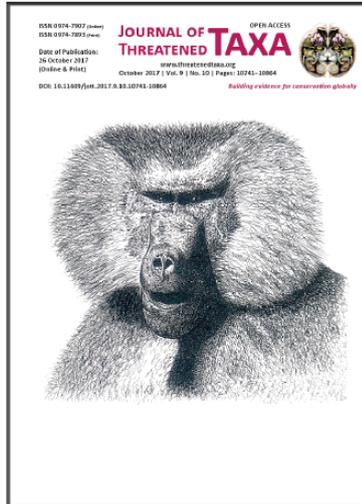


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## Journal of Threatened Taxa

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ISSN 0974-7907 (Online) | ISSN 0974-7893 (Print)

### ARTICLE

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26 October 2017 | Vol. 9 | No. 10 | Pp. 10757–10770

10.11609/jott.3172.9.10.10757–10770



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## POLLINATION ECOLOGY OF *RHYNCHOSIA CANA* (WILLD.) DC. (FABACEAE), AN ERECT SUB-SHRUB, IN PENINSULAR INDIA

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ISSN 0974-7907 (Online)  
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**Abstract:** *Rhynchosia cana* is a perennial erect sub-shrub. It flowers during November-January with peak flowering in December. The flowers are hermaphroditic, nectariferous, self-compatible and display explosive pollination mechanism adapted for pollination by bees. They do not fruit through autonomous selfing, but rather through manipulated selfing, geitonogamy and xenogamy mediated principally by bees and occasionally by Lycaenid butterflies. In the localities of this herb, weeds such as *Hyptis suaveolens* (Lamiaceae) and *Chromolaena odorata* (Asteraceae) show luxuriant growth and flower simultaneously, and their intense flowering and high flower density ensures that most flower-visiting insects visit their flowers. In this situation only two bee species, *Nomia* and *Anthidium* exhibited fidelity to *R. cana* flowers. Un-tripped flowers fall off while tripped ones set fruit. In open-pollinations, fruit set was 81% and seed set was 54%. Seed dispersal occurs by explosive pod dehiscence. Perennial root stock resurrects back to life and restarts its reproductive cycle during the rainy season. Seeds also germinate at the same time but their continued growth is subject to the availability of soil moisture content. This study suggests that *R. cana* is unable to compete with the co-flowering weed species for pollinators, and also has regeneration constraints due to nutrient-deficient rocky habitats with prolific growth of weeds.

**Keywords:** Entomophily, explosive pollination mechanism, explosive seed dispersal, hermaphroditism, *Rhynchosia cana*.

DOI: <http://doi.org/10.11609/jott.3172.9.10.10757-10770>

Editor: Cleofas Cervancia, University of Philippines Los Baños College, Laguna, Philippines.

Date of publication: 26 October 2017 (online & print)

Manuscript details: Ms # 3172 | Received 27 November 2016 | Final received 01 August 2017 | Finally accepted 18 September 2017

Citation: Raju, A.J.S. & K.V. Ramana (2017). Pollination ecology of *Rhynchosia cana* (Willd.) DC. (Fabaceae), an erect sub-shrub, in peninsular India. *Journal of Threatened Taxa* 9(10): 10757–10770; <http://doi.org/10.11609/jott.3172.9.10.10757-10770>

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Funding: The work reported was carried out from self-funding sources.

Competing interests: The authors declare no competing interests.

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Author Contribution: Both the authors contributed to a similar extent overall.

Acknowledgements: We thank the Andhra University, Visakhapatnam, for providing physical facilities.



## INTRODUCTION

*Rhynchosia* is a genus of the legume family Fabaceae, subfamily Faboideae, tribe Phaseoleae, and subtribe Cajaninae (Lackey 1981; Jayasuriya 2014). It consists of approximately 200 species and occurs in both the eastern and western hemisphere in warm temperate and tropical regions (Gear 1978). In the Eastern Ghats, 12 species of this genus have been reported to be occurring almost in one region, Seshachalam Hills of southern Eastern Ghats of Andhra Pradesh. They include *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*. These species are either climbers or shrubs (Madhavachetty et al. 2008). Of these, *R. cana* is distributed only in India and Sri Lanka.

Franco (1995) provided floral details of a species of *Rhynchosia* in Brazil. He reported that it is autogamous, limited by spatial segregation between stigma and anthers. Levels of out-crossing are maintained by retention of a pollination mechanism. *Hypanthidium* sp. and *Centris* sp. are the primary pollinators, and pollen is deposited on the ventral part of their abdomen when the flower is probed. Craufurd & Prins (1979) reported that *Rhynchosia sublobata* is self-compatible and pollinated by *Xylocopa* bees. Etcheverry et al. (2011) reported that *Rhynchosia edulis* and *R. senna* var. *texana* display valvular pollination mechanism; the former is facultative xenogamous while the latter is obligately xenogamous. There is no other information on flowering phenology, breeding systems, pollen presentation mechanisms, pollination mechanisms, pollinators and fruiting ecology of any species of *Rhynchosia*. There is one detailed study on the biochemical and nutritional aspects of *R. cana*, *R. filipes*, *R. rufescens* and *R. suaveolens*, which suggests that their seeds have significant protein content although they are under-utilized legumes (Kalidass & Mohan 2012). Keeping this in view, the present study of the floral biology, sexual system, breeding systems, pollinators and fruiting ecology of *R. cana* was conducted. This information is useful to take up breeding programs aimed at improving the nutritional quality of legumes involving *Rhynchosia* species and *Cajanus cajan*.

