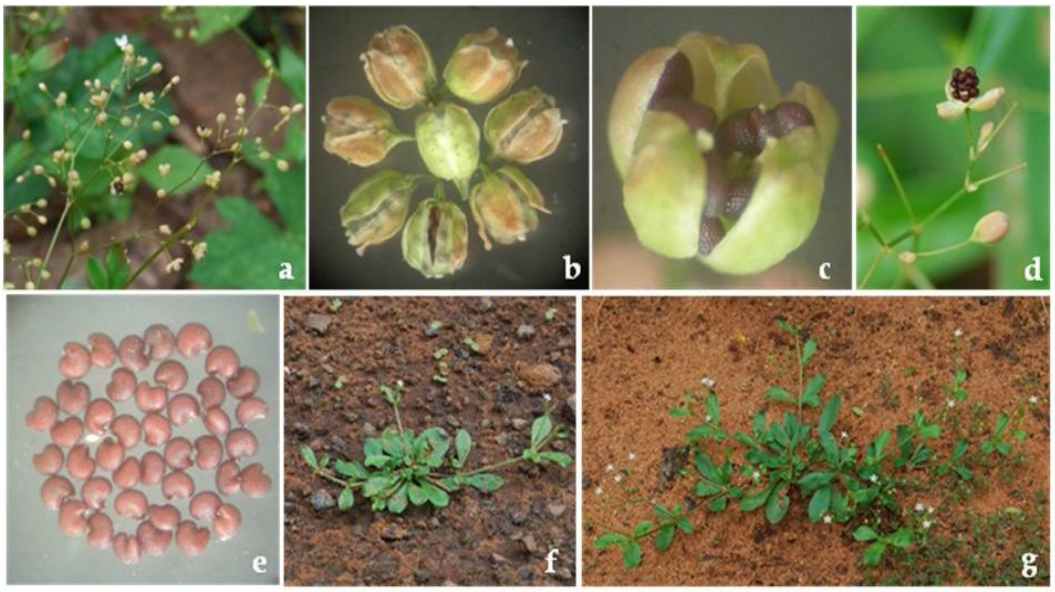

Plate 14. *Mollugo pentaphylla*: a. Fruiting phase, b. Maturing fruits, c. Dehisced fruit capsule, d. Dehisced fruit capsule with seeds intact, e. Seeds, f. & g. New plants.

Table 19. Natural fruit and seed set rate in *Mollugo pentaphylla*

Flower type	Number of flowers sampled	Number of flowers set fruit	Fruit set (%)	Seed set (%)
3-stamened	250	220	88	83
4-stamened	150	130	87	84
5-stamened	75	62	83	86

Table 20. Consolidated list of insect foragers on the studied plant species

Order/Family	Insect species	*Glinus*	*Glinus oppositi-folius*	*Mollugo nudic-aulis*	*Mollugo pentap-hylla*	*Forage sought* P: Pollen, N:Nectar
Hymenoptera						
Apidae	Apis cerana F.	+	+	+	+	P + N
	Apis florea F.	+	+	+	+	P + N

	Trigona iridipennis Smith	+	-	+	+	P + N
	Ceratina smaragdula F.	-	+	-	-	P + N
	Ceratina sp.	+	+	+	+	P + N
	Thyreus histrio	-	-	-	+	P + N
Halictidae	*Halictus* sp.	-	+	+	-	P + N
Megachilidae	*Megachile* sp.	-	+	-	-	P + N
Formicidae	*Camponotus* sp.	+	+	-	-	N
	Crematogaster sp.	+	+	-	-	N
Diptera						
Syrphidae	*Eristalinus* sp.	-	-	+	-	N
Muscidae	*Musca* sp.	-	-	+	-	N
Lepidoptera						
Lycaenidae	*Castalius rosimon* F.	-	-	-	+	N
	Zizula hylax F.	+	+	+	+	N
	Zizeeria karsandra Moore	+	+	+	+	N
	Zizina otis F.	+	+	+	+	N
	Freyeria trochylus Freyer	+	+	+	-	N
	Chilades laius Stoll	+	+	-	-	N
	Chilades pandava Horsfield	+	+	+	+	N

