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POLLINATION ECOLOGY, BREEDING SYSTEMS AND SEED DISPERSAL IN *Passiflora foetida* L. (PASSIFLORACEAE), A PERENNIAL HERBACEOUS CLIMBER WEED IN SOUTHERN PARTS OF ANDHRA PRADESH, INDIA

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ABSTRACT

Passiflora foetida L. (passion fruit) of the Passifloraceae family is an herbaceous climber weed which grows up to 1.5 - 6.5 m tall and is able to climb up until about 3 to 9 m high. This weed grows in riverbeds, wastelands, forest floors, crop fields, and roadsides. The peak flowering season is in July to December. Regular field visits and observations helped to understand the flowering phenology, fruit formation and seed distribution. Experimentation, testing and examination recorded pollen grain output, morphology and stigma receptivity duration. *Passifloraceae* flowers exhibited three various kinds of stigma positions in the same plant with different frequencies which determined the fertility rate of the flower. The stigma positions observed were: 1. Stigma below the anthers 64% (fully curved); 2. Stigma above the anthers 16% (no curvature); and 3. Stigma above anthers 20% (partially curved). Observation on *P. foetida* flowers showed both self-pollination and cross-pollination. Stigmas curved below the anthers had high fertility rate (fruit set 66.66% and seed set rate 75.05%). *Xylocopa latipes* (carpenter bee) visited the flowers more frequently compared with other forages. The fruits spread 5 m radial distance of the plant and the seeds were dispersed at quite a distance by animals (zoochory). The edible fruits of *P. foetida* were observed to have great nutrients content. *P. foetida* also retains pharmaceutical content. This study focused on phenology, flower morphology, floral biology, pollination mechanism, breeding systems, insect pollination, fruiting ecology, and seed ecology of *P. foetida*. It is expected that this study will provide knowledge on reproductive biology of passion fruit.

Keywords: cross-pollination, edible fruit, fertility rate, fruit set, herbaceous climber, passion fruit, seed set, self-pollination

INTRODUCTION

Passiflora foetida L. is one of herbaceous vine which is extensively found in tropical and subtropical regions. The particular name, *foetida,* means strong and small which name comes from the damaged foliage (Guzzo *et al.* 2004). Even though the family Passifloraceae is widely distributed in East Asia, South America, and New Guinea, it is a native species of the South and Central America. More than 500 species were identified up to the genus level (Fischer & Rezende 2008). Most of them are spread throughout Central and South America (Amorim 2011). Colombia has been a center for the diversity of genus *Passiflora* in which more than 100 *Passiflora* species are found in Colombia (Ocampo *et al.* 2007). In the 15th century, a Spanish scientist compared the spectacular flowers with the passion of Christ and named the flower as passion flower (Miyasaka *et al.* 2009).

P. foetida was firstly recorded as an invasive weed species by the Australian Agricultural Department in 1921 due to the findings of the plants' flower invaded forest areas, roadsides and disturbed fields in the state of Queensland in Australia, Western Australia. Genus *Passiflora*, which bears edible fruit, has the highest number of species within the family of Passifloraceae (Martin & Nakasone 1970). Aside from *P. foetida*, *P. alata* and *P. edulis* are the only species forming edible fruits (Noriega *et al.* 2011).

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Passiflora sp. generally are cultivated for their edible fruits, ornamental flowers, and pharmaceutical uses. Currently, in Spain, *P. caerulea* grows vigorously. However, *P. edulis* and *P. flavicarpa* are introduced to several tropical areas as a profit-oriented crop. Moreover, *Passiflora* sp. are used in the traditional medicinal application (Miroddi *et al.* 2013).

Previous research discussed about the reproduction system in purple passion fruit (Gulupa fruit). Those research stated that 80% of the flower anthesis occurs from 06:00 to 08:00 a.m., in which prevailing flowers forms fully curved style 66.4%, then fruit formation occurs in geitonogamy 86% (Rendon *et al.* 2013). Pollinators play a key role in crop production (Kearns *et al.* 1998), which pollinate 35% of crop varieties (Klein *et al.* 2007). *Xylocopa* spp., a dominant pollinator on *P. edulis,* is attracted by the sweet nectar of the passion fruit. The sticky pollens are impregnated on the body of passion fruit from the dehisced anthers (Nishida 1963).

Accessible information on phenology, breeding systems, pollination modes, pollinators, fruit formation and seed dispersal of *Passiflora foetida* L. (Passifloraceae) is lacking. In this framework, the study aimed to obtain information about pollination ecology of *Passiflora foetida*.

MATERIALS AND METHODS

Study Site

The study on *Passiflora foetida* L. was conducted in a deciduous forest ecosystem, an integral part of the Southern Eastern Ghats of Andhra Pradesh, India (15°33’25.37” N and 80°02’07.18” E) (Fig. 1).

Methods

Twenty-five flowers of *P. foetida* were tagged and observed daily to record the number of florets produced and the flowering phenology. Fifty fresh florets were examined to determine the floret type, color, odor, shape, symmetry, floret sex, and other characters (Aluri & Mallikarjuna 2016a).

Twenty-five tagged flowers were observed to document the time of anthesis and anther dehiscence and the availability of nectar. Nectar existence were observed by making gentile rapture on the corolla to take out the nectar by inserting micropipette through the flower corolla and measuring the nectar volume. The volume of collected nectar from ten flowers were measured. The mean of the total volume of nectar per flower is denoted as µL (Mallikarjuna 2017).