## MATERIALS AND METHODS

### Study site

The study region is located in the southern Eastern Ghats of Andhra Pradesh in peninsular

India at 13.68333056 N & 79.31666667 E. This area constitutes the forest cover of Tirumala Hills in the Seshachalam Hill Range in Chittoor District, which is primarily deciduous forest. The site is characterized by a combination of rocky, undulating and steep terrain. In this area *Rhynchosia cana* grows in small populations or as scattered individuals in open areas, intermingled prominently with two prolific weeds, *Hyptis suaveolens* and *Chromolaena odorata*.

### Flowering and floral biology

The flowering season was defined via regular field trips. Anthesis was initially recorded by observing 25 marked mature buds in the field. These observations were repeated five times on different days in order to determine an accurate anthesis schedule for each species. Similarly, the mature buds were monitored to record the time of anther dehiscence. The presentation pattern of pollen was also investigated by recording how anthers dehisced and confirmed by observing the anthers under a 10x hand lens. Details of flower morphology such as flower sex, shape, size, colour, odour, sepals, petals, stamens and ovary were described based on 25 flowers randomly collected from five plants. Careful observations were made regarding the position and spatial relationships of stamens and stigma in mature buds, at anthesis and during flower lifespan with reference to self and/or cross-pollination.

### Pollen output

Thirty mature but un-dehisced anthers from five different plants were collected and placed in a petri dish. Single anthers were removed, placed on a clean microscope slide (75x25 mm) and dabbed with a drop of lactophenol-aniline-blue. Anther tissue was observed under the microscope for pollen; if pollen was present the pollen mass was drawn into a band and the total number of grains was counted under a compound microscope (40x objective, 10x eye piece). This procedure was followed for counting the number of pollen grains in each anther collected. Based on these counts, the mean number of pollen produced per anther was determined. The mean pollen output per anther was multiplied by the number of anthers in the flower for obtaining the mean number of pollen grains per flower. The characteristics of pollen grains were also recorded.

### Pollen-ovule ratio

The pollen-ovule ratio was determined by dividing the average number of pollen grains per flower by the

number of ovules per flower. The value thus obtained was taken as pollen-ovule ratio (Cruden 1977).

### Nectar characters

The presence of nectar was determined by observing mature buds and open flowers. Ten flowers were used to determine the average volume of nectar per flower expressed in  $\mu\text{L}$ . Flowers used for this purpose were bagged at the mature bud stage, opened after cessation of nectar secretion and nectar was squeezed into micropipette to measure the volume. Nectar sugar concentration was determined using a Hand Sugar Refractometer (Erma, Japan). Ten samples were used for examining the range of sugar concentration in the nectar. For the analysis of sugar types, the paper chromatography method described by Harborne (1973) was used. Nectar was placed on Whatman No. 1 filter paper alongside standard samples of glucose, fructose and sucrose. The paper was run in ascending order for 24 hours with a solvent system of n-butanol-acetone-water (4:5:1), sprayed with aniline oxalate spray reagent and dried at  $120^{\circ}\text{C}$  in an electric oven for 20 minutes for the development of spots from the nectar and standard sugars. Sugar types present and the most dominant type were recorded based on the area and colour intensity of spots. The sugar content/flower is expressed as the product of nectar volume and sugar concentration per unit volume,  $\text{mg}/\mu\text{L}$ . This is 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  $\text{mg}$  of sugars present in  $1\mu\text{L}$  of nectar.

### Stigma receptivity

In visual method, the stigma physical state (wet or dry) was considered to record the commencement of receptivity.  $\text{H}_2\text{O}_2$  test as given in Dafni et al. (2005) was followed for the confirmation of stigma receptivity period.

### Breeding systems

Mature flower buds of five inflorescences on five individuals were tagged and enclosed in paper bags. The breeding systems were repeated second time with the same number of inflorescences and individual trees. They were tested in the following way, and the number of flower buds used for each mode of pollination is given in Table 1.

1. The flowers were fine-mesh bagged without hand pollination for autonomous autogamy.

2. The stigmas were pollinated with the pollen of the same flower manually just five minutes after anthesis at 11:30hr by using a brush; they were bagged and followed to observe fruit set in manipulated autogamy.

3. The stigma in each emasculated flower was hand-pollinated with the pollen of two anthers of a different flower on the same plant at 11:30hr by using a brush; they were bagged and followed for fruit set in geitonogamy.

4. The stigma in each emasculated flower was hand-pollinated with the pollen of two anthers of a different plant at 11:30hr by using a brush; they were bagged and followed for fruit set in xenogamy.

All these categories of flower pollinations were followed for fruit set for three weeks. If fruit set is there, the percentage of fruit set was calculated for each mode.

