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Anemophily, entomophily and geophily in facultative xenogamous polychorous species, *Gisekia pharnaceoides* L. (Gisekiaceae)

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ABSTRACT

Gisekia pharnaceoides is an annual herbaceous ruderal and agrestal weed with prostrate and creeping habit. This weed displays prolific growth, flowering and fruiting during rainy season. The flowers are small, nectariferous, actinomorphic, bisexual and facultative xenogamous. The flowers facilitate the occurrence of spontaneous autogamy, anemophily, thripsophily, entomophily and geophily. Entomophily involves small-bodied honey bees and carpenter bees, ants and small lycaenid butterflies. The percentage of fruit and seed set is highest in open-pollinations. Fruits are non-fleshy capsules which split into five indehiscent mericarps. Seed dispersal modes include barochory, anemochory and hydrochory. The ability to reproduce sexually throughout the year, production of highest seed set rate, function of different seed dispersal modes and production of new plants as soon as seeds are dispersed enable the weed to occupy ruderal and agrestral sites. This weed has economical, medicinal and ecological values and hence its exploitation is an excellent remedy to control its menace in agricultural sites. Further, it is important as a pioneer species to control soil erosion, add soil fertility and rehabilitate dry or arid habitats to wet habitats.

Keywords: *Gisekia pharnaceoides*, hermaphroditism, anemophily, entomophily, geophily, barochory, anemochory, hydrochory.

1. INTRODUCTION

The genus *Gisekia* was initially included in Phytolaccaceae, later placed in Aizoaceae and then in Molluginaceae (Klaus et al., 1993). Finally, *Gisekia* has been placed in a separate family Gisekiaceae (APG III, 2009). It is distributed in arid regions of Africa and Asia (Bissinger et al., 2014). Joshi and Rama Rao, (1936) reported that *Gisekia* is a small genus of African herbs comprising only five species. Gilbert, (1993) reported that Gisekiaceae family is represented by *Gisekia* genus which is mainly African with an extension into southern Asia. The genus consists of seven species, *G. pharnaceoides* L., *G. diffusa* M. Gilbert, *G.*

paniculata Hauman, *G. africana* (Lour.) Kuntze, *G. haudica* M. Gilbert, *G. scabridula* M. Gilbert and *G. polylopha* M. Gilbert. Within *G. pharnaceoides*, there are two varieties var. *pharnaceoides* L. and var. *alata* M. Gilbert and within *G. africana*, there are three: var. *africana* (Lour.), Kuntze, var. *pedunculata* (Oliv.) Brenan and var. *decagyna* Hauma. Of these, *G. pharnaceoides* and *G. africana* are widely distributed.

Joshi and Rama Rao, (1936) reported that *Gisekia pharnaceoides* is extended to a greater part of India with confinement mostly to sandy soils but it is not common everywhere. Berry and Bjorkman, (1980) and Prasad et al., (2006) reported that *T. portulacastrum* is a C_4 prostrate herb and has a greater capacity to photosynthesize at high temperatures in comparison to C_3 species. Ramadas and Raghavendra, (1972) observed a CO_2 compensation point typical of C_4 photosynthesis for *G. pharnaceoides*. Bissinger et al., (2014) confirmed that *G. pharnaceoides* performs C_4 photosynthesis based on CO_2 compensation point measurements. Despite its wide distribution, it has not been investigated for its sexual reproduction and hence the present study is an occasion to provide a comprehensive account on this aspect in *G. pharnaceoides*.

2. MATERIALS AND METHODS

Gisekia pharnaceoides L. populations growing in dry and wet areas near foothills of Visakhapatnam were selected for the study during wet season in 2019 and 2020. Phenological schedules, anthesis, anther dehiscence, floral morphology, flower closing behavior with reference to self-mediated autogamy, nectar and pollen characters, essential and non-essential amino acids, in vitro pollen germination, pollen-ovule ratio, stigma receptivity, flower visitors and their role in pollination, pollen carryover efficiency of insects to promote vector-mediated pollination rate, fruit and seed set rates in open-pollinations, fruit and seed characters and seed dispersal were examined very carefully according to the protocols provided in Dafni et al., (2005).

