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Melittophily and censer seed dispersal mechanism in *Argemone mexicana* L. (Papaveraceae)

Suvarna Raju P[1], Henry Jonathan K[2], Sravan Kumar S[3], Solomon Raju AJ[4]

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Author Affiliation:
[1]Department of Health, Safety and Environmental Management, International College of Engineering and Management, Muscat, Sultanate of Oman, Oman
[2]Department of Transportation, Logistics and Safety Management, Faculty of Business and Economics, Modern College of Business and Science, Muscat, Sultanate of Oman, Oman
[3]Department of Basic Sciences & Humanities, Baba Institute of Technology & Sciences, P.M. Palem, Visakhapatnam 530 048, India
[4]Department of Environmental Sciences, Andhra University, Visakhapatnam 530 003, India

***Corresponding author:**
A.J. Solomon Raju,
Email: solomonraju@gmail.com

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ABSTRACT

Argemone mexicana is a widespread herbaceous weed. It is a potential candidate in eco-restoration of ecologically disturbed, deteriorated and damaged habitats since it prefers well-drained sandy soils with low water and nutrient content. The flowers are self-compatible, nectarless and scentless and melittophilous. The flower closing mechanism facilitates the occurrence of autonomous autogamy which serves as fail-safe mechanism when pollinating bees are either not reliable or available to set seed. The vector-dependent and non-vector dependent pollination ensures reproductive success to invade and build up through seed. Censer mechanism of seed dispersal functional in this species is wind-driven in natural conditions. However, rain water, humans and animals also have a role in seed dispersal. *A. mexicana* with autonomous autogamy, melittophily and seed dispersal by different agents is able to build up populations in different habitats that present different ecological conditions. In Oman, *A. mexicana* as a naturalized species in certain habitats is most likely to provide pollen to bees in general and honey bees in particular due to saucer-shaped corolla of the flower with well exposed stamens with dehisced anthers. Specific studies on this aspect is recommended to evaluate the potential of *A. mexicana* as an important pollen source for bees.

Keywords: *Argemone mexicana*, hermaphrodite, melittophily, autonomous autogamy, censer mechanism

1. INTRODUCTION

The genus *Argemone* (Papaveraceae) has 24 (Schwarzbach and Kadereit 1999) or 32 (Ownbey 1997) species. It is native to Americas and is distinguished from other genera of Papavaraceae by its collective possession of trimerous perianth parts sepal horns, united styles and acrocidal anther dehiscence of the capsules (Ownbey 1958, 1961). This genus includes important weed species which are valued in traditional medicine due to the presence of secondary metabolites which make up mostly alkaloids. These alkaloids are present in all tissues of the members of this genus (Martinez-Delgado et al.

2022). *Argemone* species grow well in regions of low rainfall or soils of low water holding capacity. Studies on the reproductive ecology of *Argemone* are rare in the literature (Schneider and Nichols 1984). Literature survey indicated that *A. aurantiaca* flowers show anthesis over three consecutive days with flowers opening early morning and closing in the late afternoon. In this species, the flowers protogynous with attainment of stigma receptivity in the early morning of first day flowers and anther dehiscence taking place in the late morning. The stigma becomes non-receptive and the anthers shrivel by late evening of the 2nd day. The petals and stamens abscise on the 3rd day. The flowers are pollinated by hymenopterans (*Dialictus* and *Halictus*) and coleopterans (*Euphoria* and *Lytta*), the former are the effective cross-pollinators while the latter facilitate self-pollination (Schneider and Nichols 1984). In *A. munita*, the flowers are self-incompatible and display an inherent mechanism with which self-pollen tube penetration is inhibited when it touches the female tissue (Bilinski and Kohn 2012). *A. mexicana* L. is indigenous to South America but has widespread distribution in tropical and subtropical regions of the world (Ibrahim and Ibrahim 2009). It has received much attention owing to reports of epidemic dropsy, cardiovascular manifestations, and mutagenic and carcinogenic effects caused by toxic alkaloids produced by the plant (Schneider and Nichols 1984 and the references therein). Pathak et al. (2021) documented that the varied climatic conditions present in India enabled this plant to become widespread in varied habitats. It prefers light sandy well-drained soil and also grows nutritionally poor acidic, neutral and basic soil. Kaul (1972) reported that *A. mexicana* is self-compatible and strikingly protandrous as anthers dehisce one day before anthesis and the stigma attains receptivity at anthesis. In this species, autonomous autogamy occurs during flower-opening and closing. It is pollinated by pollen collecting insects belonging to hymenoptera, coleoptera, hemiptera and dermaptera. These insects effect mostly cross-pollination. Pathak et al. (2021) noted that *A. mexicana* is entomophilous but the details of insects effecting pollination are not mentioned. Maheshwari and Kanta (1961) reported that intra-ovarian pollination done manually in *A. mexicana* produces high seed set rate but it is low when compared to natural seed set rate. With this backdrop, the present study is an attempt to provide certain details of ecological aspects of pollination syndrome and seed dispersal mechanism in *A. mexicana* and discuss the findings of this study taking into consideration the published information on the same aspects in *Argemone*.