DISCUSSION

Pollination ecology of *Glinus lotoides* and *G. oppositifolius*

Glinus lotoides and *G. oppositifolius* are prostrate, spreading, annual herbs that carpet the ground in open sandy soils and agricultural lands. They occur throughout the year and show vegetative, flowering and fruiting phases in different areas. But, their robust growth, profuse flowering and fruiting is confined to wet season. The flowers borne in axillary cymes in *G. lotoides* and axillary fascicles in *G. oppositifolius* stand erect above the foliage and display their prominence. In both the species, the stems produce many branches and each branch produces several cymes or fascicles. Since the plants 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.

Several anonymous authors provided the floral descriptions of *Glinus* species. Ronse De Craene (2010) stated that *Glinus* species have five sepals in quincuncial aestivation. In the present study, *G. lotoides* and *G. oppositifolius* have been found to have five tepals as common and six tepals as rare. The study also indicates that the word "tepal" is the appropriate word since it acts as petal adaxially and sepal abaxially. This is further substantiated by two different colours displayed on adaxial and abaxial surface. The tepals are whitish green on adaxial surface and green abaxial surface in *G. lotoides* and creamy white on adaxial surface and brownish orange on abaxial surface in *G. oppositifolius*.

Hoffman (1994) stated that the stamen number is unstable among different species of *Glinus* and the number varies from five to several series which includes outer staminodes. Brockington *et al.* (2013) used the word "petaloid" for "staminode" in *Glinus*. These authors reported that in this genus, petaloid number can fluctuate enormously and can either be antisepalous replacing a fertile stamen or alternisepalous as an appendage of upper stamen. They also stated that the outer stamens are replaced by petaloid structures. Weberling (1989) noted that the stamens that lost their function as producers of viable pollen have become staminodes or petaloids in this genus. Ronse De Craene (2010) reported that the androecium of *G. lotoides* is extremely variable. Further, he reported that the flower material he examined showed that the alternisepalous whorl is complete with staminodes and odd stamen opposite to petals. Sharma (1963) mentioned that *G. lotoides* flowers produce rarely more than five stamens while *G. oppositifolius* produce 10-13 stamens in three whorls. He also suggested a tendency for reduction with the loss of the outer stamen whorl in androecium. In the present study, *G. lotoides* flowers have 8-12 functional stamens arranged in two whorls and they are usually antitepalous. The flowers also have 5-7 staminodes arranged in outer whorl and they are usually alternitepalous. In *G. oppositifolius*, the flowers have 4-6 functional stamens arranged in one whorl and they are alternitepalous; the staminodes are 5-6 arranged in outer whorl and they are antitepalous. In both the species, the staminodes are petaloids indicating the fusion of two adjacent stamens that lost the function of producing viable pollen in course of the evolution of flowers. These staminodes are integral features of floral morphology and appear to have evolved to serve as attractants to pollinators, reduce self-pollination rate and optimize the available nutrients for enhanced reproductive output in water and nutrient deficient habitats. Further, the production of staminodes appears to be an adaptation to reduce pollen production per flower, increase efficiency of pollen dispersal by limiting pollen removal by individual pollinators and enable precise contact between pollinators and pollen presenters or pollinators and stigmas. Therefore, the petaloid staminodes are evolved to perform different roles in the flowers and are unique for *Glinus* within Molluginaceae (Stebbins 1974; Ronse De Craene and Smets 1993, 1995; Ronse De Craene 2013).