3. RESULTS

Phenology

It is a common prostrate or creeping semi-succulent annual herb of sand dunes, sandy soils, cultivated lands and ruderal places (Figure 1a). It is well-branched with pubescent cylindrical stems. Leaves are simple, solitary and in clusters of 3 to 7 and petiolate. Leaf blade is elliptic, lanceolate or spatulate with white raphides covering both upper and lower surface and apex obtuse or sub-acute. The plant appears throughout the year with different phases of growth, flowering (Figure 1b) and fruiting but it thrives well during July-October by showing prolific growth, flowering and fruiting. Inflorescence is sessile, axillary and terminal, cymosely-branched, few-flowered (3-7) at leaf-axils and many-flowered (9-15) at terminal positions. The cymose-branched inflorescences at leaf-axils complete anthesis within 2-4 days while those at terminal portions complete anthesis within 4-7 days (Figure 1c).

Flower morphology

The flowers are pedicellate (7-9 mm long), small, 2.2 ± 0.41 mm long, 3.6 ± 0.5 mm wide, odourless, actinomorphic and bisexual. They possess monochlamydeous perianth with 5 greenish-creamy white tepals with pink margins, which are free, glabrous, ovate with acute apex, 2.6 ± 0.5 mm long, 1 mm wide. The stamens are 5 and arranged alternate to tepals; the filaments are greenish-yellow, 1.08 ± 0.24 mm long and 0.5 ± 0.1 mm wide, dilated at base and flattened above and tipped with light pink dithecous anthers with versatile fixation. The ovary is apocarpous, pentacarpellary and pentalocular superior ovary. Each carpel has a style with simple wet and shiny bent stigma and both style and stigma are papillate (Figure 1f). Each locule has one ovule arranged on axile placentation (Figure 1i). The tepals are flat with the free carpels exposed and the stamens extending above the stigmas.

Floral biology

Mature buds open during 0600-1200 h with high percentage of flower-opening during 0700-1000 h (Table 1). The event of anthesis from the initiation to complete opening of tepals exposing the sex organs occurs within 20 to 30 minutes (Figure 1d, e). The anthers dehisce during anthesis by longitudinal slits; all anthers in a flower dehisce within 15 minutes (Figure 1g). The number of pollen grains per anther is 403 ± 29.3 while pollen output per flower is 2015 ± 146.5. The pollen-ovule ratio is 403:1 flowers. The pollen grains are white with light pink tinge, 3-nucleate, 32.37 ± 2.62 µm in diameter (Figure 1h). In vitro pollen viability test showed that pollen grains are viable from 0700 h with 99% viability to 2100 h with 4% viability (Table 2). The stigma attains receptivity after anthesis and continues until noon of the following day. The nectar is secreted in traces. The nectar has 6 essential amino acids which included threonine, valine, leucine, isoleucine, histidine and arginine. Further, it has 9 non-essential amino acids which included alanine, amino-butyric acid, cysteine, cystine, glutamic acid, glycine, hydroxy-proline, proline and serine (Table 3). The tepals close back slowly enclosing the sex organs by late evening (1600-1700 h); however, flower closure is not complete leaving the possibility

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for probing by insects in the consecutive days. The stamens, styles and stigmas wither away and their dried parts remain inside the closed flowers throughout the period of fruit development while the carpels grow into mericarps which are enclosed by persistent tepals.