### Flower visitors

Flower foragers included bees and butterflies. The hourly foraging visits of each species were recorded on three or four occasions, and the data were tabulated for further analysis. Plants in full bloom were selected to record the foraging visits of insects. The data obtained was used to calculate the percentage of foraging visits made by each species per day, and also to calculate the percentage of foraging visits of each species per day in order to understand the relative importance of each species. Their foraging behaviour was observed on a number of occasions for the mode of approach, landing, probing method, the type of forage collected, contact with essential organs to result in pollination, inter-plant foraging activity in terms of cross-pollination.

### Determination of pollen carryover efficiency of insects

Ten specimens of each species were captured from flowers and brought to the laboratory. Each specimen was washed first in ethyl alcohol and the contents stained with aniline-blue on a glass slide and observed under microscope to count the number of pollen grains present. From this, the average number of pollen grains carried by each species was calculated to know its pollen carryover efficiency.

### Natural fruit set, seed set, seed dispersal and seedling ecology

Flowers on 50 plants were tagged prior to anthesis and followed for fruit set rate in open-pollinations. The same fruits were used to record seed set rate. Fruit maturation period, fruit dehiscence and seed dispersal aspects were observed to the extent possible. Field observations were also made on fruit and seed dispersal

modes, seed germination and seedling establishment to the extent possible.

### Photography

Plant habitat, flowering inflorescences, and flower and fruit details were photographed with Nikon D40X digital SLR (10.1 pixel) and TZ240 stereo zoom microscope with SP-350 Olympus digital camera (8.1 pixel). Olympus binoculars (PX35 DPSR Model) was also used to make field observations. Magnus compound microscope - 5x, 10x, 40x and 100x magnification was used for studying the pollen characteristics.

## RESULTS

### Phenology

It is a perennial erect sub-shrub with slender stem that grows in open, rocky areas. The branchlets are glandular, sticky and velvet-hairy. The plant re-grows from below ground perennial root stock and from the seed during June–October (Image 4c). The plants show almost complete vegetative growth by the end of October (Image 1b). *Hyptis suaveolens*, a weedy labiate also shows profuse growth simultaneously and its individuals are intermingled with the individuals of *R. cana* in many places (Image 1a). In this situation, *H. suaveolens* stands out prominently while *R. cana* with comparably low height is not prominent in appearance. In *R. cana*, the leaves are trifoliate with reticulate venation. The leaflets are petiolate, ovate, pointed, pubescent, especially beneath. The flowering occurs during November–January with peak flowering in December (Image 1c). The flowers are yellow, stalked (5mm) and borne in pairs in leaf-axils. The plants wither and disappear in late March/early April. In *H. suaveolens*, the flowering occurs during November–February with peak flowering during November–January. It produces multi-flowered cymes with violet-blue flowers and attracted most of the local insect foragers, which exhibit fidelity to this floral source. In some areas *Chromolaena odorata* and *R. cana* were in full bloom simultaneously, and the former species deprived the latter of insect foragers. *H. suaveolens* and *C. odorata* with their profuse flowering outcompete *R. cana* when all the three occur in the same habitat, hence *R. cana* with paired flowers in leaf axils attracted few insects even during its peak flowering phase. In areas where *H. suaveolens* and *C. odorata* flower simultaneously with *R. cana*, seeds produced by the latter species appear to be mainly derived from self fertilization via autogamy and geitonogamy.



Image 1. *Rhynchosia cana*: a - Habitat showing individual plants mixed with the dense population of *Hyptis suaveolens*; b - Vegetative phase; c - Flowering initiation. © A.J. Solomon Raju

### Flower morphology

The flowers are pedicellate, small ( $9.2 \pm 0.7$  mm long and  $7.6 \pm 0.5$  mm wide), yellow, odorless, papilionaceous, zygomorphic and bisexual. The calyx is green with yellow tinge and consists of five free, lanceolate, hairy, 5–6 mm long sepals. 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 ( $8.3 \pm 0.6$  mm long and  $6.7 \pm 0.4$  mm wide), yellow streaked with purple veins outside and inside but prominent at the bottom of the inside mid-region 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 petals ( $7.4 \pm 0.5$  mm long and  $3.7 \pm 0.4$  mm wide), called wing petals surround the two bottom petals, called keel petals ( $7.2 \pm 0.4$  mm long and  $3.4 \pm 0.5$  mm wide). The keel petals form a proximal cylindrical part and a distal part consisting of a pressed angular pouch, with an acute 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 10,  $5.4 \pm 0.5$  mm long, diadelphous; nine filaments are fused by the basal part into a sheath open along the upper side while the tenth filament is free and lies on the others (Image 2f). The distal parts of the filaments are free and contain 1mm long uniform dithecous anthers. The ovary is sessile, green, villous,  $3.4 \pm 0.5$  mm long and lies in the sheath of the filaments along the cylindrical part of the keel (Image 2h). It is monocarpellary and monolocular with two ovules or rarely three ovules arranged on marginal placentation (Image 2j,k). It has a long glabrous style with a capitate wet shiny stigma (Image 2i), both together accounts for a length of  $4.3 \pm 0.4$  mm. The stigma is situated at the height of 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 1030–1530 h with peak anthesis during 1130–1230 h (Table 1; Image 2a-d; l-o). Unfolding of the standard petal and wing petals indicates flowering opening. The keel petals do not unfold and remain in their original position as in mature bud stage (Image 2e). All the 10 anthers in a flower dehisce at the same time by longitudinal slits in mature bud stage. The number of pollen grains per anther is  $867 \pm 68.06$  and per flower is 8670. The pollen-ovule ratio is 4,335:1. The pollen grains are monads, spheroidal,  $31.52 \pm 3.80$   $\mu$ m in size, powdery and tricolporate, angulaperturate with reticulate exine (Image 2g). A nectariferous disc is present at the base of the ovary. The initiation of nectar secretion occurs during mature bud stage and its cessation occurs an hour after anthesis. Individual flowers produce  $2.3 \pm 0.16$   $\mu$ l of nectar with 0.66mg of sugar. The nectar sugar concentration is 26% (Range 25–28 %) consisting of sucrose, glucose and fructose with the first as dominant. Nectar is deeply concealed and it is open through two windows between the joined and the free filaments at the flower base. These windows allow access to the nectar. The stigma attains receptivity during anthesis and remains receptive for about three hours. After three hours of anthesis, the standard, wing and keel petals gradually move close to each other enclosing the reproductive organs (Image 2p–r). The closed flowers remain so even during most part of the 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.

