



Pollination ecology of a rare prostrate herb, *Rhynchosia capitata* (Heyne ex Roth) DC. (Fabaceae) in the Southern Eastern Ghats, Andhra Pradesh, India

Aluri Jacob Solomon Raju^{1✉}, Banisetti Dileepu Kumar², Kunuku Venkata Ramana³

1. Department of Environmental Sciences, Andhra University, Visakhapatnam 530 003, India

2. Department of Botany, M R College (Autonomous), Vizianagaram 535 002, India

3. Department of Botany, Andhra University, Visakhapatnam 530 003, India

✉Correspondent author:

A.J. Solomon Raju,
Department of Environmental Sciences, Andhra University,
Visakhapatnam 530 003, India
Email: solomonraju@gmail.com

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ABSTRACT

The current study aims to investigate the pollination mechanism, sexual system, breeding system, pollinators and seed dispersal in *Rhynchosia capitata*, a rare prostrate herb in the southern Eastern Ghats, Andhra Pradesh, India. The study indicated that *R. capitata* is a prostrate, climbing herb and winter season bloomer. It is hermaphroditic, self-compatible and facultatively xenogamous which is essentially vector-dependent. The flowers are papilionaceous with zygomorphic symmetry and exhibit explosive pollination mechanism associated with primary pollen presentation pattern. Nectar analysis showed that the flowers are sucrose-rich with moderate sugar concentration indicating that the plant is melittophilous which is substantiated by field observations. Bees trip the keel petals that release the reproductive column due to which pollination takes place. Dry pods dehisce explosively but seeds remain attached to the pod wall. The seeds fall to the ground gradually and germinate during rainy season. But, many seedlings soon perish due to rocky habitat, intermittent rains and long dry spells within rainy season. The perennial root stock also produces new growth and initiates reproductive cycle.

Keywords:

Rhynchosia capitata; hermaphroditism; explosive pollination mechanism; melittophily

1. INTRODUCTION

The genus *Rhynchosia* L. consists of approximately 200 species and distributed in both the eastern and western hemisphere in warm temperate and tropical regions (Gear, 1978). In India, Madhava Chetty et al. (2008) reported that 12 *Rhynchosia* species, *R. beddomei*, *R. rufescens*, *R. suaveolens*, *R. cana*, *R. albiflora*, *R. capitata*, *R. courtollensis*, *R. densiflora*, *R. heynei*, *R. minima*, *R. rothii*, *R. rufescens*, *R. suaveolens* and *R. viscosa* occur in the southern Eastern Ghats of Andhra Pradesh. Of these, *R. capitata* has been reported to be distributed in the hills of Cuddapah and Ananthapur in Andhra Pradesh and Coimbatore in Tamil Nadu, India (Gamble, 1935). Later, different authors reported that *R. capitata* is an emerging annual summer weed and indigenous to Pakistan, India and Sri Lanka (Jahan et al. 1994; Dogra et al. 2009; Ali et al. 2012).

Little information is available on the pollination ecology of *Rhynchosia*. Franco (1995) reported that *Rhynchosia* is autogamous and pollinated by *Hypanthidium* sp. and *Centris* sp. Craufurd and Prins (1979) reported that *R. sublobata* is self-compatible and pollinated by *Xylocopa* bees. Etcheverry et al. (2011) reported that *R. edulis* with facultative xenogamy and *R. senna* var. *texana* with obligate xenogamy exhibit valvular pollination mechanism. Solomon Raju and Venkata Ramana (2017) reported that *R. cana* is self-compatible and principally pollinated by bees. Keeping this state of information in view, the present study was carried out on the pollination ecology of *R. capitata* distributed in the southern Eastern Ghats of India. This species is a rare non-prolific prostrate climbing herb confined to rocky terrain. It is used in traditional medicine (Ahmad, 2014; Sarvalingam and Rajendran, 2015), in food preparations (Tayade and Patil, 2006) and as fodder (Vardhana, 2006). The work reported in this paper is useful to understand the pollination ecology of *R. capitata* and its limitations contributing to its rarity in the study region.

2. MATERIALS AND METHODS

The study area

Populations of *Rhynchosia capitata* populations growing in Sahasra lingalakona and Srikalahasti in Chittoor District, Andhra Pradesh, India (13°41'N latitude and 79°42'E longitude, 2,401 ft altitude) were used for study during July 2015-July 2017. The site is characterized by a combination of rocky, undulating terrain with some litter content formed from grass and other herbaceous plants in the crevices and cracks of the rocks (Figure 4a-c). The climate is chilly in winter and cool and pleasant during summer. The Southwest monsoon (June-September) accounts the major proportion of the rainfall and the study areas receive high rainfall (1115 mm) when compared to other nearby places which receive on average 600 mm of rainfall. The temperature ranges from 40°C to 42°C during March to May at foot hills while that at the top of the hills ranges from 30°C to 37°C (Madhavachetty et al. 2008).