2. MATERIALS AND METHODS

Argemone mexicana growing in the wild patches at Visakhapatnam Steel Plant area, Visakhapatnam District, Andhra Pradesh, India, were selected for the study during November-May 2021. The phenological events, vegetative growth, flowering and fruiting were carefully observed. Fifteen flowers from each plant species were used to note the floral morphological traits. Fifty mature buds were tagged and followed to record the timing of anther dehiscence and stigma receptivity. Observations on visitors to flowers were made during day to record their scientific names, the foraging behavior and forage collected. All observations recorded were described systematically and discussed with the relevant works that have already been published.

In Oman, many habitats are characterized by different environmental stress factors, serpentine, shallow and rocky soils, alkaline or saline, low phosphorus and nitrogen content, low precipitation, low moisture and high temperature (Zaffermann et al. 2015). Majority of alien plants recorded in this country are from South America. Annual or perennial herbs largely prevail among alien plants. One such species is a herbaceous weed, *Argemone mexicana*. It is naturalized and restricted to a few habitats indicating that it is not an invasive species (Patzelt et al. 2022). The study findings on *A. mexicana* in the study area in India have been interpreted in the light of its occurrence and role in providing food for bees in general and honey bees in particular.

3. RESULTS AND DISCUSSION

It is an erect annual herb with muti-branched prickly stem. Lower leaves are borne in a rosette form with short petioles while the stem leaves are apetiolate, long, alternate and serrate with spiny margins. Flowering occurs during January-May with peak flower production during February-March (Kaul 1972) (Figure 1a). Flowers are solitary, borne at the distal ends of the axillary branches, scentless and bisexual (Figure 1b,c). The calyx is 3-vaulted and spiny. The corolla has 6 obovate glabrous bright yellow petals arranged in 2 whorls, each with 3 petals. The stamens are many, free and yellow. The pistil consists of a compound 4-6 carpelled many ovuled ovary with long soft bristles and a compound style tipped with 4-6 dark red turgid stigmatic lobes with unicellular glandular papillae.

Mature buds are open during 0800-0900 h (Kaul 1972). The flowers are bowl-shaped when open fully. Anthers dehisce by extrorse mode by curling basipetally backwards and eventually they shrivel. The pollen grains are tri-zonicolpate and the colpi membrane is heavily crustate with reticulate exine surface with rounded ends. Both sterile and fertile pollen grains produced, the fertile pollen production rate is high during January-March and low later on if flowering is continued (Kaul 1972). The stigmatic

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lobes are white in bud and dark red with turgid unicellular papillae at anthesis; the latter state of the stigma is an indicator of stigma receptivity. The state of loss of papillae turgidity and blackened stigmatic lobes is an indicator of loss of stigma receptivity.