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 and 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 *Glinus* 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 in the afternoon. Further, the flowers are too small, lack corolla, tepals not vividly coloured and stay open for a brief period, for three hours in *G. lotoides* and four hours in *G. oppositifolius* 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. The specific timing of anthesis in the late afternoon is a likely mechanism to filter out generalist pollinators most active at midday, rather targeting specific group of insects, primarily bees, still active in the late afternoon. The present study indicates that afternoon anthesis in *Glinus* species is probably evolved in course of time to avoid competition for pollinators in pollinator-deprived environment, especially in habitats where other herbaceous plant species flower simultaneously, show anthesis during forenoon period and attract insect pollinators with their vivid floral colours. *Glinus* species provide sufficient forage for insect pollinators in the afternoon period and accordingly bees, ants and lycaenid butterflies collect forage and pollinate flowers. Bees and butterflies are generalists which visit a wide range of flowers and hence are polylectic. Since they are active throughout day, they soon switch to fresh forage available in the habitat. *Glinus* species with afternoon anthesis readily provide forage, and bees and butterflies begin to shift to these floral sources and concentrate on forage collection from them. Therefore, afternoon anthesis in *Glinus* species ensures insect pollination and reciprocate the insect pollinators with pollen and/or nectar.

Watson and Dallwitz (1992) stated that Molluginaceae members are entomophilous. These authors considered nectar secreting tissue and showy tepals in several species as adaptations for entomophily. In *Glinus* species, the floral characters such as the erect position of flowers above foliage, adaxial surface of the tepals, petaloid staminodes and nectar secreting tissue between the ovary base, connate part of staminal filaments and scabrate ornamentation of pollen grains appear to be adaptations for insect pollination. The bees while collecting pollen and butterflies while collecting nectar effect sternotribic pollination. Further, the bees and ants while collecting nectar effect nototribic pollination. In both *G. lotoides* and *G. oppositifolius*, the pollen output per anther varies with the number of functional stamens present in the flowers; it increases with a decrease in the stamen number. The pollen output per flower in *G. lotoides* is more than double the amount produced per

flower in *G. oppositifolius*. The variation in pollen production in these plant species is partly attributable to the number of stamens produced. The varied 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 collection 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, ants and lycaenid butterflies to visit flowers across population(s) due to which both self- and cross-pollinations occur. *Glinus* species appear to be important sources of pollen for bees, especially for honey bees. Aldeen (2014) also noted that *G. lotoides* is an important pollen source for honey bees in Radom area, South Darfur State, Sudan. Further, these plant species in the study area are important nectar sources for ants and lycaenid butterflies. Among butterflies, lycaenids are the smallest, low-flying and appropriate pollinators for prostrate herbs such as *Glinus* species. Grund (1998) reported that the lycaenid butterfly, *Zizeeria karsandra* uses both *G. lotoides* and *G. oppositifolius* as larval host plants in South Australia. This report suggests that this butterfly uses *Glinus* species as both larval and nectar host plants. Studies on the life cycle of other lycaenid butterflies visiting *Glinus* species may throw more light on the relationships between *Glinus* species and lycaenid butterflies.

In both *Glinus* species, the flowers are weakly protandrous because there is a brief gap between anther dehiscence and commencement of stigma receptivity. Since both male and female sexes mature almost at the same time, the flowers in these plant species can be stated as homogamous. Further, the stamens and stigmas are spatially separated in both the species; such a situation suggests that the flowers are also herkogamous. Herkogamy does not facilitate the occurrence of spontaneous autogamy despite the flowers being homogamous. However, 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. Further, the movement of tepals together with stamens towards the pistil during flower closure facilitates contact between the sex organs and effects spontaneous autogamy if pollen is still available in the dehisced stamens. *In vitro* pollen germination test for *G. oppositifolius* indicated that pollen is viable for a brief period only from the time of anther dehiscence to the time of flower closure suggesting that there is no possibility for the occurrence of spontaneous autogamy after flower closure. However, 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. *In vitro* pollen germination test for *G. lotoides* was not done. Since it is an allied species of *G. oppositifolius*, it is possible that its pollen also displays the same duration of viability and thrips may effect pollination in the closed flowers. Therefore, *G. lotoides* and *G. oppositifolius* while keeping the options open for spontaneous or vector-mediated

selfing exhibit polyphily involving bees, ants, butterflies and thrips as pollinators.