Flowering phenology and morphology

Observations regarding the organization of inflorescences, the spatial positioning of flowers, and their position on the plant in the field. Ten inflorescences, one each on a different plant were tagged and followed to quantify the daily flower production rate and

record the length of flowering and the number of flowers produced. Twenty five mature buds were marked and followed to record anthesis rate at each hour during anthesis period and the same flowers were used to record the time of anther dehiscence. The presentation pattern of pollen during anther dehiscence was observed visually and confirmed by observing the anthers under a 10x hand lens. The details of flower morphology such as flower sex, shape, size, colour, odour, sepals, petals, stamens and ovary were described based on a sample of twenty flowers collected randomly from ten plants. Ten plants selected at random were tagged prior to the commencement of flowering and followed daily to record the number of flowers produced during their flowering period. The total numbers of flowers produced were compiled week- and month-wise to understand the flowering pattern.

Floral biology

Twenty mature but un-dehiscent anthers were collected from five randomly chosen plants and placed in a Petri dish. The pollen output per anther and pollen-ovule ratio was calculated using the protocol given by Cruden (1977). Individual volumes of nectar were recorded for twenty five flowers and then the average volume of nectar per flower was determined and expressed in μl . The flowers used for this purpose were bagged at mature bud stage, opened after anthesis and squeezed nectar from each flower into micropipette to measure the volume of nectar. The nectar sugar concentration was determined using a Hand Sugar Refractometer (Erma, Japan). Nectar analysis for sugar types was done as per the Paper Chromatography method described in Dafni et al. (2005). The sugar content/flower is expressed as the product of nectar volume and sugar concentration per unit volume, $\text{mg}/\mu\text{l}$. This was done by first noting the conversion value for the recorded sugar concentration on the refractometer scale and then by multiplying it with the volume of nectar/flower. Table 5.6 given in Dafni et al. (2005) was followed for recording the conversion value to mg of sugars present in one μl of nectar. Stigma receptivity duration was tested using the protocol given by Dafni et al. (2005).

Breeding system

Fifty mature buds, five each from ten plants were used for each breeding system. The buds were bagged without manual pollination for autonomous autogamy; the stigmas were pollinated with the pollen of the same flower manually for autogamy; the emasculated buds were pollinated with the pollen of a different flower on the same plant for geitonogamy and with the pollen of another plant for xenogamy. Then, all these pollinated flowers were bagged and followed to record fruit set rate. Further, one hundred and sixty seven flowers on fifty plants were used to record fruit set rate in open-pollinations.

Insect activity and pollination

The flower visitors included bees only. They were collected and identified with the representative identified bee specimens available with the Department of Environmental Sciences, Andhra University, Visakhapatnam. The bees were observed carefully for ten hours in a day for ten days in different weeks each year. During the days of observation, the hourly foraging visits of each species were recorded for which approximately seventy flowering inflorescences were selected. The data obtained was used to calculate the percentage of foraging visits made by each species per day. Simultaneously, the bees were observed for their foraging behavior such as mode of approach, landing, probing behaviour, the type of forage they collected, contact with essential organs to result in pollination, inter-plant foraging activity. The bees were captured from the flowers during 1000-1200 h on five different days for pollen analysis in the laboratory. For each bee species, 10 specimens were captured, washed 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 to record their pollen carrying capacity.

Fruiting ecology, seed dispersal and germination

Fifty fruited flowers were tagged and followed to record the duration of fruit maturation. Seed characteristics were examined carefully to note their adaptations for dispersal mode. Field visits were made continuously at weekly intervals to record the time of seed germination. Further, observations were made on the root stock remains of the plants to record whether new growth occurs and if so, whether they continue vegetative growth, flowering and fruiting. Quantitative studies were not done on seed germination and seedling aspects at the study site because of restrictions imposed by the local forest authority.