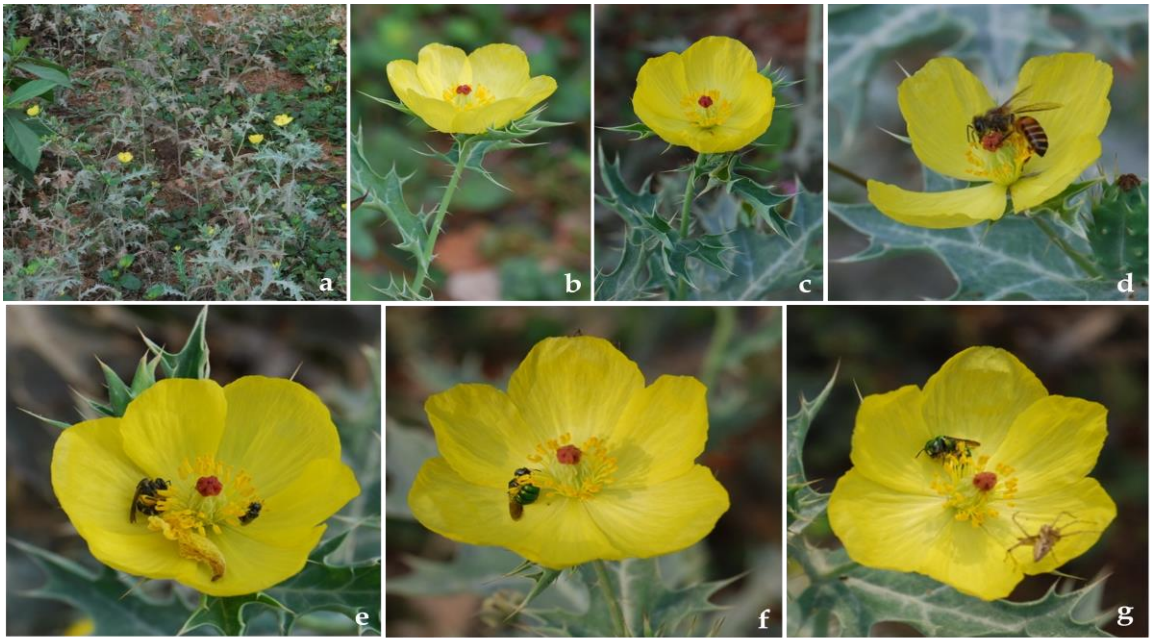

Figure 1. *Argemone mexicana*: a. Habit - flowering phase, b. & c. Flowers, d. *Apis cerana* collecting pollen, e. *Apis florea* (left) collecting pollen and *Trigona iridipennis* (right) collecting pollen, f. & g. *Pithitis binghami* collecting pollen.

Kaul (1972) reported that in *A. mexicana*, pollination occurs at anthesis, pollen germinate immediately and the pollen tubes stretch over the stigmatic papillae ectotrophically and finally reach the ovary within 10 hours. This author also reported that the flowers are nectarless, protandrous, self-compatible and self-pollination is inevitable. The closed state of petals effect autogamy and after that, the petals are open. The anthers dehisce a day before anthesis and are placed close to the stigma at the time of anther dehiscence and deposit their pollen on the stigma. When the flower opens, the anthers curve backwards during which the remaining pollen falls on the concave surface of petals. In the evening, the petals close over the pistil due to which the inner surface beset with pollen comes into direct contact with the stigma which is still in receptive state effecting pollination. In this study, it is found that *A. mexicana* is hermaphrodite, nectarless, protogynous and self-compatible. The flowers are strikingly protogynous since the dark red stigmatic surface indicating receptivity is evident about 5-6 hours before flower-opening and the dehiscence of anthers occurs after anthesis. There is no close contact betwee the stigma and anthers even during bud stage because of the placement of the stigma slightly above the level of anthers but such a placement of sex organs may provide scope for the occurrence of autonomous autogamy to a minimum level. Since anther dehiscence occurs after anthesis, the pollen falling on the inner surface of petals during bud or at the time of anthesis is totally ruled out. But, there is scope for the occurrence of autonomous autogamy during flower closure which is a function of closing of petals enclosing the sex organs as reported by Kaul (1972).

In this study, *A. mexicana* flowers are of open dish-bowl shape which allows easy landing and access to pollen for flower-visiting insects because of well exposed androecial and gynoecial organs. Since the flowers provide only pollen as forage, all flower-visiting insects are pollen foragers only. Further, each flower with many stamens provide copious amount of pollen and hence, the visiting insect is well rewarded in return for the pollination service rendered by it. Kaul (1972) reported that *A. mexicana* is visited by pollen collecting insects, *Andrena, Halictus, Osmia, Callosobruchus, Dasyscytus* and *Forficula* of which three bee species effect mostly cross-pollination while the other insects facilitate most self-pollination. Pathak et al. (2021) reported that *A. mexicana* is entomophilous but these authors have not provided details of insects involved in the pollination of this species. In this study, it is found that *A. mexicana* is exclusively pollinated by bees, *Apis cerana* (Figure 1d), *A. florea* (Figure 1e), *Trigona iridipennis* (Figure 1e) and *Pithitis binghami* (Figure 1f,g) indicating that this plant species is obligately melittophilous. The bright yellow corolla might be reflecting ultraviolet activity which is visible to bees and the corolla as a whole appears to be functioning as a guide to direct bees to the reproductive center of the flower (see Schneider and Nichols 1984). In Oman, *A. mexicana* as an alien herb grows in certain habitats with environmental stress factors such as serpentine, shallow and rocky soils, alkaline or saline, low phosphorus and nitrogen

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content, low precipitation, low moisture and high temperature (Zaffermann et al. 2015). Since this species is now naturalized and able to grow together with local plant species, the flower visitors, especially the pollen collecting bees might have long been habituated to utilize the pollen of this species as an important food. Further, *A. mexicana* flowers are nectarless, the pollen collecting bees should find nectariferous flowers growing simultaneously in the same habitats in order to collect liquid food. In *A. aurantiaca*, the flowers are pollinated by bees along with beetles but the former act as effective cross-pollinators while the latter facilitate self-pollination (Schneider and Nichols 1984). In *A. munita*, the flowers being self-incompatible display an inherent mechanism with which self-pollen tube penetration is inhibited when it touches the female tissue (Bilinski and Kohn 2012).