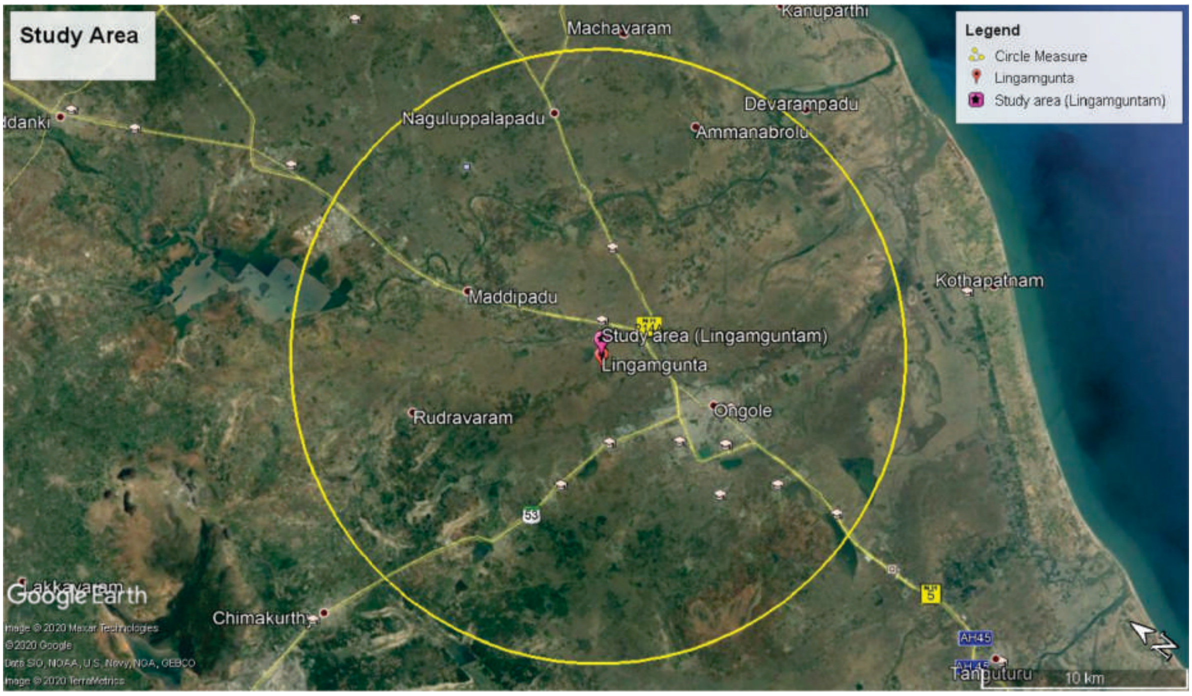

Figure 1 The study site of *Passiflora foetida*

Pollen per anther and flower were determined by using the Cruden method (Cruden 1977) and the pollen grain characters were recorded simultaneously. The timing and stigma receptivity were recorded by using the H_2O_2 test (Dafni *et al.* 2005). Moreover, the stigma physical circumstances observed up to the end of the flower life to confirm the duration period of stigma receptivity.

The visiting frequency of the foragers were recorded from morning to evening, every ten days during the peak flowering phase to list the foragers (Aluri & Mallikarjuna 2016b). The foraging activities were recorded every 10 minutes per hour for 24 hours. The observation of foraging activities was repeated every ten days. The activities patterns of each forager species were tabulated. From this tabulation, we calculated the visit percentage for each forager and categorized each forager's activities patterns each day. Simultaneously, we recorded the forager approach time, mode of association, touch down pattern, exploring behavior and contact with the essential organs for pollination and inter-plant foraging pursuit (Mallikarjuna & Aluri 2017). During the peak foraging spell, ten individual insects were collected when they were foraging the pollen or nectar on the flowers.

To evaluate the relative pollen carry-over ability and pollination efficiency, the trapped insects were carried to the laboratory. Ethyl alcohol was used to rinse the pollen from the insect body. The pollens were then stained with aniline-blue and counted the number of pollens under a microscope (Mallikarjuna *et al.* 2017).

To calculate the fruit and seed set, one hundred flowers were marked and recorded for determining the frequency of three different types of flowers (based on sigma position). After that, we marked 25 of each type of flower for verification and fruit maturation aspects. For seed formation aspects, the fruits were collected to examine the complete and un-complete seeds). Seed features were recorded to assess the mode of dispersal. Seed germination aspects were confirmed by visiting the study area at frequent intervals (Aluri *et al.* 2016).

RESULTS AND DISCUSSION

Phenology

Passiflora foetida is a very common herbaceous climber weed (Fig. 2a-c) which grows up to 1.5 - 10.5 m tall in wastelands. *P. foetida* often occurs in open fields, roadsides, and wastelands in rainy and winter seasons. The plant is able to regrow from the perennial root below in the ground soon after the first rainy days in June (Fig. 2e) or gingerly comes out from the seed (Fig. 2d) in the period of June - September. In stony and parched areas, seeds germination occur late, while the growth of new plants depends on soil nutrients and moisture environment. Robust climbing plants are found in soil having sufficient moisture.