3. RESULTS

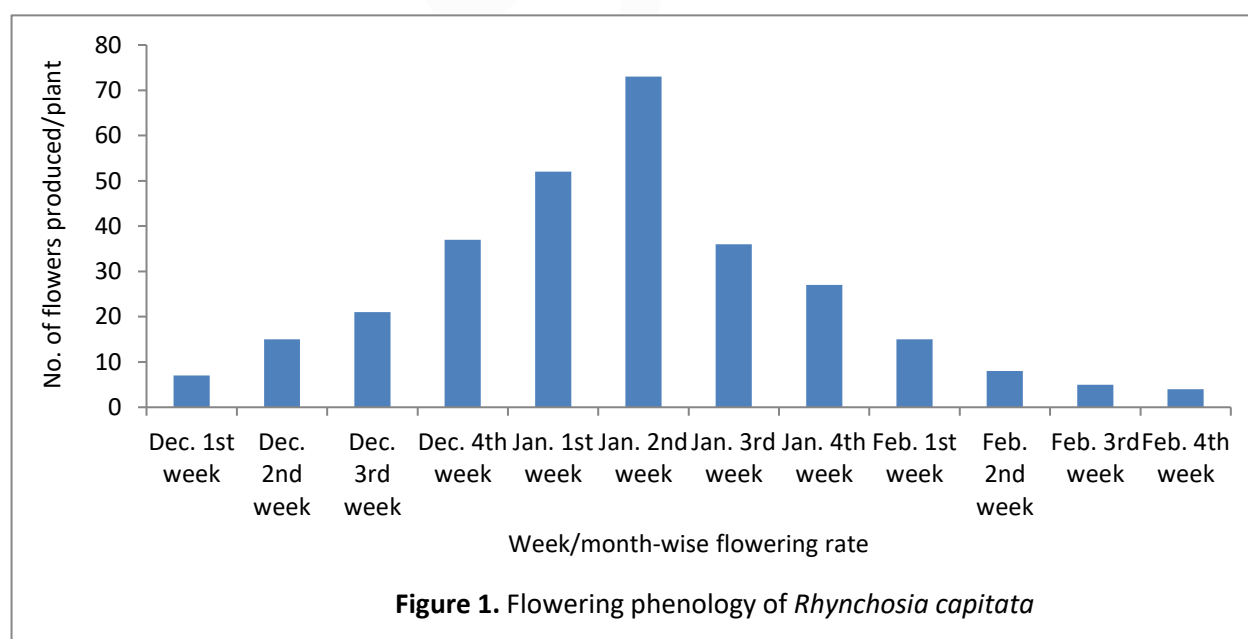
Phenology

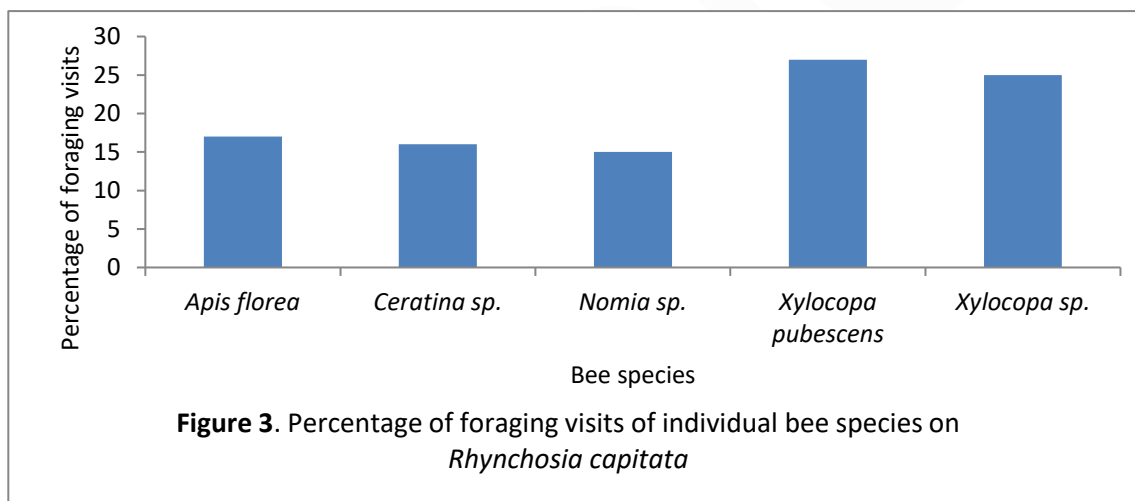
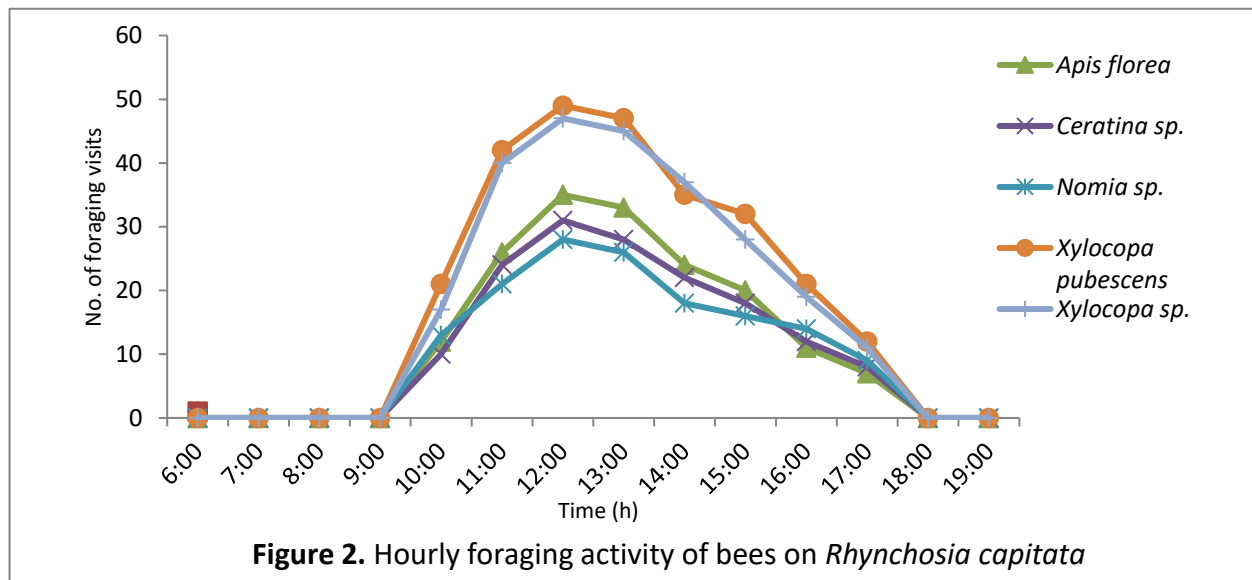
It is a perennial prostrate, climbing herb with hispid spreading branches and branchlets. It grows in cracks and crevices of rocks with little soil content; it can be seen climbing the rocks during growing season. The plant re-grows from perennial root stock embedded in rocky areas and from the seed during wet season from July to October during which growth and leaf flushing occurs. Cordate,