Maheshwari and Kanta (1961) reported that in *A. mexicana* intra-ovarian pollination done manually resulted in high seed set rate with 140 seeds per fruit against natural seed set rate with 150-200 seeds per fruit. These authors put a slit in the ovary and injected pollen grains manually; then the pollen germinated and fertilized the ovules. If this is the case, then what is the role of stigma and style in enabling pollen to germinate, form tube and reach the ovary? What factors present in the ovary enabled the pollen to germinate and form tube for fusion with the ovules? These questions require a thorough scientific study. In this context, it is appropriate to mention that certain enzymes and chemicals present in stigma and style trigger and enable the pollen to germinate and form tube to proceed further until it reaches the ovary to fertilize the ovules.

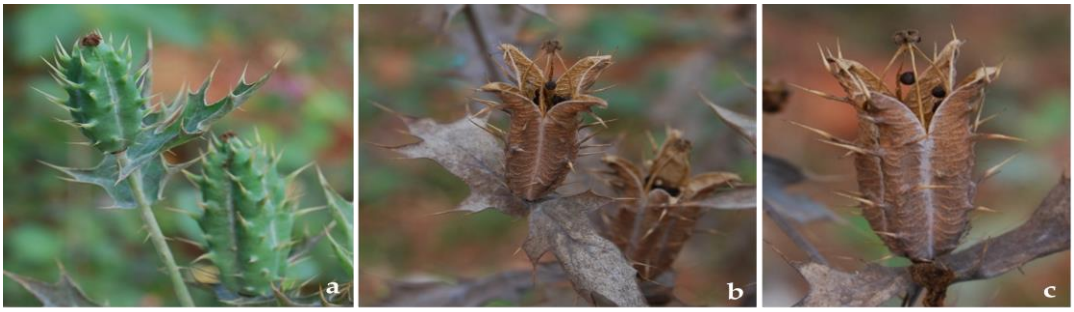

Figure 2. *Argemone mexicana*: a. Maturing fruit, b. & c. Fruit dehiscence and seed dispersal.

In this study, it is found that *A. mexicana* fruits develop and mature within 3 weeks from the time of fertilization (Figure 2a). Fruit is an ellipsoid 4-6 valved erect prickly many-seeded capsule dehiscing acrocidally from the apex to about 1/3; the valves separate from the framework vascular elements and the persistent style and stigma remain attached to the elements. The seeds are globular, finely net-veined and blackish brown. When the brisk wind strikes the dehisced fruits violently, the seeds fall off in small aggregates by jactitation but all seeds do not disperse at once. This wind-driven seed dispersal is called censer mechanism (Figure 2b,c). Most of the seeds fall within the vicinity of parental sites. The seeds settled in the soil are dispersed by water during rainy season, humans due to adhering of mud to shoes or chappals, livestock and farming machinery.

4. CONCLUSIONS

Argemone mexicana is a widespread herbaceous weed which grows well in different habitats, especially in sites characterized by light sandy well-drained and nutritionally poor acidic, neutral and basic soils (Pathak et al. 2021). Since it prefers well-drained sandy soils with low water content, this species is a potential candidate for consideration in eco-restoration of ecologically disturbed, deteriorated and damaged habitats where soil is mostly exposed and deficient in nutrients and moisture content. It is hermaphroditic species with self-compatible, nectarless and scentless flowers adapted for melittophily which ensures cross-pollination in addition to self-pollination. The flower closing mechanism facilitates the occurrence of autonomous autogamy which serves as fail-safe mechanism when pollinating bees are either not reliable or available to set seed. The vector-dependent and non-vector dependent pollination ensures the success of sexual reproduction and invade and produce population in the presence or absence of pollinators. Censer mechanism functional in this species for seed dispersal is wind-driven in natural conditions. However, rain water, humans and animals also have a role in seed dispersal. *A. mexicana* with melittophily, autonomous autogamy and seed dispersal by different agents is able to spread very easily and build up populations in different habitats that present different ecological conditions. In Oman, *A. mexicana* as a naturalized species in certain habitats is most likely to provide pollen to bees in general and honey bees in particular due to saucer-shaped corolla of the flower with well exposed stamens with dehisced anthers. Apart from this, its ability to grow in environmental stress factors is advantageous for the charging of the soil with organic matter, accumulation of soil moisture and carbon sequestration.

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Authors contributions:
All authors contributed equally.

Ethical approval
Argemone mexicana from Visakhapatnam District, Andhra Pradesh, India is reported in the study. The ethical guidelines for plants & plant materials are followed in the study for sample collection & identification.

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Conflicts of interests
The authors declare that there are no conflicts of interests.

Data and materials availability
All data associated with this study are present in the paper.

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