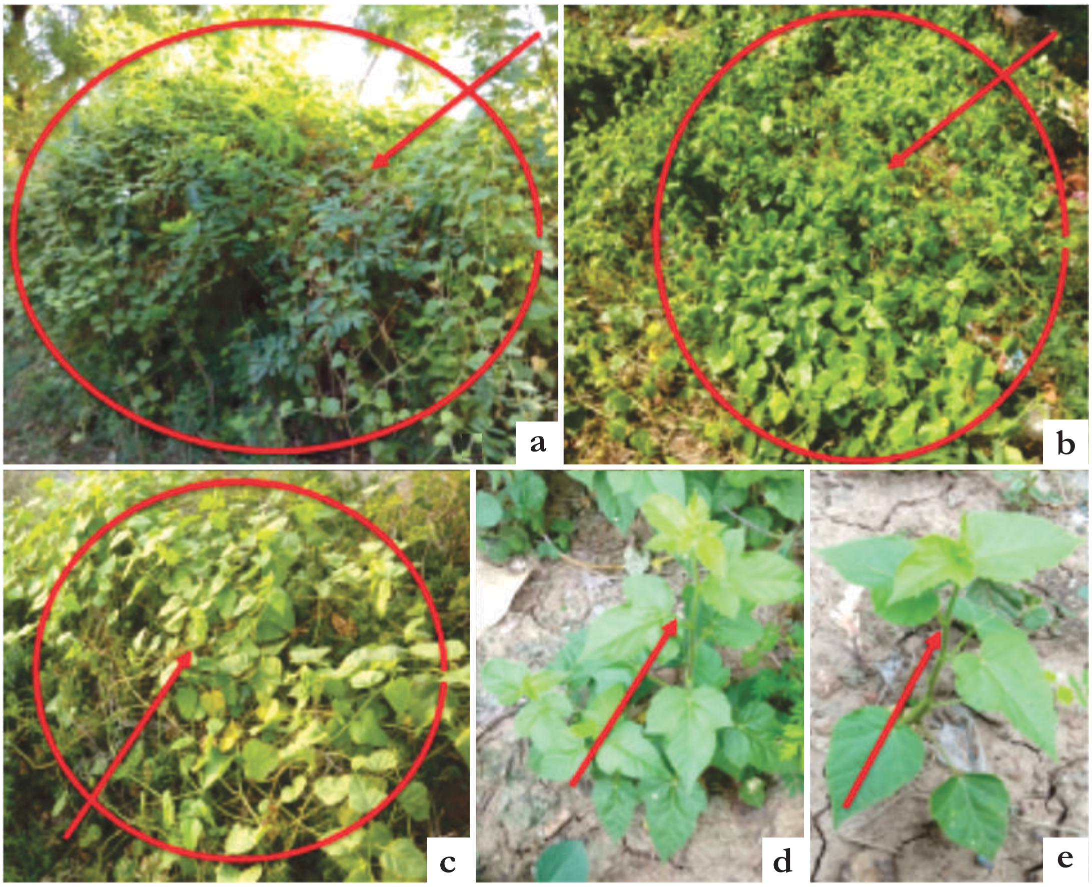

Figure 2 *Passiflora foetida* growing habit
Notes: a = climbing habit (vine); b & c = creeper habit; d & e = juvenile individual plant samplings.

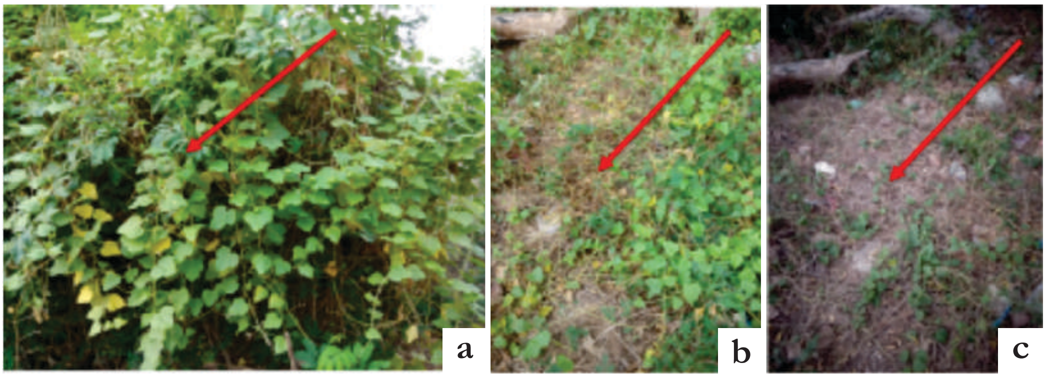

Figure 3 Different drying phases of *Passiflora foetida*

Our observation showed that fruit ripening season starts in October. Thereafter, the density of the flowering phase gradually decreases and the plant becomes dry in the period of April - May (Fig. 3a-c).

Flower Morphology

Our study showed that the flower blooming season (Fig. 4a-d) occurs earlier from the plants, emerged from the rootstock. Flowering season starts in August and ends in December, depending on soil types and moisture conditions.

The flower of *P. foetida* had dichromatic color by the corolla. The white flowers (Fig. 4b-d) were marked with a ring of radially oriented purple streaks as nectar guide (corolla). The flower was pedicellate (31 mm long), solitary, axillary. The flower occurred abundantly with dispersed pattern in individual flower. The flower was quite attractive during the flowering season.