hispid and 2-3 mm long stipules are present at the base of the leaves. The plant produces compound trifoliolate leaves with reticulate venation; the obovate-suborbicular and slightly coriaceous leaflets are attached to the tip of the elongated and hispid petiole. The flowering occurs during December-February with peak flowering in January. The plants wither and disappear in late-March/April. At plant level, the flower production rate gradually increased from the 2nd week of December to 2nd week of January and then onwards gradually decreased until flowering ceased. The flower output per plant averaged to 283 (Range 280-302) out of which 27% was recorded in December, 63% in January and 10% in February (Figure 1). The flowers are pedicellate (5-6 mm long) and borne in pedunculate (20-30 mm long) axillary umbellate racemes which are situated opposite to petiolate compound leaves. Individual racemes produce 6-8 flowers which open over a period of 3-4 days (Figure 1d,e).

Flower morphology

The flowers are small (17.8 ± 0.9 mm long and 20.7 ± 1.1 mm wide), yellow, odorless, papilionaceous, zygomorphic and bisexual. The calyx is purplish brown, pilose, gland-dotted and consists of 5 free oblong sepals; the lower sepal is 19 mm long while all other four sepals are 7-8 mm long. The corolla is bright yellow, pubescent, specialized and consists of upper standard petal, two wing petals and two keel petals. The standard petal is large (14.4 ± 0.3 mm long and 13.6 ± 0.4 mm long), yellow, obovate with scattered reddish-brown lines which serves as nectar guide; the petal base is clawed and consists of two inflexed fingernail auricles. The standard petal envelops the rest of the petals in bud but reflexes when the flower blooms. The two adjacent yellow petals (14.9 ± 0.7 mm long and 4.2 ± 0.5 mm wide), called wing petals surround the two bottom white petals, called keel petals (13.8 ± 0.6 mm long and 4.4 ± 0.4 mm wide). The keel petals form a proximal cylindrical part and a distal part consisting of a pressed angular pouch, with porate tip in which the stamens and stigma are housed. The keel and the wing petals are attached by means of two notched folds. The wing petals serve as alighting platform for insects visiting the flowers. The stamens are ten, 16.9 ± 0.9 mm long, diadelphous (Figure 4n,o); nine filaments are fused basally into a sheath while they are open along the upper side while the tenth filament is free and lies on the others. The distal parts of the filaments are free and tipped with 1.4 ± 0.5 mm long uniform dithecous anthers. The ovary is sessile, green, villous, 3.7 ± 0.7 mm long and lies in the sheath of the filaments along the cylindrical part of the keel (Figure 5a,b). It is monocarpellary and monolocular with two ovules arranged on marginal placentation (Figure 5d,e). It has a long glabrous style with a capitate wet shiny stigma (Figure 5c), both together measure 13.2 ± 0.4 mm in length. The stigma is situated slightly above the anthers. The distal portion of free filaments and style and stigma are incurved and clamped into the keel petals.





Floral biology

Mature buds open during 1000-1500 h with peak anthesis at 1100 h (Table 1; Figure 4k). Unfolding of the standard petal from wing petals is a sign of anthesis (Figure 4j). The keel petals remain in folded position as in mature bud stage (Figure 4f-i, l,m). All anthers in a flower dehisce simultaneously by longitudinal slits in mature bud stage (Figure 4p). The pollen out per anther is $1,936.2 \pm 128$ and per flower is 19,362. The pollen-ovule ratio is 9,681 : 1. The pollen grains are monads, spheroidal, $30.43 \pm 4.04 \mu\text{m}$ in size, powdery, yellow and tricolporate, angulaperturate with reticulate exine (Figure 4q). Nectar secretion is initiated during mature bud stage by a nectary disc present at the base of the ovary and its secretion ceases an hour after anthesis. A flower produces $1.4 \pm 0.03 \mu\text{l}$ of nectar with 0.44 mg of sugar. The nectar sugar concentration is 28% (Range 26-31%) consisting of sucrose, glucose and fructose with the first one as dominant. The ambient temperature during this period varied from 25 to 30°C while the relative humidity varied from 81 to 65%. Nectar is deeply concealed and it is open through two windows between the joined and the free filaments at the flower base. The stigma is receptive during anthesis and ceases its receptivity after three hours. Then, the standard, wing and keel petals gradually close back enveloping the reproductive organs. The closed flowers remain so even during fruit development. The calyx initially encloses the ovary and subsequently turns light brown and discloses the ovary since the latter gradually bulges and develops into a seeded pod.



Figure 4. *Rhynchosia capitata*: a-c. Study area – Sahasralingala Kona near Ramapuram village, Srikalahasti – Prostrate climbing herb in flowering phase, d. Twig with spent flowers, e. Flowering inflorescence, f-i. Different stages of flower development, j. Standard petal (dorsal side), k. Flower, l & m. Wing and keel petals together with stamens and stigma inside, n & o. Diadelphous stamens and stigma, p. Dehisced anthers, q. Pollengrain.