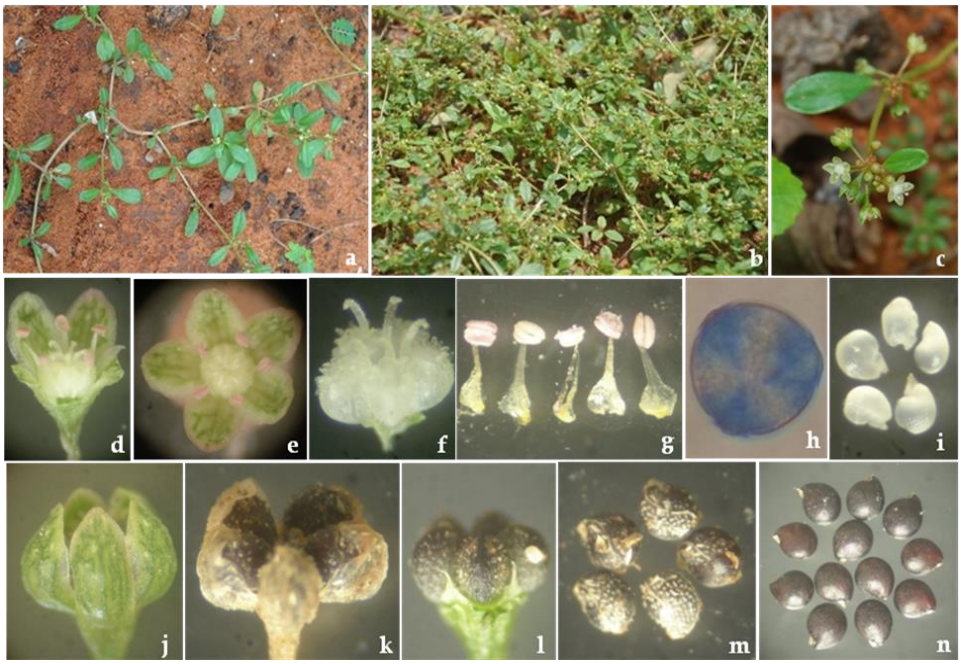

Figure 1 *Gisekia pharnaceoides*: a. Habit, b. Flowering phase, c. Buds and flowers, d. & e. Anthesis stages, f. Ovary with five styles tipped with bent stigmas, g. Dehisced dithecous stamens, h. 3-nucleate pollen grain, i. Ovules, j. Mature fruit, k. Fruit dehiscence, l-n. Seeds

Table 1 The percentage of anthesis as a function of time in *Gisekia pharnaceoides*

Time	No. of flowers anthesed	Percentage of anthesis
0500	0	0
0600	18	9
0700	58	29
0800	48	24
0900	36	18
1000	26	13
1100	10	5
1200	4	2
1300	0	0
1400	0	0

Table 2 In vitro pollen germination in *Gisekia pharnaceoides*

Time (h)	No. of pollen grains in the sample	No. of pollen grains germinated	Germination (%)
0600	-	-	-
0700	378	370	98
0800	359	329	92
0900	315	278	88

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1000	310	267	86
1100	245	176	72
1200	213	140	66
1300	178	91	51
1400	154	65	42
1500	145	54	37
1600	123	41	33
1700	98	30	31
1800	78	21	27
1900	43	10	23
2000	39	5	13
2100	25	1	4
2200	23	0	0
Modified Brewbaker and Kwack's medium			

Table 3 Essential and non-essential amino acids present in the nectar of *Gisekia pharnaceoides*

Essential amino acids		Non-essential amino acids	
Amino acid type	Present (+)/ Absent (-)	Amino acid type	Present (+)/ Absent (-)
Threonine	+	Alanine	+
Valine	+	Amino butyric acid	+
Methionine	-	Aspartic acid	-
Leucine	+	Cysteine	+
Iso leucine	+	Cystine	+
Lysine	-	Glutamic acid	+
Phenyl alanine	-	Glycine	+
Histidine	+	Hydroxy proline	+
Arginine	+	Proline	+
Tryptophan	-	Serine	+
		Tyrosine	-

Flower behavior and pollination

Mature buds about to open their tepals show the stamens in erect state and positioned above the stigmas. With the initiation of unfolding of tepals, the anthers dehisce making available self-pollen for the possibility of occurrence of spontaneous autogamy consequent upon the attainment of receptivity to pollen by the stigmas of the same flower. As the stigmas become receptive immediately after anthesis, there are plenty of possibilities for the occurrence of spontaneous autogamy which is further promoted by versatile anthers which facilitate pollen dispersal by wind. After anthesis, the tepals gradually expand and become nearly flat during which the styles with bent stigmas take different orientations in erect state and the stamens move away from the styles/stigmas in order to minimize the occurrence of self-pollination either spontaneously or by wind and to provide opportunity for the occurrence of cross-pollination. Towards evening, the tepals close back gradually bringing back the stamens close to the stigmas; this positional shift of stamens and their placement above the stigmas facilitate again the occurrence of self-pollination either by the fall of dry pollen downwards on the stigmas which are still in receptive state, accelerated either by gravitation or by wind. The possibility and extent of self-pollination at flower closure time depends on the availability levels of pollen in the anthers. Further, the closed flowers keep an opening terminally which facilitates probing by insects during the forenoon period of the following day for the occurrence of self- and/or cross-pollination. Therefore, the flower behavior involving movements of tepals and stamens and different orientations of styles/stigmas provide ample opportunities for the occurrence of spontaneous or vector-mediated self- and/or cross-pollination.