Inflorescences were reduced to a single flower with opposite tendrils, 3 bracts, glandular pilose apically. Flowers were white with 31.0 ± 4.2 mm long and 53.2 ± 1.4 mm wide, solitary and had a minty fragrance. Radially symmetrical, bisexual flowers, 5 green sepals (25.6 ± 2.25 mm long and 9.2 ± 1.1 mm wide), 10 petals (18.0 ± 1.0 mm long and 7.9 ± 1.0 mm wide), 5 stamens (6.7 ± 0.7 mm long), corona with 3 - 5 seriate, filamentous, two outer series (10 mm long), inner three series 1 - 2.5 mm; operculum 1 - 1.5 mm, membranous; disk copular, gynoecium (20.2 ± 0.8 mm tall), 5 stamens (6.7 ± 0.7 mm long) coherent at the base, flat; anther oblong, ovary (3.4 ± 0.6 mm long), short stipitate, ellipsoid, glabrous; chambered ovary composed of three carpels (ovule-bearing segments), ovules (41.66 ± 5.47 mm long) attached to the inner ovary walls, 3 styles (8.4 ± 3.5 mm long) with green color, stigma capitate, green, ovoid-globose (2.4 mm long), glabrous. Seeds (23.33 ± 7.21 mm long), light brown to black, elliptic, 5.2 ± 0.8 mm long and 3.2 ± 0.7 mm wide.

Floral Biology

Our study showed that flowers on different individuals exhibited similar floral events. Mature buds opened in the early morning between 05:30 to 06:00 a.m. with the rise of the sun. All mature buds of the plant opened at the same time. No other single flower opened after 06:00 a.m.

The anthesis started from mature bud to completely open flower which took 30 minutes. Inside the mature bud (Fig. 4a), the corolla was wrapped and rotated. The anther dehiscence showed longitudinal slit at the time of anthesis and the pollens were unloaded on the stigmas.

The number of pollen grains per anther were 2,041.8 ± 25.83; per flower were 10,209.0 ± 129.15. The pollen-ovule ratio was 10,209.0 : 41.66. Pollen grains were light yellow, initially appeared sticky and later powdery.

The stigma attained receptivity at the mature bud and it continued up to the next 06:00 p.m. The stigma was captivating, shiny and sticky in the course of the receptive stage and occurred in three different heights with the anthers.

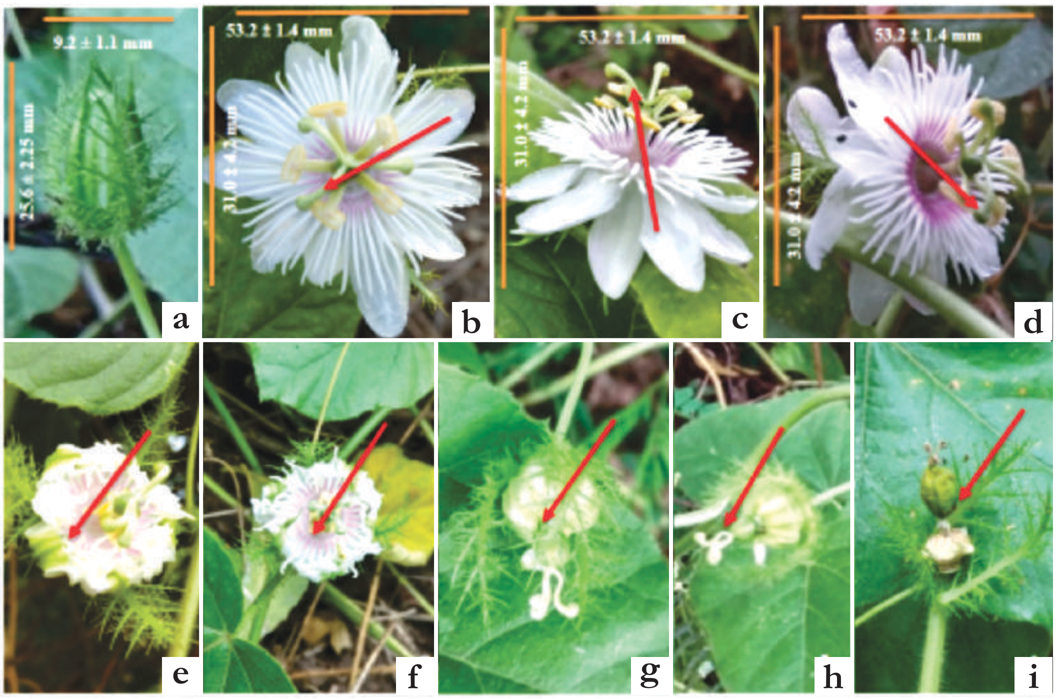

Figure 4 *Passiflora foetida* flowering mechanism
Notes: a = mature bud; b = flower (anthers below); c = flower with anthers above; d = flower with anthers below); e-f = Different phases in flower closing; g-h = closed flowers and fully curved stigma; i = unfertile flower or sterile flower in fruit formation.

In some cases, the stigma came back straight (90°) after the anthesis at 06:00 a.m. (Fig. 4g). In some cases, the stigma stayed the same. The ring-shaped nectar guide appeared on the corolla (Fig. 4b-d), nectar occurred around the ovary base and nectar quantity is good. The corolla closed and the stigma stood with the ovary (Fig. 4h) and protected with three bracts up to fruit mature. The pollinated and fertilized flowers remained and un-pollinated flowers fell off from the plant (Fig. 4i).