Table 1 Anthesis as a function of time in *Rhynchosia capitata*

Time (h)	No. of flowers anthesed	Percentage of Anthesis
0900	0	0
1000	21	16
1100	39	30
1200	32	24
1300	21	16
1400	13	10
1500	5	4
1600	0	0

No. of mature buds tagged: 131

Pollination mechanism

The reproductive column is held under pressure within the keel in open flowers and gets exposed when the pollinator presses the wing and the keel petals downwards. When insects land on the wing petals, the latter causes the keel petals to release the reproductive column violently. In consequence, the reproductive column snaps forward against the standard petal causing most of the pollen instantly released and the pollen thus released comes into contact with the ventral side of the insect body. Since the incurved stigma is situated above the height of the anthers, it strikes the insect body first due to which cross-pollination occurs if the insect carried pollen of other flowers on its ventral side and also then the pollen ejected from the anthers powders the ventral side of the insect instantly. If it is the first visit for the insect to the flower, then it effects self-pollination upon explosive release of

reproductive column from the keel petals. With the departure of the insect from the flower, the reproductive column does not return back to its former position but the keel moves forward partly covering the stamens and stigma. The downward movement of keel petals occurs in each subsequent foraging visits by appropriate insects. If the flower is untouched or tripping to keel did not occur, the reproductive column remains enclosed in the keel petals and falls off subsequently upon withering without fruit set.

Breeding systems

In mature buds and flowers, spontaneous autogamy is totally absent. Fruit set is 22% in hand-pollinated autogamy, 36% in geitonogamy, 90% in xenogamy and 42% in open-pollination (Table 2).

Bee pollinators and pollination

Insects visited the flowers from the time of anthesis and until 1700 h with peak foraging activity during 1200-1300 h. The foraging activity gradually increased with the gradual increase in the anthesis rate and later there is a gradual decrease in foraging visits due to a gradual increase in the number of closed flowers (Figure 2). Insects were exclusively bees, *Apis florea*, *Ceratina* sp., *Nomia* sp., *Xylocopa pubescens* and *Xylocopa* sp (Table 3). Of the total foraging visits, *Xylocopa* bees made 52% while the other bee species made 48%. Individually, *A. florea* 17%, *Ceratina* sp. 16%, *Nomia* sp. 15%, *Xylocopa* sp. 27% and *X. pubescens* 25% of total foraging visits (Figure 3). The bees showed variation in the pollen carrying capacity; the average pollen carried by *A. florea* was 78.4, *Ceratina* sp. 24.7, *Nomia* sp. 288.7, *Xylocopa pubescens* 1,552 and *Xylocopa* sp. 1,123 (Table 4). The flowers were visited several times by bees but new visits lasted shorter than the first one. Sometimes, the bees abandoned their intention of browsing on previously visited flowers upon landing. With respect to their behavior, the bees landed on the wing petals and the keel, with their head near the standard petal. They then exerted pressure with legs on the wing petals until these and the keel bent downwards, and then proceeded to collect nectar during which the bee's abdomen appeared pollen-smothered. The pollen collecting bees took "U" turn after nectar collection and proceeded towards the stamens to collect pollen.

Table 2 Results of breeding systems in *Rhynchosia capitata*

Pollination mode	No. of flowers pollinated	No. of fruits formed	Fruit set (%)
Autogamy (un-manipulated and bagged)	50	0	0
Autogamy (hand-pollinated and bagged)	50	11	22
Geitonogamy	50	18	36
Xenogamy	50	45	90
Open-pollination	167	71	42

Table 3 List of insect foragers on *Rhynchosia capitata*

Order	Family	Sub-family	Genus	Species	Common Name	Foraging schedule	Forage collected
Hymenoptera	Apidae	Apinae	<i>Apis</i>	<i>florea</i> F.	Dwarf honey bee	1000-1700	Nectar + Pollen
			<i>Ceratina</i>	sp.	Small carpenter bee	1000-1700	Nectar + Pollen
		Nomiinae	<i>Nomia</i>	sp.	Alkali bee	1000-1700	Nectar + Pollen
		Xylocopinae	<i>Xylocopa</i>	<i>pubescens</i> Spinola	Large carpenter bee	1000-1700	Nectar
			<i>Xylocopa</i>	sp.	Larger carpenter bee	1000-1700	Nectar

Table 4 Pollen recorded in the body washings of bee foragers on *Rhynchosia capitata*

Bee species	Sample size (N)	Number of pollen grains		
		Range	Mean	S.D
<i>Apis florea</i>	10	22-184	78.4	62.6
<i>Ceratina</i> sp.	10	15-42	24.7	8.65
<i>Nomia</i> sp.	10	231-324	288.7	32.8
<i>Xylocopa pubescens</i>	10	926-2167	1552	454.0
<i>Xylocopa</i> sp.	10	678-1568	1123	367.9



Figure 5. *Rhynchosia capitata*: a. Gynoecium, b. Ovary covered with hair, c. Capitulate stigma, d & e. Ovary with two ovules, f. Fruited inflorescence, g. Fruit, h. Re-growth from perennial root stock, i. New plant from seed.