**Table 1. Anthesis as a function of time in *Rhynchosia cana***

Time (h)	No. of flowers anthesed	Percentage of Anthesis
0930	0	0
1030	5	8
1130	15	25
1230	26	43
1330	9	15
1430	4	7
1530	1	2
1630	0	0
No. of mature buds tagged: 60		

### Pollination mechanism

The reproductive column is held under pressure within the keel part in open flowers, and it is exposed when the pollinator presses against the wing and the keel petals. When bees land on the wing petals the keel petals release the reproductive column explosively. Consequently, the reproductive column snaps forward against the standard petal, causing most of the pollen to be instantly released. The pollen thus released comes into contact with the ventral side of the bee body. Since the incurved stigma is situated above the height of the anthers, it strikes the bee's body first due to which cross-pollination occurs if the bee visited the other flowers previously and carried pollen on its ventral side and also then the pollen ejected from the anthers powders the ventral side of the bee instantly. If it is the first visit for the bee to the flower, then it effects self-pollination upon explosive release of reproductive column from the keel boat. With the departure of the bee 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 visit by bees. Lycaenid butterflies were found to visit the flowers for nectar but they were ineffective to trip the keel petals to cause explosive pollen release. If the flower is untouched or the keel is not tripped, the reproductive column is never exposed and remains enclosed in the keel boat. Such flowers wither and fall off.

### Breeding systems

In mature buds, anthers dehisce but autonomous autogamy does not occur. Fruit set is absent in un-manipulated autogamy, 18% in hand-pollinated autogamy, 46% in geitonogamy, 90% in xenogamy and 81% in open-pollination (Table 2). In open-pollination, seed set rate is 54% (Table 3).



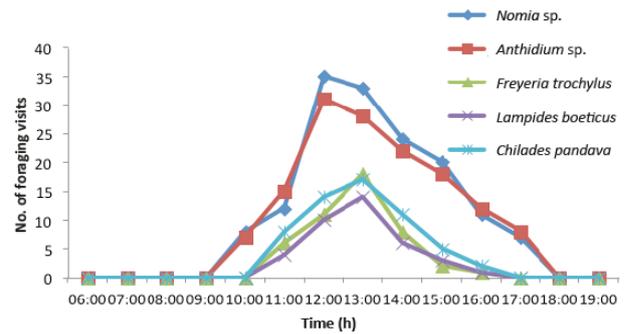
Image 2. *Rhynchosia cana*: a–d - Different stages of anthesis from bud to flower; e - Keel and wing petals with stamens and stigma inside; f - Diadelphous condition of stamens; g - Pollen grain; h - Ovary; i - Capitate stigma, j–k - Ovules, l–o - Different stages of anthesis; p–r - Different stages of flower closure. © A.J. Solomon Raju.

Table 2. Results of breeding systems in *Rhynchosia cana*

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	9	18
Geitonogamy	50	25	46
Xenogamy	50	44	90
Open-pollination	1000	807	81

### Insect foraging activity and pollination

The flowers were foraged by bees for both nectar and pollen, and by butterflies for nectar (Table 4). The bees showed foraging activity from 1000h onwards when the mature buds are still in the process of anthesis and stopped visiting flowers at 1700h (Fig. 1). The bees included Apidae and Megachilidae of Hymenoptera. The bees included *Nomia* sp. (Apidae) (Image 3a) and *Anthidium* sp. (Megachilidae) (Image 3b–d); they were almost consistent foragers during the flowering season. Butterflies were not consistent foragers and they showed foraging activity during 1100–1600 h with peak foraging activity 1200–1300 h (Fig. 1). The foraging activity pattern of insects indicated that their flower-visiting rate is directly related to the availability of flowers; the peak anthesis time is confined to noontime hours when humidity is usually low and light intensity is high. Bees accounted for 68% and lycaenid butterflies 32% of total foraging visits (Fig. 2). Among bees, *Nomia* sp. made 35% while *Anthidium* sp. made 33% of total foraging visits. The body washings of foraging bees and butterflies showed variation in the pollen carrying capacity; the average pollen recorded on *Nomia* sp. was 168.2, *Anthidium* sp. 125.4, *F. trochylus* 32.8, *L. boeticus* 40.7 and *C. pandava* 45.1 (Table 5; Image 3e,f). The flowers were visited several times by bees but new visits lasted shorter than the first one. With respect to their behavior, the bees landed on the wing petals and the keel, with their head near the standard. They then exerted a certain 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 (sternotribic pollen deposition). The bees took "U" turn after nectar collection and proceeded to the stamens to collect pollen. In case of butterflies, they attempted to visit both un-tripped and tripped flowers. They never tripped keel petals due to their light weight and also could not access nectar due to protection of nectar by the standard petal.