Pollination Mechanism

The stamens and stigmas stayed in three different heights in a flower (Fig. 5b-d). The anthers dehisced in the mature bud and discharged the pollen grains into anther tube. In this phase, the style erected by the anthers, while the stigma opened its branches into the stigmas and started curvature toward the anthers. Thus, the branched stigmas lay in three different positions in an individual flower. Sixty four percent of the flower's stigmas curved below the anthers (Fig. 5b). Simultaneously, the stigma attained receptivity, came closer and touched the anthers. Besides, this plant favored pollinators to landing on flowers and probed the nectar. Thus, the flowers exhibited autogamy and geitonogamy.

In the case of the second type flowers (Fig. 5c), the stigma stayed in an erect position (angle 70° to 90°). Stigma did not move toward the anthers. Thus, it impossible for pollen to contact with the stigma, unfavorable for pollination, very few get pollen, and most of them become sterile (Fig. 5i).

Finally, in the third type of flowers (Fig. 5d) the stigma curved partially above the anthers (angle between 0° and 45°). Thus, the stigmas did not have contact with the anthers, but it facilitated pollinator to landing and getting pollen from pollinators, which means the flowers avoiding self-pollination and promoting cross-pollination.

The bees approached the flowers to collect pollen and nectar by hovering. The bees actively bushed off the anthers to free the pollen from their anthers, to bind with the vertical sides of the insect body. The stigma was located above the anthers.

In this case, the body of the visiting forager got brash first. As a result, cross-pollination took place in the case the forager overtook another flower before the former. On the other hand, if the flower was the first visit for the pollinator, it ended with self-pollination. The nectar is robbed by bees which ruptured the nectar chamber wall and collected nectar.

Throughout the course, the style and its stigma branches (Fig. 5b-g) which were extended by anthers in the first 3 hours, would become erect and the tips were curved (Fig. 5d). In few situations, stigmas never came back to erect; it remained with the fruit and dried.

Breeding Systems

Anthers dehisce occurred in mature buds (Fig. 4a). Wild fruit set and seed set rated in flowers (Table 1) with fully curved stigma flowers (below the anthers) were 68% and 82.14%, respectively. The flowers facilitated favorable conditions for autogamy and geitonogamy and showed the highest fruit and seed set rate. In non-curved stigma flowers (above the anthers), the flowers exhibited 16% fruit set and 61.11% seed set rate. These lower fertilization rate was due to the absence of autogamy and in very few cases geitonogamy occurred (Table 1). Most of the time the flowers became sterile. Partially curved stigma flowers (above the anthers) displayed fruit and seed set rate of 44% and 73.07%, respectively, due to autogamy and geitonogamy (Table 1).

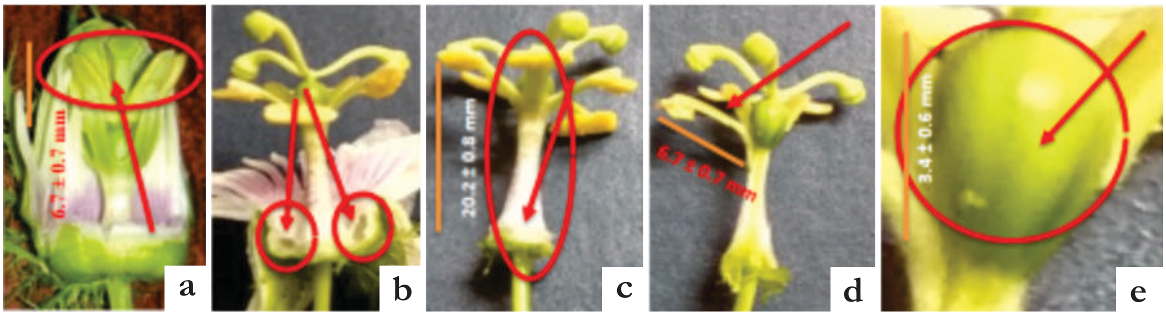

Figure 5. *Passiflora foetida* pollination mechanism
Notes: a = position of stigma and anthers in mature bud; b = clear view of nectar glands; c = gynisium; d = stamens; e = ovary.

Table 1 Seed set rate in a natural breeding experiment

Flower type in the plant	Observed flowers	Flowering frequency (%)	No. of flowers tagged	No. of fruits formed	No. of seeds formed	Fruit set (%)	Seed set rate (%)
Flowers with a fully curved stigma (below the anthers)	100	64	25	17	391	68.00	82.14
flower with non-curved stigmas (above the anthers)	100	16	25	04	44	16.00	61.11
Flower with partially curved stigmas (above the anthers)	100	20	25	11	209	44.00	73.07

Insect Pollination

Flower is the attraction unit for insect foragers. White flowers (Fig. 4b-d) marked with a ring of radially oriented purple streaks as nectar guide (corolla), are captivating to direct the insect foragers to nectariferous flower for collecting nectar/pollen. Bees visited flowers for nectar and pollen, while butterflies for nectar (Table 2).