Fruiting ecology and seed dispersal

The fruits mature within three weeks (Figure 5f,g). The sepals enclose the growing fruit initially and the fruit bulges out of the sepals later. Fruit is a pod which is green initially and brown to dark brown when ripe and dry. It is non-fleshy, transversely striated or wrinkled, softly pilose, glandular, circular to narrowly oblong, 12.9 ± 1.4 mm long, 11.3 ± 0.9 mm wide, compressed with one or two-seeds.

The bi-valvate dry fruits dehisce elastically exposing the seeds. The seed is reddish brown to black, compressed, sub-reniform, glabrescent, 4.5 ± 0.5 mm long, 3.6 ± 0.4 mm wide and shiny with a prominent strophiole. Depending on the state of seed in terms of its dryness, the seed is either scattered into the air or remains attached to the fruit wall. Seeds germinate during wet season which starts from June onwards (Figure 5i). Seedlings grow continually but their growth is regulated by the moisture status of the soil. Further, the root stock embedded in the crevices and cracks of the rocks (Figure 5h) produce new growth quickly and initiate flowering prior to the plants produced by seed. However, the flowering in both cases is confined to December-February only.

4. DISCUSSION

Rhynchosia capitata is a prostrate climbing herb which shows growth from perennial root stock embedded in the soil of rocky caves, crevices and cracks during rainy season. It also produces new plants from seed stock at the same time. Full leaf flushing occurs by the end of October and then onwards, floral bud initiation takes place. The flowering season is well defined and confined to winter season. Flowers are quite prominent due to their bright yellow colour and borne opposite to the petiolate trifoliate compound leaves which are horizontally spread on the rock surface. But, the plant has scattered distribution with small patches and isolated individuals here and there and in effect, it is not able to attract many species of insects.

In *R. capitata*, the flowers are homogamous, self-compatible and autogamy takes place only when flower foragers trip the keel petals to release the reproductive column. Fruit set in this mode is evidenced in manual pollinations. This situation indicates that

the receptive stigma inside keel petals blocks the germination of self-pollen and it requires rupture on its surface by pollinators for regulating self-pollination rate and promoting cross-pollination rate. Lloyd and Schoen (1992) reported that the stigmatic membrane prevents spontaneous self-pollination in certain members of the tribe Phaseoleae. The peri-stigmatic hairs present in these members facilitate maximization of out-crossing by preventing self-pollen deposition on the stigmas during the stages of anthesis. In these members, the stigmatic membrane has thick cuticle and requires a rupture which is caused by the pollinator during flower visit. Shivanna and Owens (1989) stated that the rupture of the stigmatic surface by pollinators permits the pollen to germinate in the flowers of Phaseoleae members with thick stigmatic cuticle. In *R. capitata*, the stigmatic surface appears to have thick cuticle and does not have the mechanism of causing spontaneous rupture to facilitate spontaneous autogamy. In effect, the tripping of keel petals appears to be essential to cause rupture on the stigmatic surface by the tripping agent due to which there is more likelihood of the occurrence of either geitonogamy or xenogamy. The fruit set rates recorded in hand-pollinated geitonogamy and xenogamy also substantiate that the plant is facultative xenogamous, a breeding system that is flexible and keeps the options open for both selfing and out-crossing mediated by pollen vectors.

Schrire (1989) stated that the ecological and evolutionary success of Leguminosae is related to biotic pollination mechanisms. The three sub-families within this family have achieved a characteristic floral architecture but the plants in the sub-family Papilionoideae have developed the most complex floral mechanism and also have zygomorphic flowers that are mainly melittophilous (Westerkamp, 1997) and followed by ornithophily and cheiropterophily (Ortega-Olivencia et al. 2005). In melittophilous flowers of this sub-family, each part of the corolla is specialized, the standard petal for pollinator attraction, keel petals for protection to androecium and gynoecium and wing petals together with keel petals for providing a landing platform for the insects; the wing petals also work as levers that raise or lower the keel petals (Stirton, 1981). As a Fabaceae member, *R. capitata* has papilionaceous corolla and performs the same functions as mentioned above. Further, its flowers with zygomorphic symmetry, yellow corolla with nectar guide, nectar hidden at the corolla base and pollen in keel petals conform to melittophilous pollination syndrome.

Howell et al. (1993) reported that primary and secondary pollen presentations Papilionoideae sub-family. In plants with primary pollen presentation, pollen is delivered directly from the anthers to the vector's body while in plants with secondary pollen presentation, pollen is delivered first on a floral part and then on the body of the vector accurately. Yeo (1993) stated that primary and secondary pollen presentation patterns are associated with the four types of basic pollination mechanisms - valvular, pump, explosive and brush; each mechanism is associated with a particular floral architecture and kinetics. In the valvular type, pollen presentation is primary, whereas in the other three mechanisms, it is secondary. In *R. capitata*, the flowers display primary pollen presentation associated with explosive pollination mechanism in which pollen is delivered directly from the anthers to the bee's body when keel petals are tripped by the foraging bee. But the efficiency of explosive pollination mechanism depends on the ambient weather. Since *R. capitata* flowers during winter season, it commences anthesis from noon onwards by which time the ambient air will be relatively dry and hence is conducive for the efficient functioning of the explosive pollination mechanism. The foraging bees also commence their foraging activity from noon onwards and continue forage collection until the flowers close back. The concealment of the stamens within the keel petals until it is tripped is an advantage for the plant to secure pollen from unusual rains and ambient moisture conditions during winter season (Peter et al. 2004).