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Insect visitors and pollination

Thrips-pollination

The terebrantian thrips, *Megalurothrips distalis* Karny and *Frankliniella schultzei* Trybom (Family: Thripidae, Sub-family: Thripinae) were found to use the buds for their breeding. They came out during the process of anthesis with the unfolding of the tepals resulting in the exposure of sex organs. These thrips remained on the plant as resident foragers and foraged for both pollen and nectar which were available or accessible during and after anthesis and also after flower closure. Bud infestation with thrips was 67%. The forage collection and crawling of the thrips within and between flowers on the same plant were considered to be effecting autogamy and geitonogamy. The thrips also moved to adjacent plants by crawling on the leaves that connected the leaves of nearby conspecific plants and also by flying in order to collect pollen and nectar from different plants and this forage collection behavior was considered to be effecting cross-pollination also. The papillate stigmas capture the pollen with great ease from the pollen-laden thrips when the latter crawl on the stigmas ensuring the occurrence of pollination.

Bees, ants and butterfly-pollination

The flowers were foraged regularly by bees, weaver ants and butterflies during day-time (Table 4). The foraging activity of these insects was very high at profuse flowering phase during rainy season. Of these, bees and weaver ants foraged during 0700-1700 h with maximum activity at 1200-1300 h (Figure 4) while butterflies commenced their foraging activity along with bees and weaver ants at 0700 h but continued until 1600 h only with maximum activity at 0900-1000 h (Figure 5). The bees collected both pollen and nectar mostly in the same visit to the flowers while ants and butterflies collected only nectar. The bees were *Apis florea* (Figure 2a), *Trigona iridipennis* (Figure 2b) and *Ceratina* sp. (Figure 2c). The ants represented only one species, *Oeocophylla* sp. (Figure 2d). The butterflies represented lycaenids only which included *Zizula hylax, Pseudozizeeria maha* (Figure 2e), *Zizeeria karsandra* (Figure 2f, g), *Zizina otis* and *Chilades pandava* (Figure 2h). Of the total foraging visits made by insects, bees made 56%, ants 17% and lycaenid butterflies 27% (Figure 6). The pollen carrying efficiency evaluated by body washings (except corbiculae on hind legs in case of bees) of captured insects indicated that the bees were more efficient in carrying pollen than ants and butterflies. *A. florea* carried 83.8 ± 15 pollen grains, *T. iridipennis* 56.4 ± 11.5 pollen grains, *Ceratina* sp. 50.7 ± 9.4 and *Oecophylla* sp. 20.4 ± 5.3 pollen grains. The average number of pollen grains recovered in the washings of head, proboscis and body of lycaenid butterflies varied from 18.9 ± 4.7 to 34.3 ± 8.8 (Table 5).

The forage collection activity by all insect species was found to be resulting in self- and/or cross-pollination depending on the pollen source from the same or different conspecific individual plants. The foraging activity of thrips for nectar as well as pollen was found to be compelling the bees to make multiple visits to the same and/or different flowers on the same or different conspecific plants in the habitat in order to collect forage to the extent possible before the closure of flowers at the end of the day. Therefore, insect activity involving thrips, bees, ants and butterflies was treated as very important to maximize pollination rate in addition to spontaneous self-pollination, gravitational and wind-pollination.

Table 4 List of Insect foragers on *Gisekia pharnaceoides*

Family	Genus	Species	Common name	Forage sought
Hymenoptera				
Apidae	*Apis*	*florea* Fabricius	Dwarf Honey Bee	Pollen + Nectar
	Trigona	*iridipennis* Smith	Stingless Honey Bee	Pollen + Nectar
	Ceratina	sp.	Small Carpenter Bee	Pollen + Nectar
Formicidae	*Oeocophylla*	sp.	Weaver ant	Nectar
Lepidoptera				
Lycaenidae	*Zizula*	*hylax* Fabricius	Tiny Grass Blue	Nectar
	Pseudozizeeria	*maha* Kollar	Pale Grass Blue	Nectar
	Zizeeria	*karsandra* Moore	Dark Grass Blue	Nectar
	Zizina	*otis* Fabricius	Lesser Grass Blue	Nectar
	Chilades	*pandava* Horsfield	Plains cupid	Nectar

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Table 5 Pollen recorded in the body washings of insects on *Gisekia pharnaceoides*

Insect species	Sample size (N)	Number of pollen grains		
		Range	Mean	S.D
Apis florea	10	62-116	83.8	15.0
Trigona iridipennis	10	36-82	56.4	11.5
Ceratina sp.	10	30-68	50.7	9.4
Oeocophylla sp.	10	11-28	20.4	5.3
Zizula hylax	10	9-34	26.3	6.7
Pseudozizeeria maha	10	10-25	18.9	4.7
Zizeeria karsandra	10	13-38	28.7	7.0
Zizina otis	10	8-31	23.1	6.1
Chilades pandava	10	15-47	34.3	8.8