The bees foraged at 08.00 to 12.00 a.m. with peak foraging activity occurred from 10.00 to 11.00 a.m. (Fig. 6). During this period the flowers contained a good quantity of nectar with mint or sweet smell which attracted the foragers to come toward the flowers. Finally, carpenter bees were the highest pollen grain carriers and dominant pollinator (Table 3).

Bees (84.82%) were the regular and consistent foragers, while the remaining were inconsistent foragers. Predominant forage visits were observed in peak flowering season. The bees were *Xylocopa latipes* L. (56.25%) and *Anthophora bicinta* F. (28.57%). The butterfly was *Danaus chrysippus* L. (16.32%) occasionally visited the flowers, but unable to collect nectar (Table 4).

Table 2 Insect foragers on *Passiflora foetida*

Order	Family	Scientific name	Vernacular name	Forage target
Hymenoptera	Anthophoridae	*Xylocopa latipes* L.	Carpenter bee	Nectar
		Anthophora bicincta F.	Blue-banded bee	Pollen+ Nectar
Lepidoptera	Nymphalidae	*Danaus Chrysippus* L.	Plain tiger	Nectar

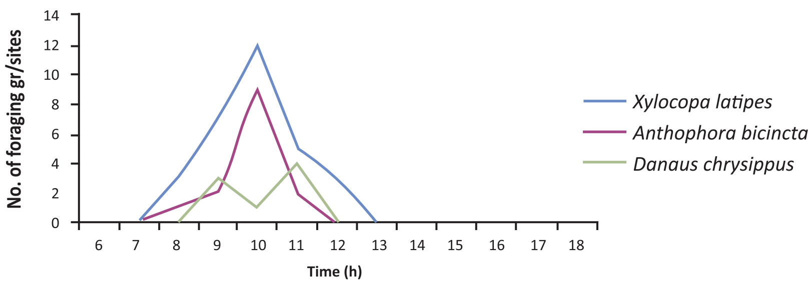

Figure 6 Hourly foraging activity of insects on *Passiflora foetida*

Table 3 Pollen production through the body rinsing experiment on bees and butterflies

Name of the insect species	Sample (N)	Number of pollen grains		
		Range	Mean	SD
Bee				
Xylocopa latipes	10	22 - 64	47.5	22.39
Anthophora bicincta	10	41 - 92	71.2	24.25
Butterflies				
Danaus chrysippus	10	26 - 64	35.6	12.55

Table 4. Percentage of pollinator visits during the flower opening time

Pollinator name	No. of times pollinator visited the flower	Percentage of pollinator visits
Xylocopa latipes	27	56.25
Anthophora bicincta	14	28.57
Danaus chrysippus	08	16.32

Notes: Pollinator visits were counted from 06.00 a.m. to 06.00 p.m. The percentage of pollinator visits were calculated by using the formula: (Each pollinator visit/total visits of the pollinators) x 100%. The observation was carried out for 25 days and given average values.

Fruiting Ecology

The plant produced fruits starting from October. Each plant bore 48.33 ± 26.85 fruits (Fig. 7a). Fruits were spread radially around 5 m from the mother plant. The fertilized flowers produced numerous ellipsoid-seed fruits within four weeks (Fig. 7g-h). The fruits (21.4 ± 4.8 mm long and 17.1 ± 3.8 mm wide) were initially green. After ripening, the fruit color turned to red or orange (Fig. 7b-d), surrounded by finely dissected, needle-like bracts, pulpy sweet taste covered by thick skin (Fig. 7f). Each fruit contained 23.33 ± 7.21 seeds (Fig. 7f). Although young fruits are toxic and cyanogenic, ripen fruits are edible and taste like *Passiflora edulis* L. fruits. Matured and ripened fresh fruits were eaten and dispersed by birds, animals, and humans (Fig. 8a-j).