Percival (1961) stated that plants with deep-tubed flowers tend to produce sucrose-rich nectar. Baker and Baker (1983) stated that flowers with long corolla tube possess more sucrose in their nectar. In *R. capitata* with short corolla tube presents sucrose-rich nectar because the nectar is hidden and enclosed by standard petal in flower phase. This concealment of nectar is benefits the plant to maintain control over its chemical composition in order to maximize pollination rate by appropriate pollinators (Herrera et al. 2008). Honey bees prefer the flowers with sucrose as chief constituent of nectar (Kevan, 1995). The flowers pollinated by long-tongued bees produce sucrose-rich nectar (Baker and Baker, 1990). In line with this, *R. capitata* also produces sucrose-rich nectar which is utilized exclusively by long-tongued bees. *Apis*, *Ceratina*, *Nomia* and *Xylocopa* bees have been documented as long-tongued bees (Cruden et al. 1983; Roubik, 2006). Bee-flowers tend to produce small volume of nectar with higher sugar concentration than the nectar of flowers pollinated by other animals (Opler, 1983; Cruden et al. 1983). Honey bees prefer sugar concentration of 20 to 40% in the nectar (Waller, 1972). On the contrary, Baker and Baker (1983) noted that honey bees prefer sugar concentration of 30 and 50% in the nectar. The honey bees have the ability to regurgitate liquid onto concentrated or even crystallized nectar, in this way, reduce its concentration so that it may be imbibed. The preferred sugar concentrations of nectar by other categories of bees have not been found in the literature. But, Pyke and Waser (1981) stated that the nectar sugar concentration of flowers pollinated by bees is generally higher than that of flowers pollinated by butterflies and hummingbirds; bee-pollinated flowers tend to produce nectar with sugar concentration more than 35% while butterfly or hummingbird pollinated flowers tend to produce nectar with sugar concentration ranged between 20 and 25%. In line with these reports, the present study

shows that the flowers of *R. capitata* produce small volume of nectar with 28% sugar concentration. Further, the energy yield from nectar appears to be in tune with the requirement of energy by bees in general and carpenter bees in particular due to their larger body size. In case of carpenter bee visits to *R. capitata* is further substantiated by the reports of Baker (1975) and Heinrich and Raven (1972) that these bees, being large in size and requiring high energy reach the floral reward only if the energetic reward is proportional to the energy expended. Therefore, *R. capitata* flowers with explosive pollination mechanism, primary pollen presentation, and hidden nectar and pollen have evolved to discourage other foragers from visiting the flowers and to ensure that the bees get the floral rewards. Accordingly, the flowers never received visits from other categories of insects.

In *R. capitata*, the keel tripping process is not self-activated to effect pollination. The flowers depend on bees for tripping of the keel petals to enable the working of explosive pollination mechanism. The flowers that were not tripped by external agents subsequently fall off. This situation explains that the plant is obligately dependent on bees for pollination. Of the bees, carpenter bees and the rock honey bee being large in size are more efficient in tripping the flowers than other bees. Carpenter bees are also more efficient in lifting the flag petal to access the nectar situated at the flower base. Since these bees collect only nectar and more efficient in tripping the flowers to effect pollination, they are classified as principal pollinators. All other bees although trip the flowers and effect pollination are treated as next-rank pollinators because they reduce the availability of pollen by pollen collection. The scarcity or non-availability of reliable floral resources during winter season in the study area further enforces fidelity to *R. capitata* by bees, in particular pollen collecting ones due to which the pollen availability for pollination gets very much reduced. Mishra and Rajesh Kumar (1997) reported that the pollen has great importance for a bee colony as pollen provides proteins, which are essential for worker honey bees to secrete glandular food (royal jelly) for rearing brood. Availability of enough pollen directly helps in more brood rearing, which ultimately leads to gradual colony build up. *R. capitata* is a promising source of pollen for honey bees and other bees during winter season.

Cruden (1977) used the pollen-ovule (P/O) ratios as indicators of breeding systems of plants. He provided P/O ratios for different breeding systems - 168.5 + 22.1 for facultative autogamy, 798.6 + 87.7 for facultative xenogamy and 5859.2 + 936.5 for xenogamy. Several workers followed these P/O ratios to classify breeding systems of the plant species studied by them. Arroyo (1981) stated that the P/O varies according to the pollination mechanism within Papilionoideae. These authors suggested that the plants with explosive mechanism have a low P/O because a single pollinator visit is needed for efficient transference of pollen; this low P/O is a consequence of the highly specialized, irreversible pollination mechanism, which allows only one effective exchange of pollen with pollinators. Small (1988) stated that *Medicago* species of the tribe Trifolieae with explosive pollination mechanism displays the lowest pollen-ovule ratios. Lopez et al. (1999) recorded explosive pollination mechanism with highest pollen-ovule ratios in certain genera of the Fabaceae such as *Cytisus*, *Pterospartum*, *Teline*, *Ulex*, *Stauracanthus* and *Cytisophyllum*. Etcheverry et al. (2011) stated that the Fabaceae plants which they studied with explosive pollination mechanism had intermediate pollen-ovule ratios. These authors mentioned that *Rhynchosia edulis* and *R. senna var. texana* have valvular pollination mechanism with primary pollen presentation. Both the species are classified as obligate xenogamous based on P/O ratio but *R. edulis* has been found to be facultative xenogamous in hand-pollination tests. Craufurd and Prins (1979) reported that *R. sublobata* is self-compatible, facultative xenogamous and pollinated by *Xylocopa* bees. In the present study, *R. capitata* shows highest P/O ratio even when compared to that of xenogamy used by Cruden (1977). It seems that the P/O is not always a good indicator of breeding system. The highest P/O ratio in this plant species appears to be a consequence of pollen collection activity by bees other than carpenter bees and the beetle, *Popillia impressipyga*. Therefore, it is inevitable for *R. capitata* to produce high P/O to compensate the pollen loss caused by pollen collectors and ensure the function of its vector-dependent facultative xenogamous breeding system.