Figure 1. Hourly foraging activity of insects on *Rhynchosia cana*

Their visits to un-tripped flowers did not contribute to any pollination. However, their visits to tripped flowers contributed to pollination due to contact between their proboscis/forehead and the exposed stamens and stigma; as the flowers were already tripped, nectar windows were exposed at the base of the standard petal and hence butterflies were able to collect nectar. Both bees and butterflies were found to make inter-plant flights frequently due to production of a few flowers per plant and in this process individuals flowers appeared to be visited more than one or several visits enhancing the pollination rate.

### Fruiting behavior

Fruit growth and development begins immediately after pollination and fertilization. The fruits mature within three weeks (Image 3g–i). The sepals enclose the growing fruit initially and the fruit emerges out of the sepals gradually. Fruit is green initially and brown when ripe and dry. It is a non-fleshy, hairy, oblong,  $15.7 \pm 0.6$  mm long,  $6.7 \pm 0.5$  mm wide, compressed between seeds, rounded and apiculated pod. The pods produced 1 or 2 or 3 seeds or none; 1-seeded pod set is 91.57%, 2-seeded pod set 7.19%, 3-seeded pod set 0.62% and pod set without seeds 0.62% (Table 3; Image 3j–p).

### Seed ecology

Mature and dry fruits with bi-valvate configuration dehisce explosively to eject seeds violently due to which they fall well away from the parent plant (Image 4a,b). The seed is brownish black, reniform, finely pubescent,  $3.7 \pm 0.5$  mm long and  $2.8 \pm 0.3$  mm wide and shiny with cushioned strophiole (Fig. 3q). Seeds germinate during rainy season which starts from June. Seedlings grow continually but their growth rate is subject to the availability of moisture status of the soil (Image 4d-h).



Image 3. *Rhynchosia cana*: a - *Nomia* sp. collecting nectar; b-d - *Anthidium* sp. collecting pollen from un-anthesed flowers (b), collecting nectar from open flower (c), collecting pollen from open flower (d); e & f - Lycaenid, *Chilades pandava* collecting nectar; g-i - Different stages of fruit development before maturity; j - 1-seeded pod; k - 2-seeded pod; l - 3-seeded pod (not dehiscent); m-p - Dehiscent 3-seeded, 2-seeded and 1-seeded pods; q - Seeds. © A.J. Solomon Raju.

**Table 3. Natural fruit/seed set rate in *Rhynchosia cana***

No. of flowers sampled	No. of flowers set fruit	Fruit set (%)	Seed set (%)	Rate of seed set/fruit							
				No. of 1-seeded fruits	1-seeded fruit set (%)	No. of 2-seeded fruits	2-seeded fruit set (%)	No. of 3-seeded fruits	3-seeded fruit set (%)	No. of seedless fruits	Seedless fruits (%)
1000	807	81	54	739	91.57	58	7.19	5	0.62	5	0.62

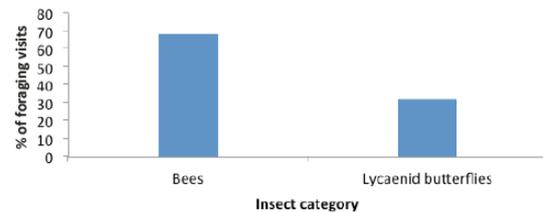
No. of ovules/flower = Two; rarely Three

**Table 4. List of insect foragers on *Rhynchosia cana***

Order	Family	Sub-family	Genus	Species	Common Name	Foraging schedule	Forage collected
Hymenoptera	Apidae	Nomiinae	<i>Nomia</i>	sp.	Alkali bee	1000–1700	Nectar + Pollen
	Megachilidae	Megachilinae	<i>Anthidium</i>	sp.	Potter bee	1000–1700	Nectar + Pollen
Lepidoptera	Lycaenidae	Polyommatae	<i>Freyeria</i>	<i>Trochylus</i> Freyer	Grass Jewel	1100–1600	Nectar
			<i>Lampides</i>	<i>boeticus</i> L.	The Pea Blue	1100–1600	Nectar
			<i>Chilades</i>	<i>Pandava</i> Horsfield	The Plains Cupid	1100–1600	Nectar

**Table 5. Pollen recorded in the body washings of bee foragers on *Rhynchosia cana***

Bee species	Sample size (N)	Number of pollen grains		
		Range	Mean	S.D
<i>Nomia</i> sp.	10	76-281	168.2	67.62
<i>Anthidium</i> sp.	10	58-185	125.4	48.87
<i>Freyeria trochylus</i>	10	21-47	32.8	8.70
<i>Lampides boeticus</i>	10	23-56	40.7	11.50
<i>Chilades pandava</i>	10	31-59	45.1	9.26