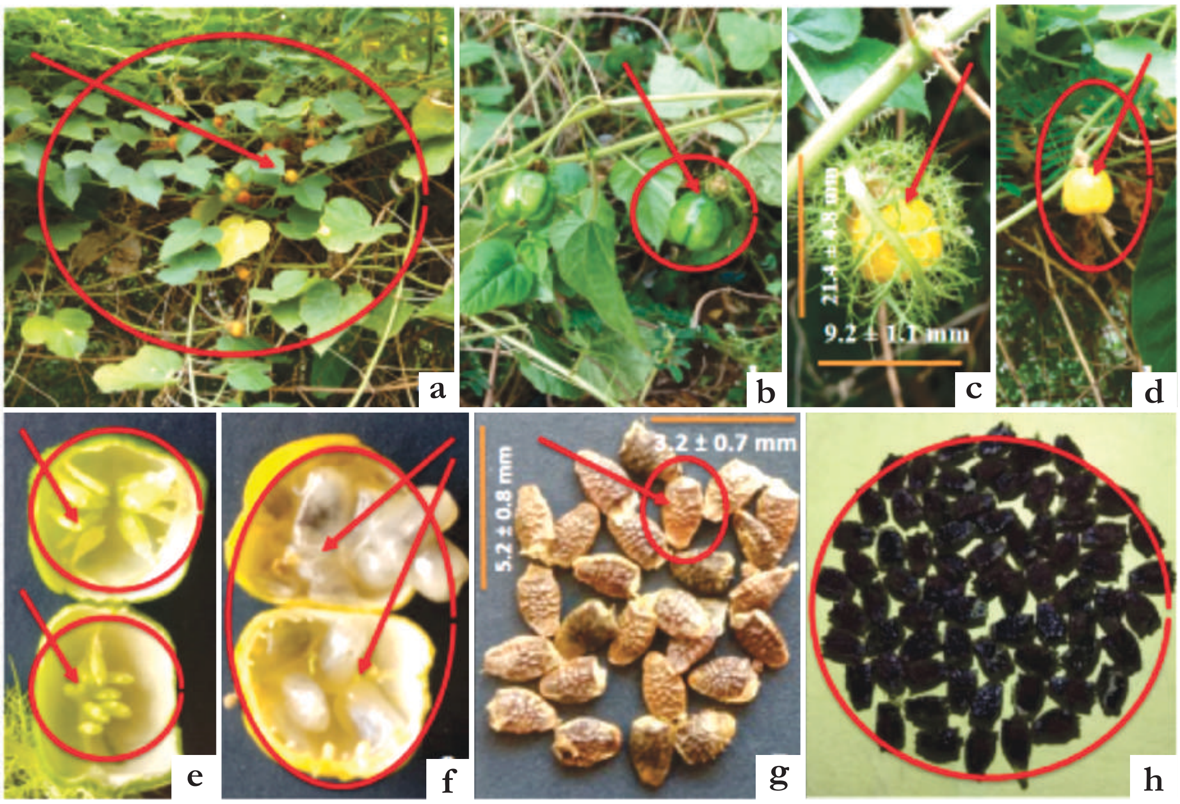

Figure 7 *Passiflora foetida* fruiting ecology
Notes: a-b = fruiting phase of the plant; c-d = ripened fruit with and without bract; e = immature fruit seeds; f = ripened fruits with pulpy seeds; g = seeds in brown color; h = seeds in black color.

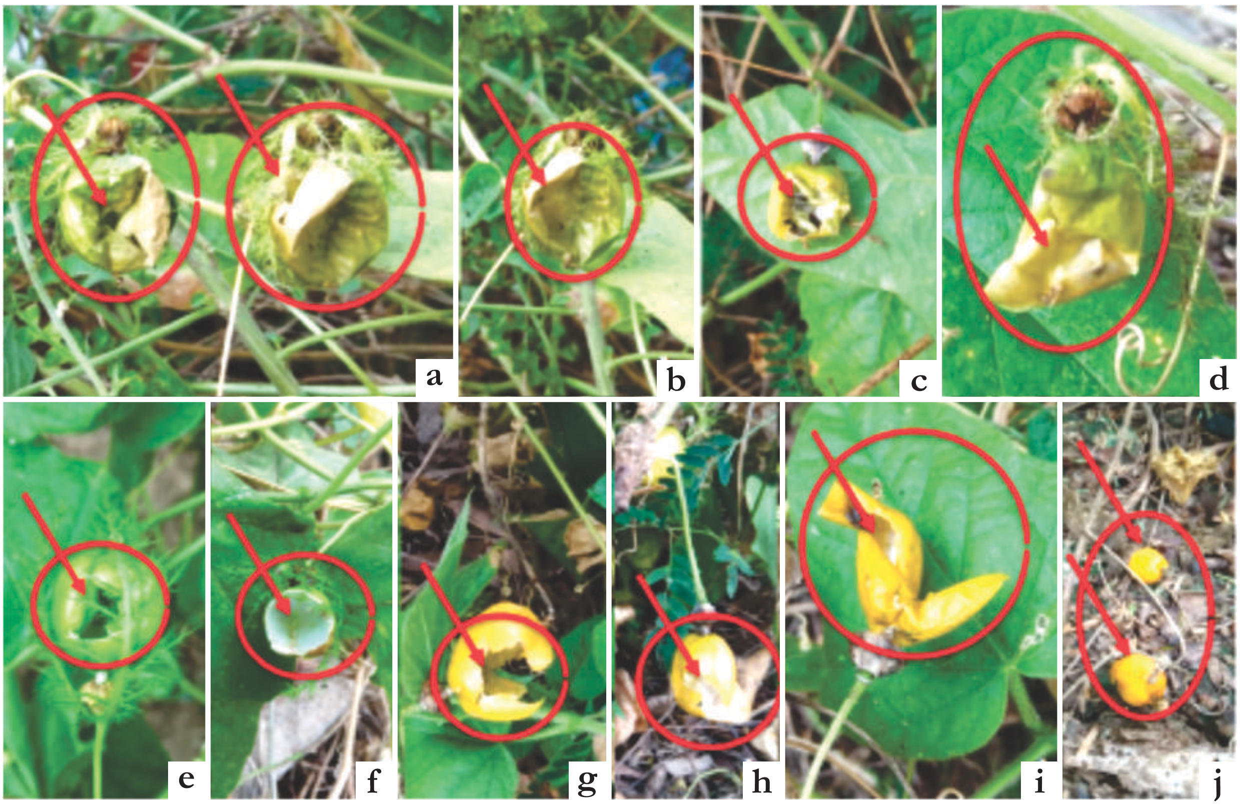

Figure 8 *Passiflora foetida* fruit eaten and dispersed
Notes: a-i = fruits ruptured by birds, bats and animals for the sweet pulp; j = ripened fruits fell and dispersed from the mother plant.