Figure 2 *Gisekia pharnaceoides:* a. *Apis florea*, b. *Trigona iridipennis*, c. *Ceratina* sp., d. *Oecophylla* sp., e- h. Lycaenid butterflies – e. *Pseudozizeeria maha*, f. *Zizeeria karsandra*, g. *Zizeeria karsandra* (in mating state), h. *Chilades pandava.*

Figure 3 *Gisekia pharnaceoides:* a. & b. new plants

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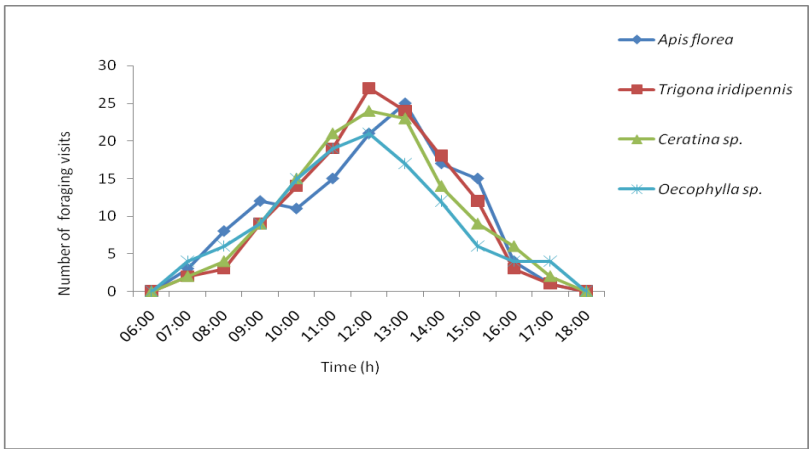

Figure 4 Hourly foraging visits of bees and ants on *Gisekia pharnaceoides*

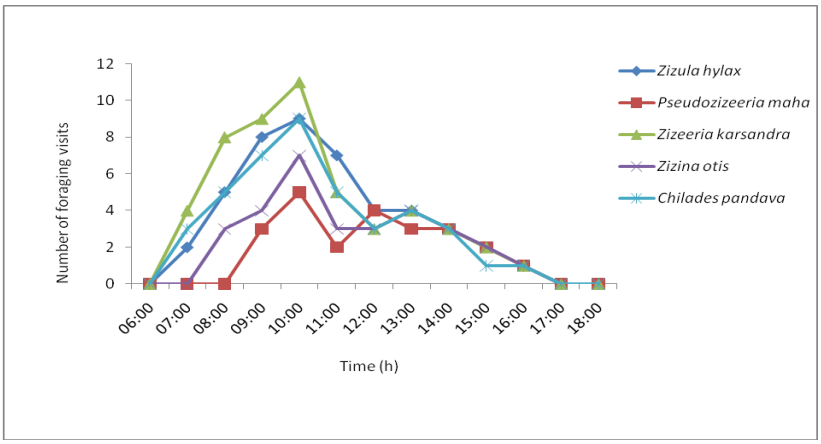

Figure 5 Hourly foraging visits of lycaenid butterflies on *Gisekia pharnaceoides*

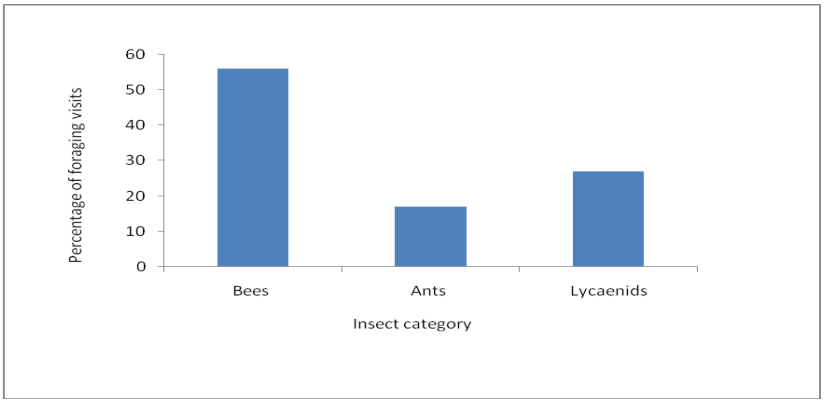

Figure 6 Percentage of foraging visits of bees, ants and lycaenid butterflies on *Gisekia pharnaceoides*