**Figure 2. Relative percentage of foraging visits of bees and butterflies on *Rhynchosia cana***

**DISCUSSION**

The present study shows that *Rhynchosia cana* is a dry deciduous species and grows in rocky areas with little litter content. In the absence of information on the habitats of its occurrence, it is not possible to evaluate whether it has the ability to grow in diverse habitats or not. It is an erect sub-shrub, which shows growth from perennial root stock during the rainy season. It also produces new plants from seed stock at the same time. Full leaf flushing is complete by the end of October and then onwards, floral bud initiation takes place. The flowering period is confined to winter season. Individual plants produce a small number of flowers during their lifetime due to production of only a pair of flowers in leaf axils. The plant during flowering phase attracts only two bee species consistently and three species of butterflies occasionally due to simultaneous flowering of the weeds *Hyptis suaveolens* and *Chromolaena odorata*, which produce large populations with prolific flowering. These

species outcompete *R. cana* in attracting a wide array of insects to their flowers, limiting pollinator availability.

In *R. cana*, the hermaphroditic sexual system is functional due to production of fertile pollen grains and functional ovaries. The flowers display near-synchronous hermaphroditism or homogamy due to the occurrence of anther dehiscence in the mature bud stage, and receptivity of stigmas during anthesis. The entire reproductive column stays inside the keel petals even after anthesis; in this situation, there is a likelihood of autonomous autogamy. Nevertheless, hand pollination tests indicated that autonomous autogamy does not occur despite self-compatibility, although it remains functional because fruiting occurred when stigmas were brushed with their own pollen. Such a situation suggests that the flowers are essentially dependent on flower foragers for fruit set through self- as well as cross-pollination. It appears that the stigma, although receptive, blocks the germination of the self-pollen while it is in keel petals and hence it essentially requires the rupture of its surface by a pollinator to allow the self- or cross pollen to germinate. Such a stigmatic regulatory