Seed Ecology

The elliptic seeds were pulpy (5.2 ± 0.8 mm long and 3.2 ± 0.7 mm wide) with black or brown color (Fig. 7g-h) and crowned thick seed coat. Seedling growth is determined by the soil moisture and soil nutrients availability. Seeds generate easily and produce mature plants in two to three months after its start flowering and fruiting. Field observations showed that seeds did not have dormancy, germinated in two weeks after dispersal. The seeds usually germinate during the rainy season (June). When the seeds are sowed in pots and watered regularly, the seeds germinate after 6 months. In natural areas, the plants can grow up to two to three generations in a year based on the soil moisture and nutrient availability.

Flowering and Fruiting Mechanisms

Passiflora foetida grows in deciduous climatic regions with both wet or dry and rocky sites. Leaf flushing is followed by flowering and fruiting. Each plant produces dichromatic solitary white flowers and a clear investigation of the flowers in the same or different plant population identified that three different types of flowers (heteromorphous). *P. foetida* exhibits three various heights of the stigma concerning anthers positions. Based on the curvature of style in floral opening or anthesis, the pollination mode, fruit set, and seed set are determined. *Passiflora foetida* produces fruits by induced self- and open pollination. In self-pollination, the floral biology we conducted indicated three different types of flowers-based stigma position variation which produce different fruit set and seed set (Rendon *et al.* 2013). The same study showed the highest percentage of fruit formation found in geitonogamy (86%).

In passion fruit (*P. edulis* f. *flavicarpa*) pollen viability stays up to 24 hours from flower anthesis (Santos *et al.* 2011). Subsequently, fruit set depends on the flower opening time in *P. foetida* flower opening with the sunrise (Garcia & Hoc 1998). However, in other species, such as *P. edulis* f. *flavicarpa* (passion fruit), the anthesis starts after 12: 00 noon in most production areas (Santos *et al.* 2011).

Among the Brazilian states, Bahia stands out for the significant occurrence of *Passiflora* species. *Passiflora capsularis* reproductive systems exhibit self-pollination (62.5%), intra-specific (68.7%), and inter-specific (48.4%) fertilization in flowers. *P. rubra*, however, exhibites 67.2% self-pollination, 62.5% intra-specific, and 46.9% inter-specific, respectively, which means the *Passiflora* genus can reproduce both by self-pollination and cross-pollination with a success rate of ≤ 50% (Amorim *et al.* 2011).

A previous study on *Passiflora foetida* L. breeding systems showed that sexual reproduction promoted both cross-pollination and autogamy, depending on the requirement (Raju PS & Raju AJS 2022). Soares *et. al.* (2015) conducted experiments on reproductive systems and pollen viability in this regard. Eleven Passifloraceae species were tested under controlled pollination in field conditions. Among all 11 species, the 6 species were self-incompatible and 5 species were self-compatible species. The same study explained inter-specific hybridization possibilities successfully and produced fruits and seeds (Soares *et. al.* 2015).

The flowers encourage cross-pollination and neglect self-pollination which means pollinators play a key role in fruit formation. *Xylocopa latipes* L. is the major pollinator for *P. Foetida* flowers. *Anthophora bicinta* F. and butterfly *Danaus chrysippus* L. occasionally visit the flowers in pollination aspects.

In Central Brazil, research recorded 27 pollinators (bees) on yellow passion fruit flowers, 12 effective and 5 occasional pollinators in between 2004 to 2007 (Yamamoto *et al.* 2012). Garcia and Hoc (1998) stated that Hymenoptera species are the most often and constant visitors. *Ptiloglossa tarsata* (Colletidae) always touches the anthers and the stigmas while aspirating nectar, hold a high percentage of *P. foetida* pollen and visit flowers. *Pseudaugo chloropsis* sp. (Halictidae) rarely contacts anthers and stigmas while puncturing the limen to access the nectar. They are nectar robbers. *Augochlorella* sp. (Halictidae) gathers pollen without touching the stigmas. They are pollen thieves (Garcia & Hoc 1998). *Passiflora foetida* hosted the larva of *Acraea violaae* butterfly and in the same research explained no seed dormancy period. Seeds germinate 3 - 10 days after the swoon (Lade *et al.* 2015).

The administration of *P. foetida* extract enhances the antioxidant levels in diabetic rats

(Ravi *et al*. 2015). Genetic hybrids were developed in *Passiflora* for achieving ornamental potential (Santos *et al*. 2011). CSIRO Ecosystem Science in Australia conducted research project to understand the invasive possibilities, threats and solution on *Passiflora foetida* L. invasion in Kimberley and Pilbara.

Results of our study showed that P*assiflora foetida* dispersed a longer distances through birds, bats and other animals due to its seductive pulp-protected seeds. Souza *et.al*. (2022). conducted an experiment to cultivate the passion fruit by supplying saline water to the *P. foetida* L. roots tocks and injurious effects were observed in plant growth (Souza *et al*. 2022).

CONCLUSION

Passiflora foetida is herbaceous seasonal climber weed, hermaphrodite, self-compatible and facultative xenogamous species. Flowers facilitate melittophily pollination mechanism. The ripened fruits were eaten by birds and animals, which disperse the seeds to farther distances.

The seeds germinate and start to grow with old perennial root stocks and continue to propagate. *P. foetida* flowers are used for decoration and fruits are edible. India has good possibilities like other countries to cultivate passion fruit as agricultural products.

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