Fruiting ecology

The pollinated and fertilized flowers grow continually and produce fruits within two weeks. Natural fruit set rate is 96% while seed set rate is 90%. Fruit is a green to light cream colored stalked non-fleshy 5-angled capsule splitting at length into 5 indehiscent mericarps (Figure 1k), 2.72 ± 0.3 mm long and 2.98 ± 0.16 mm wide (Figure 1j). It consists of 1 to 5 one-seeded spiny tuberculate reniform mericarps. The seeds are black, ovoid to sub-orbicular, smooth, minutely pitted and very light in weight (Figure 1l-n). They gradually fall off to the ground on their own by gravity and are also dispersed by wind. Further, the seeds also float in water and migrate to new habitats during rain fall period. Individual plants produce seeds throughout the year if the soil is favorable in terms of moisture and nutrients. Seeds dispersed from the plants germinate immediately within two weeks and produce new plants either in the vicinity of parental sites or away from parental sites in new areas (Figure 3a, b). The ability of seed production

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throughout the year and seed germination soon after their dispersal is an important character that enables the plant to populate in the habitat where it grows and in other habitats where its seeds migrate and settle.

4. DISCUSSION

Joshi and Rama Rao, (1936) reported that *Gisekia pharnaceoides* is extended to a greater part of India confining mostly to sandy soils. Godfrey, (1961) stated that *G. pharnaceoides* is a ruderal species. Yoganarasimhan, (2000) noted that *G. pharnaceoides* is found in sandy places only in India. Godfrey, (1961) documented that *G. pharnaceoides* grows as a ruderal species. In the present study, *G. pharnaceoides* is found to be growing in diverse habitats representing sand dunes, sandy soils, ruderal sites and agricultural sites. Its growth in different habitats indicates that this species is a ruderal and agrestal herb species (Vaidya et al., 1978). Its prostrate and creeping habit and ability to grow throughout the year enables it to spread fast and emerge as a successful weed. However, this weed displays prolific growth, flowering and fruiting during rainy season, especially in agricultural lands where soil is sufficiently wet.

In this study, it is found that *G. pharnaceoides* produces flowers in leaf axils as well as in terminal portions of the branches. But flower production rate varies with the position on the plant and the cymosely-branched inflorescence is few-flowered at leaf-axils while it is many-flowered at terminal portion. Field observations indicate that the flowers produced at the terminal position of the branches are more attractive than those produced at leaf axils as insects visiting the flowers made frequent visits to the flowers produced at the terminal position than those produced at the leaf axils. Joshi and Rama Rao, (1936) reported that in *G. pharnaceoides*, the flower rudiment first appears as a rounded structure which is surrounded by floral parts in acropetal succession, the 5 tepals appear first, followed by 5 stamens and 5 carpels. The present study also found the same sequence of appearance of floral parts with the stamens arranged alternate to tepals and ovary with free carpels, each with a style and stigma. Glover, (2011) mentioned that the betalains are found exclusively in Caryophyllales, and in no other plant species in the plant kingdom. The betalains are not major floral pigments but when produced give red colour to flowers. Hatlestad and Lloyd, (2015) mentioned that plants produce betalain pigments to attract pollinators to flowers. Sivarajan and Gopinathan (1985) mentioned that *G. pharnaceoides* flowers produce betalain pigments. The present study reports that *G. pharnaceoides* flowers produce tepals with pink-colored margins and stamens with pink-colored anthers; the pink-colored tepal margins and anthers could be attributable to the production of betalain pigments by the plant in order to attract pollinators to flowers.

In animal-pollinated plants, reduction of 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). Re-allocation of resources to more, smaller flowers and/or adaptations that increases pollen dispersal efficiency is likely to prompt the plant to reduce pollen production per flower through stamen loss. In *G. pharnaceoides*, the flowers are small and actinomorphic with a single whorl of five distantly spaced stamens collectively producing moderate amount of pollen. These traits limit pollen removal and pollen packaging by individual pollinators but maximize pollen dispersal while facilitating more precise contact between pollinators and anthers or pollinators and stigmas. These structural and functional traits enhance the proportions of pollen grains delivered to stigmas (Harder and Thomson, 1989). Cruden, (1977) stated that pollen-ovule ratios can serve as a reliable indicator of the breeding system. High pollen-ovule ratios are normally associated with obligate out-crossing behaviors, moderate pollen-ovule ratios with facultatively xenogamy and low ratios with obligate autogamy. In *G. pharnaceoides*, the pollen-ovule ratio tallies with the moderate pollen-ovule ratio provided for facultative xenogamy by Cruden, (1977). Further, the stigma receptivity extends until the noon of the 2nd day from the time of anthesis providing opportunities for self- and/or cross-pollination although the tepals close back; the closure of tepals is not absolute and hence facilitates probing by insects. Therefore, the pollen-ovule ratio and stigma receptivity duration indicate that facultative xenogamy is functional in this plant.