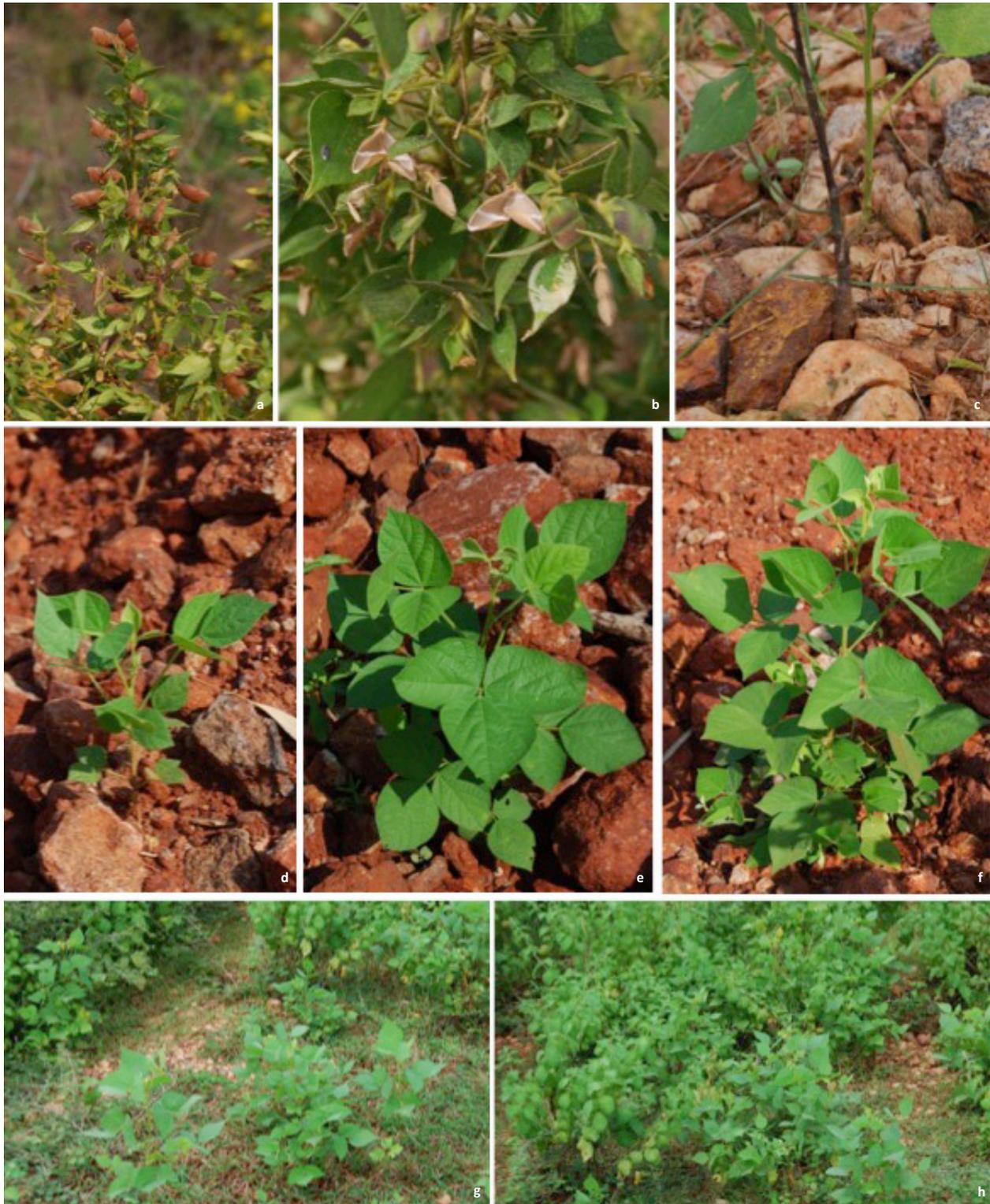


Image 4. *Rhynchosia cana*: a - Dry fruits; b - Explosive pod dehiscence; c - Emergence of new branches from perennial root stock; d-f - Growth of new plants; g & h - Established seedlings from seeds. © A.J. Solomon Raju.

function appears to have evolved to discourage selfing and promote out-crossing. Shivanna & Owens (1989) stated that the rupture of the stigmatic surface by

pollinator permits the pollen to germinate in the flowers of Phaseoleae members with thick stigmatic cuticle. On the contrary, Castro & Agullo (1998) reported that in

*Vigna*, a member of the tribe Phaseoleae, autonomous self-pollination may occur by spontaneous rupture of the stigmatic membrane. Similar stigmatic surface that prevents self-fertilization has also been reported in *Vicia faba* (tribe Viciaeae) (Lord & Heslop-Harrison 1984) and in *Medicago scutellata* (tribe Trifolieae) (Kreitner & Sorensen 1985); however, in these species auto-fertile lines have been reported to have thin stigmatic cuticles allowing spontaneous disruption and self-fertilization. In *R. cana*, the stigmatic surface appears to have thick cuticle and does not have the mechanism of causing spontaneous rupture to facilitate autonomous self-pollination. 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 has been related to biotic pollination mechanisms. The three sub-families within this family have achieved a characteristic floral architecture, in which plants within the subfamily Papilionoideae have developed the most complex floral mechanisms. Plants within the Papilionoideae have zygomorphic flowers that are mainly bee-pollinated (Westerkamp 1997); although bird pollination and bat pollination have also been recorded within the subfamily (Ortega-Olivencia et al. 2005). In bee-pollinated flowers of Papilionoideae, it is assumed that each part of the corolla is specialized for a particular role in pollinator attraction and the success of pollination. The flag or standard petal attracts pollinators; the keel protects androecium and gynoecium and, together with the wings, provides a platform for the insects to land on. The wings also operate as levers that raise or lower the keel (Stirton 1981). The flowers typical of pollination by the bee family Apidae are zygomorphic, bright yellow or blue with nectar guides, and frequently with hidden rewards such as those in the Lamiaceae, Scrophulariaceae, Fabaceae and Orchidaceae (Faegri & van der Pijl 1979). In the present study, the Fabaceae member, *R. cana* has papilionaceous corolla with flag, wing and keel petals; the flag petal serves as a visual attractant, wing petals provide landing platform and keel petals protect the entire reproductive column. The flowers are typical of pollination by bees since they are zygomorphic, standard petal with nectar guide, hidden

nectar at the corolla base and hidden pollen in keel petals.

Within the sub-family Papilionoideae, primary and secondary pollen presentations have been reported. In plants with primary pollen presentation, pollen is delivered directly from the anthers to the vector's body. In plants with secondary pollen presentation, pollen grains are delivered first on a floral part such as the keel petals in Papilionoideae and then on the body of the vector implying an accurate delivery of pollen on the vector's body (Howell et al. 1993). These two pollen presentation patterns are associated with the four types of basic pollination mechanisms - valvular, pump, explosive and brush, all of them are 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 (Yeo 1993). In the explosive mechanism, commonly only one pollination event occurs and it has evolved independently in several tribes (Small 1988), while in the other three mechanisms, repeated visitation is possible (Westerkamp 1997). In the present study, *R. cana* flowers have explosive pollination mechanism and deliver pollen directly from the anthers to the bee's body when keel petals are tripped by the foraging bee; this type pollen delivery is the representative of primary pollen presentation associated with explosive pollination mechanism. In the flowers, the staminal column is held under pressure within the keel, and when the tension is released by the forager, the same column snaps forward against the standard petal causing all the pollen to be instantly released. The reproductive column remains exposed and does not return back to its original state but the keel petals return back partially covering the stamens and stigma. The efficiency of explosive pollination mechanism depends on the ambient weather conditions, especially temperature and relative humidity. Since *R. cana* flowers during winter season, it accordingly commences anthesis from late morning onwards by which time the ambient air will be relatively dry and hence is conducive for the efficient functioning of the explosive pollination mechanism. Further, the bees also commence their foraging activity at about the same time 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 the flowering season of this plant (Peter et al. 2004).