In the present study, *Glinus* species show variation in the number of carpels and ovules per flower. The flowers of *G. lotoides* produce five carpels while those of *G. oppositifolius* produce three carpels. Likewise, the number of ovules also varies depending on the number of stamens and pollen output per flower; the ovules are more in *G. lotoides* than in *G. oppositifolius*. 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 through spontaneous autogamy or vector-mediated pollination. 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 the lowest pollen-ovule ratios recorded in *G. lotoides* and *G. oppositifolius* indicate that they are facultatively autogamous.

Bittrich (1990) reported that there is only one genus, *Adenogramma* which has one-seeded nutlet in Molluginaceae. All other genera produce capsules with many seeds and the capsules dehisce loculicidally to expose seeds. In *Glinus lotoides*, the capsules open when moistened with the aid of expanding keels. In the present study, in *G. lotoides* and *G. oppositifolius*, the fertilized flowers produce fruits within a week or two. The fruit is a capsule but it is 5-valved in *G. lotoides* and 3-valved in *G. oppositifolius*. In dry season, plants with ripe and dry capsules break off which are then dispersed by wind. Dry capsules break open loculicidally when tepals become wet and then expose the seeds. However, the seeds remain attached to the base of the perianth. In both the species, the seeds exposed from the capsules fall to the ground on clear sunny days. On rainy days, water drops find their way into the fruit through the distal opening and the fruit filled with water expels both water and seeds explosively. Further, seeds fallen on the ground disperse through surface water runoff during rain fall. Therefore, *G. lotoides* and *G. oppositifolius* exhibit anemochory, ombrohydrochory and hydrochory.

Narayana (1962) and Hofmann (1973) noted that *Glinus* species produce seeds with a white aril of funicular origin which develops into elongate, filiform strophiole. Ronse De Craene (2013) reported that *Glinus* genus is well characterized morphologically by its seeds with a filiform appendaged aril and indumentum of often stellate hairs. In the present study, it is found that *G. lotoides* produces small reniform, smooth and dark brown seeds with a white aril of funicular origin developed into elongate filiform strophiole. In *G. oppositifolius*, the seeds are small, sub-reniform and reddish-brown with a white aril of funicular origin formed into extensively curved scrotiform strophiole. The presence of filiform or scrotiform strophiole in *Glinus* species appears to be an adaptation for seed dispersal by ants. But, ants have not been found to use the strophiole as food and carry seeds of these species. However, further studies if taken up on this aspect may throw more light either to confirm or refute this observation.

Balcha (2009) reported that *Glinus lotoides* has short seed viability period. Teshome and Feyissa (2015) also reported that this species propagates by seed but short period of

seed viability and poor seed germination percentage are the limiting factors for its invasiveness. The present study showed that both *G. lotoides* and *G. oppositifolius* 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. Therefore, *Glinus* species appear to have short period of seed viability and also the viability may also be attributable to the extent of genetic variation achieved through vector-mediated pollination.

Pollination ecology of *Mollugo cerviana, M. nudicaulis* and *M. pentaphylla*

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. However, their robust growth, profuse flowering and fruiting is confined to wet season. 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. 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.

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 and 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 and 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 and 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 reciprocate 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 and 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 and 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*.

Dipterans mostly take nectar with a preponderance of sucrose (Goldblatt *et al.* 1997). The nectar used by most flies is characteristically hexose-rich and of relatively high sugar concentration (Kevan and Baker 1999). The sugars in nectar may crystallize, but many generalist flies are able to re-liquify the nectar with saliva and then imbibe it (Willmer 2011). Both sexes of most flies use the carbohydrates in nectar for short-term energy needs (Downes and Smith 1969), especially during periods of peak activity such as swarming, mating and oviposition, dispersal, and migration (Willmer 2011). Several authors have indicated that nectar can contain amino acids and they have a nutritional role for flies (Rathman *et al.* 1990; Gardener and Gillman 2002; Vrzal *et al.* 2010). In the present study, nectar analysis was not done for *Mollugo* species but it is most likely that their flowers produce sucrose-rich nectar with high sugar concentration and the plants grow in arid areas. Since flies in general have the ability to re-liquify the nectar with their saliva and then imbibe it, they use the traces of nectar present in *M. nudicaulis* without any difficulty to meet their short-term energy needs. Therefore, the interaction between *M. nudicaulis* and flies is mutualistic, the former achieves pollination while the latter obtains the food.