Ehrendorfer, (1976) proposed that ancestral taxa in Caryophyllales occupied "open, warm, dry and windy habitats with mineral soils". In this open, pollinator-deprived environment, wind pollination may have prevailed, and anthocyanin pigmentation that was produced by flowers to attract pollinators was lost. 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) stated 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

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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.

In the light of different propositions with respect to the production and non-production of floral pigments, anthocyanins or betalains as attractants of pollinator insects, the present study explains that G. *pharnaceoides* flowers produce pink colour which appears to be an indication of betalains which have a role in the attraction of pollinator insects. This floral pigmentation appears be an inherent and persistent trait used by *G. pharnaceoides* to attract pollinating insects, especially when it occupies agricultural sites where insect fauna thrives well. The study sites represent both ruderal and agrestal areas and support certain fauna but the insect species visiting the flowers of *G. pharnaceoides* are the same in both areas indicating that this plant species utilizes insects if present in ruderal areas that characterize open, warm and windy habitats. Since the plant has prostrate and creeping habit, it is not very prominent in appearance despite its ability to form mat-like population in areas where other wild plants grow naturally and hence it is not able to attract many insect species to its flowers even in agricultural sites. Therefore, the floral pigmentation displayed by tepal margins and anthers is important for *G. pharnaceoides* to attract insect pollinators to some extent to achieve high pollination rate.

The present study shows that *G. pharnaceoides* keeps its flowers open for a few hours for pollination on the day of anthesis after which the tepals close back. But, the tepals do not close completely at the apical position and this allows insects to probe the closed flowers on the 2nd day. The flowers have plenty of opportunities for the occurrence of spontaneous self-pollination, immediately after anthesis by which time pollen is available and stigma is receptive to pollen. Spontaneous self-pollination is further facilitated by versatile anthers which disseminate pollen by wind just after anthesis. During the open state of the flower, the spatially separated stamens and stigmas minimize or prevent the occurrence of spontaneous self-pollination and anemophily. During and after flower closure, the stamens return back to their original erect position over-arching the stigmas; this orientation facilitates the occurrence of spontaneous self-pollination by gravitational fall of the pollen from the anthers unto the stigmas if pollen is still present in the anthers. However, the possibility for the occurrence of these forms of spontaneous self-pollination during and after flower closure extends until late evening of the day of anthesis as the pollen grains become non-functional due to loss of viability thereafter. But, the possibility for geitonogamy and xenogamy in closed-flowers by pollinating insects extends until the noon of the 2nd day due to continuation of stigma receptivity until then and probing of closed flowers by forage-seeking insects. Further, the nectar and pollen-feeding activity of thrips commonly effect self-pollination within and between flowers on the same plant; they also effect cross-pollination if they move between plants by crawling on the leaves connecting the adjacent plants or by flying short distances in quest of more nectar and pollen forage.

The present study indicates that the prostrate habit of the plant and small flower form of *G. pharnaceoides* are suitable for landing and probing by small-bodied insects. Accordingly, bees representing small-bodied honey bees and carpenter bees and lycaenid butterflies which represent smallest butterflies visit the flowers of *G. pharnaceoides* for pollen and/or nectar during which they effect self- and/or cross-pollination. Further, an ant species as resident forager also effects pollination by probing the flowers for nectar collection. The nectar is a source of some essential and non-essential aminoacids for the flower visitors. These insects effect pollination during the entire period of open state of the flowers and also after flower closure until the cessation of stigma receptivity. Of these insects, bees and butterflies display highest pollen-carry over efficiency and frequent inter-plant foraging visits and hence they are treated as principal pollinators. Ants display lowest pollen-carry over efficiency with least inter-plant foraging visits and hence are treated as minor pollinators. The forage-feeding activity of thrips reduces the availability rate of standing crop of pollen and nectar in the flowers; in consequence the insect pollinators, especially bees and butterflies are forced to intensity their foraging activity maximizing pollination rate. Therefore, thrips indirectly promote cross-pollination through which genetic variation is achieved by the plant to adapt itself to habitat situation and populate different ecological niches and eventually to emerge as a successful weed.