Percival (1961) stated that plants with deep-tubed flowers tend to produce sucrose-rich nectar, whereas

those with open or shallow-tubed flowers tend to be hexose-rich. Baker & Baker (1983) stated that flowers with long corolla tube possess more sucrose in their nectar while those with short tubes possess more hexoses in their nectar. In the present study, *R. cana* with short corolla tube presents sucrose-rich nectar because the nectar is perfectly concealed and hence is not exposed for the breakdown of sucrose into hexoses. Concealment of nectar in this species is adaptive to protect against microorganisms, particularly yeasts, whose metabolic activities dramatically change nectar chemistry and the plant benefits from keeping the nectar as sterile as possible to maintain control over its chemical composition in order to maximize pollination rate by attracting appropriate pollinators (Herrera et al. 2008). Bees prefer flowers with sucrose as chief constituent of nectar (Kevan 1995). The flowers pollinated by long-tongued bees produce sucrose-rich nectar (Baker & Baker 1990). In line with this, *R. cana* with melittophilous pollination syndrome also produces sucrose-rich nectar which is utilized principally by long-tongued bees and occasionally by lycaenid butterflies. Opler (1983) and Cruden et al. (1983) noted that bee-flowers tend to produce a small volume of nectar with higher sugar concentration than the nectar of flowers pollinated by other animals. Pyke & Waser (1981) stated that the nectar sugar concentration of flowers pollinated by bees is generally higher when compared to those 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 the present study the flowers of *R. cana* produce a small volume of nectar with 26% sugar concentration. Further, the energy yield from the nectar appears to be in tune with the requirement of energy by bees. Therefore, *R. cana* 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, bees have been found to be the principal pollinators while lycaenid butterflies to be the secondary pollinators. This observation has been substantiated by their pollen carrying capacity as realized in body washings after their visits to the flowers. The foraging activity pattern of insects suggests that their peak foraging activity is correlated with peak anthesis time when humidity is usually low and light intensity is high. In the habitats of *R. cana*, the extensive populations of weeds, *Hyptis*

*suaveolens* and *Chromolaena odorata* with huge flower density diverted bee populations to their flowers; in this situation, *Nomia* and *Anthidium* bees confined their foraging visits to *R. cana* flowers and effected pollination. In *R. cana*, 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. The bees visiting the flowers seem to be efficient in tripping the flowers because the flower size and petal strength are commensurate with the bee size and the force employed to depress the wing petals to access the nectar.

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 & Prins (1979) reported that *R. sublobata* is self-compatible and facultative xenogamous in hand-pollination tests; it is pollinated by *Xylocopa* bees. In the present study, *R. cana* shows highest P/O ratio when compared to that of facultative xenogamy used by Cruden (1977). The highest P/O ratio in this plant species appears to be a

consequence of pollen collection activity by bees. It appears to be inevitable for *R. cana* 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. Further, this is substantiated by natural fruit and seed set rates evidenced in the study. The study showed that seed set rate is only 54% although natural fruit set is 81% of which the production rate of 1-seeded fruits exceed 90% despite the characteristic of production of two ovules per flower. This state of fruiting and seed set rates could be attributable to pollen and pollinator limitation, and also to nutrient environment of the soil where the plant grows. The study also showed that the flowers of *R. cana* produce three ovules rarely and such flowers could produce fruits with three seeds if pollinated. Further, the study also noted the production of fruits without seeds but the percentage of such fruits is highly negligible. However, this situation in *R. cana* indicates that the plant initiates and produces fruit cover first and then the gradual production of seeds. The production of seedless fruits can be attributed to nutrient-deficiency in the soil and to genetically inferior fertilization arising from self-pollination.

Tran & Cavanagh (1984) reported that in Leguminosae, seeds of many taxa exhibit physical dormancy due to the presence of a water impermeable seed coat. With this dormancy, they remain viable for long period of time. Ali et al. (2012) reported such physical dormancy in *Rhynchosia capitata* due to which this species is successful as a weed. Shaukat & Burhan (2000) described seed characteristics and the factors regulating germination of *R. minima* in Pakistan; it exhibits differential success in different habitats with different microclimates. Seed characteristics or dormancy studies on *R. cana* have not been made by previous workers. In the present study, it is found that the seeds of *R. cana* respond to monsoonal rains, germinate and produce seedlings. During the study period, the rainy season is characterized by erratic rainfall with long dry spells; in effect, the many growing seedlings perished while a few continued to grow in areas where water stress is not severe. In case of *H. suaveolens* and *C. odorata*, they showed quick growth and soon shaded or covered the growing seedlings of *R. cana* due to which the latter could not grow further and establish themselves. The perennial root stock of this species, however, grows continually and produces new leaf flushing and flowering almost without any hindrance. The explosive pod dehiscence in *R. cana* results in the settlement of seeds mostly in the parental sites but rain water may disperse them to new places

during rainy season but there is a deficit of rainfall due to which the migration of seeds is profoundly affected.

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. In this study, the seeds of *R. cana* have not been infested by any pod-borer or pod-fly suggesting that it has physiological resistance against insect pests. Therefore, intensive and extensive research is suggested to identify and select desirable genotypes of *R. cana* that give physiological resistance against pod or seed pests in order to use them for crop improvement in pigeon pea.

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ISSN 0974-7907 (Online); ISSN 0974-7893 (Print)

October 2017 | Vol. 9 | No. 10 | Pages: 10741–10864

Date of Publication: 26 October 2017 (Online & Print)

DOI: 10.11609/jott.2017.9.10.10741-10864

[www.threatenedtaxa.org](http://www.threatenedtaxa.org)

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