Bruchid beetles primarily utilize beans from the family Fabaceae as their hosts (Johnson, 1981). Most bruchids are oligophagous; their host range is limited to restricted plant taxa, typically tribes and sub-tribes for species utilizing the legume subfamily Faboideae (Tuda et al. 2005). The ability to use dry beans as a food resource is widespread in this family. In *R. sublobata*, the bruchid beetle infests the seeds by using the latter for its breeding (Craufurd and Prins, 1979). In *R. capitata*, the seeds are not infested by bruchid beetles or other insects and hence suggests that the seeds are resistant to infestation by seed pests.

In Leguminosae, seeds of many taxa exhibit physical dormancy due to the presence of a water impermeable seed coat and imparts survival value in that impermeable seeds are capable of remaining dormant but viable for long periods of time (Tran and Cavanagh, 1984). Shaukat and Burhan (2000) reported on fecundity, seed characteristics and factors regulating germination of *Rhynchosia minima* in Pakistan. It exhibits differential success in different habitats with different micro-climates. Ali et al. (2012) reported that in *Rhynchosia capitata*, the seed has physical dormancy due to impermeable seed coat which enables it to persist for longer periods in soil. These authors treated its seeds with dry heat, hot water, stratification and acid scarification (HCl, HNO₃, and H₂SO₄) to break dormancy but the seeds showed response only to the last treatment. The results indicated that the seed of *R. capitata* has only physical dormancy due to impermeability of its seed coat. In the study area, the rare and scattered occurrence of

individuals of *R. capitata* could be attributable to the functionality of seed dormancy due to rocky habitat with water stress. Ali et al. (2012) noted that *R. capitata* is a summer weed in Pakistan. But, in the present study this species does not appear during summer but appears when the monsoon rains occur during June. Seeds fallen in soil and moisture-rich rock caves, crevices and cracks germinate at the same time to produce new plants but many seedlings subsequently perish due to dry conditions as a consequence of insufficient rainfall and long dry spells within the rainy season. In this connection, physical dormancy of seed coat enables the seeds that fall in shallow soils within the rocky sheets to escape water stress and remain dormant persistently (Roberto et al. 2000). Further, the seeds do not disperse far away from the parental site despite the explosive break-up of pods because the seeds are usually attached to the fruit wall even after fruit dehiscence. Therefore, *R. capitata* is unable to populate itself due to several limitations during growth season.

Remanandan (1981) stated that *Rhynchosia*, being closely related to the genus *Cajanus*, some of its species can be used to provide substantial contributions towards crop improvement in pigeon pea. Furthermore, some species of *Rhynchosia* have been experimented in India to provide physiological resistance against insect pests such as pod-borer and pod-fly in pigeon pea. Since the seeds of *R. capitata* are not infested as recorded in this study, this species can be tried to evaluate its potentiality to provide physiological resistance against insect pests of pigeon pea. *R. capitata* has been reported to have medicinal, food and fodder values (Tayade and Patil, 2006; Vardhana, 2006; Ahmad et al. 2014; Sarvalingam and Rajendran, 2015). Further, this species has adaptations to survive in rocky habitats. Therefore, further studies are required to evaluate the potentiality of this herb for economic and commercial purposes while taking all possible care for its conservation and management in its natural areas.

5. CONCLUSION

Rhynchosia capitata is a prostrate, climbing herb and winter season bloomer. It is hermaphroditic, self-compatible and facultatively xenogamous which is essentially vector-dependent. The flowers with papilionaceous corolla, zygomorphic symmetry and explosive pollination mechanism associated with primary pollen presentation pattern and sucrose-rich nectar with moderate sugar concentration are adapted for melittophily. Dry pods dehisce explosively but seeds remain attached to the pod wall. Subsequently, the seeds gradually fall to the ground, usually disperse within parental sites and germinate during rainy season. But, most of the seedlings perish due to water stress and nutrient-poor environment as a consequence of rocky habitat, intermittent rains and long dry spells within rainy season. The perennial root stock also produces new growth and initiates reproductive cycle. Despite the function of these dual modes of regeneration, the plant is not able to populate itself and extend its distribution range.

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Authors contributions

All three authors contributors contributed equally.

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