In this study, it is observed that G. *pharnaceoides* produces highest fruit and seed set rates indicating the functionality of facultative xenogamy mating system and the occurrence of spontaneous and/or vector-mediated (wind and insects) pollination at anthesis, during the open state of the flower and after flower-closure due to strikingly weak protandry which characterizes homogamy. The percentage of flowers that did not contribute to fruit and seed set could be attributable to untimely pollen arrival on stigmas and deficiency of nutrients in the soil environment. Gilbert, (1993) noted that *Gisekia* species be regarded as heterocarpous because they represent two types of mericarps, "smooth" characterized by very thin pericarps that virtually lack any kind of ornamentation and "sculptured" characterized by pericarps that develop various types of ornamentation. Further, this author mentioned that African authors consistently described the mericarps of *Gisekia* as "warted, muricate or papillose". In *G. pharnaceoides* var. *pharnaceoides,* the mericarps are smooth to spiny-papillose and sutures are at most obscurely toothed while in *G. pharnaceoides* var. *alata,* the mericarps are smooth to obscurely papillose and sutures are often expanded into prominent whitish

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dorsi-ventral crests or wings. Sivarajan and Gopinathan, (1985) noted that *G. pharnaceoides* seeds are lined with punctate seed coat. In this study, *G. pharnaceoides* produces stalked non-fleshy capsules which split into five indehiscent mericarps with minutely pitted or punctate seed coat. The mericarps rely on gravity and wind for seed dispersal and the fallen seeds disperse by water indicating the function of barochory, anemochory and hydrochory. The capacity to reproduce sexually throughout the year, produce highest seed set rate through spontaneous, gravitational and vector-mediated pollination, use different seed dispersal modes and produce new plants as soon as seeds are dispersed enables *G. pharnaceoides* to occupy different ecological niches and expand its distribution range in tropical latitudes as a successful ruderal and agrestral herb species.

Ramadas and Raghavendra, (1972) reported that *G. pharnaceoides* is a C4 plant species. Bissinger et al., (2014) reported that all traditionally recognized *Gisekia* species are C4 plants with atriplicoid Kranz anatomy. *Gisekia* genus represents an isolated C4 lineage within core Caryophyllales and probably spread along the African arid corridor from a South African center of origin. *G. pharnaceoides* with C4 photosynthetic pathway uses the NAD-ME biochemical type and it is treated to be migrated along the arid areas of eastern Africa. These authors stated that all currently recognized species of *Gisekia* are to be treated as one polymorphic species or species complex of *G. pharnaceoides*. These reports indicate that *G. pharnaceoides* has evolved C4 photosynthetic pathway due to its occurrence and spread in arid areas of Africa for a long period of time. The present study shows that C4 photosynthetic system ensures *G. pharnaceoides* to occupy both dry and wet habitats and grow as a successful weed in India.

5. CONCLUSION

Gisekia pharnaceoides is an annual herbaceous ruderal and agrestal weed. The flowers are small and actinomorphic with a single whorl of five distantly spaced stamens collectively producing moderate amount of pollen. These traits limit pollen removal and pollen packaging by individual pollinators but maximize pollen dispersal while facilitating more precise contact between pollinators and anthers or pollinators and stigmas. The pollen-ovule ratio and stigma receptivity longevity indicate the function of facultative xenogamy. The flowers facilitate spontaneous self-pollination, anemophily and vector-mediated pollination. Thrips, honey bees and carpenter bees, ants and small lycaenid butterflies effect pollination while collecting pollen and/or nectar. The fruits are stalked non-fleshy capsules which split into five indehiscent mericarps with minutely pitted or punctate seed coat. Seed dispersal modes include barochory, anemochory and hydrochory.

The capacity to reproduce sexually throughout the year, produce of highest seed set rate through spontaneous, gravitational and vector-mediated pollination, use different seed dispersal modes and produce new plants as soon as seeds are dispersed enables the weed to occupy different ecological niches and expand its distribution range in tropical latitudes as a successful ruderal and agrestral herb species. *G. pharnaceoides* as C4 plant has different abilities such as tolerance to extreme heat stress, carrying out photosynthesis efficiently, broadening niches in warm environments by saving a lot energy and water resource. These abilities indicate that this plant species is a promising species to exploit its genetic pool to develop heat-tolerant crop plants in the context of rising global temperatures and the looming possibility of widespread crop failure.

Authors contributions

All work contributed by this author only.

Ethical approval

Gisekia pharnaceoides L. species from foothills of Visakhapatnam were selected & used for 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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