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 the 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 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. *In vitro* pollen germination test for *M. pentaphylla* indicated that the pollen is viable from the time of anther dehiscence and until three hours after flower closure suggesting that there is a possibility for the occurrence of spontaneous autogamy even after flower closure. 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 vector-mediated pollination during the open state of flowers.

In the present study, all the 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 from the fertilized flowers. 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 and 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.

Rama Das and Raghavendra (1973) noted that *Glinus lotoides* and *G. oppositifolius* are C_3 species. Brockington *et al.* (2009) reported that *Mollugo cerviana* is the only known C_4 species in the family Molluginaceae. Edwards and 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 *Glinus* species and *M. pentaphylla*

with C_3 photosynthesis usually occur 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 cool environments and this photosynthetic pathway is physiologically advantageous for their niche broadening in warm environments. Williams *et al.* (2013) explained the advantages of C_4 photosynthesis. C_4 plants grow faster than C_3 plants, and they require less water. In a hot climate, however, a plant can lose a lot of water through the pores in its leaves: closing these pores allows the plant to retain water, but this also reduces the supply of carbon dioxide. Under these circumstances this causes problems because RuBisCO uses oxygen to break down RuBP, instead of creating sugars, when carbon dioxide is not readily available. C_4 photosynthesis prevents wastage of a lot of energy and resources but it is more complex than C_3 photosynthesis. In C_4 plants, the mesophyll which is the region that is associated with the capture of carbon dioxide by RuBisCO in C_3 plants, contains high levels of an alternative enzyme called PEPC that converts carbon dioxide molecules into an acid that contains four carbon atoms. To avoid carbon dioxide being captured by both enzymes, C_4 plants evolved to relocate RuBisCO from the mesophyll to a second set of cells in an airtight structure known as the bundle sheath. The four-carbon acids produced by PEPC diffuse to the cells in the bundle sheath, where they are broken down into carbon dioxide molecules, and photosynthesis then proceeds as normal. This process allows photosynthesis to continue when the level of carbon dioxide in the leaves is low due to closure of pores to retain water in the plant. This specialized photosynthetic pathway allows *M. cerviana* to survive and build up its populations in warm and dry habitats or 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 and 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. *Glinus* and *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.

Different authors reported that *Glinus lotoides* and *G. oppositifolius* are commonly used as vegetables. Further, these species and all three *Mollugo* species now studied are used in traditional medicine and in recent times used in Ayurvedic system of medicine to treat different diseases and ailments. In Ethiopia and Tanzania, *G. lotoides* is given threatened status due to its regular harvest for medicinal purpose. *M. cerviana* is widely used as a pot herb in India and its extract is useful as inhibitor of corrosion of mild steel (Hamed *et al.* 1996; Parvathamma and Shanthamma 2000; Sastri 2002; Rajamanikandan *et al.* 2011; Dutta *et al.* 2012; Sahu *et al.* 2012; Arockiasamy *et al.* 2014; Bhavani 2015; Teshome and Feyissa 2015). These various uses indicate that *Glinus* and *Mollugo* species can be promoted as vegetables or medicine. *M. cerviana* can be commercially promoted as a pot herb. Further studies on the steel corrosion inhibition properties of this plant may provide more concrete information for its potentiality as inhibitor of steel corrosion. Except *M. cerviana*, all other plant species are useful as important nectar sources for almost throughout the year for the low flying lycaenid butterflies. It appears that there is a close relationship between these plants and lycaenids, and both benefit from this relationship. Bees also use these plants as a major source of pollen and a minor source of nectar. These plants in general form important forage sources during dry season. Therefore, all these plant species are ecologically and medicinally useful. Further, they are important in soil erosion control and in the initiation of eco-restoration process in dry areas where there is no vegetation and in areas where soil usually contains very little moisture.

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