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Journal of Threatened Taxa

10.11609/jott.2023.15.2.22559-22770
www.threatenedtaxa.org

26 February 2023 (Online & Print)
15(2): 22559-22770
ISSN 0974-7907 (Online)
ISSN 0974-7893 (Print)

Open Access

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

Publisher
Wildlife Information Liaison Development Society
www.wild.zooreach.org

Host
Zoo Outreach Organization
www.zooreach.org

43/2 Varadarajulu Nagar, 5th Street West, Ganapathy, Coimbatore, Tamil Nadu 641006, India
Registered Office: 3A2 Varadarajulu Nagar, FCI Road, Ganapathy, Coimbatore, Tamil Nadu 641006, India
Ph: +91 9385339863 | www.threatenedtaxa.org
Email: sanjay@threatenedtaxa.org

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Cover: Pseudo-flying animals and wind-dependent seed & spore dispersers – made with digital painting in Krita. © Melito Prinson Pinto

Journal of Threatened Taxa | www.threatenedtaxa.org | 26 February 2023 | 15(2): 22686–22694

OPEN ACCESS

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

https://doi.org/10.11609/jott.8287.15.2.22686-22694

#8287 | Received 28 November 2022 | Final received 02 January 2023 | Finally accepted 09 February 2023

COMMUNICATION

Andromonoecy functional through heterostyly and large carpenter bees as principal pollinators in *Solanum carolinense* L. (Solanaceae)

Suvarna Raju Palathoti [1] & **Aluri Jacob Solomon Raju** [2]

[1] Department of Health, Safety and Environmental Management, International College of Engineering and Management, Muscat, Sultanate of Oman, Oman.
[2] Department of Environmental Sciences, Andhra University, Visakhapatnam, Andhra Pradesh 530003, India.
[1] suvarnarajup@rediffmail.com, [2] solomonraju@gmail.com (corresponding author)

Abstract. *Solanum carolinense* is a perennial shrubby weed. In this species, andromonoecy is functional through heterostyly represented by the production of long, semi-long, medium, & short-styled flower types and another flower type lacking style & stigma completely. All plants produce long-styled flowers while all individuals do not produce other flower types. The long- and semi-long-styled flowers are functionally co-sexual and produce fruit while the other flower types are functionally female-sterile and do not produce fruit. The position of style in long- and semi-long-styled flowers facilitates the act of pollination by pollinator bees. *Xylocopa* bees are large-bodied specialist bees which collect pollen from poricidal anthers efficiently in this plant by displaying buzzing behaviour and are treated as principal pollinators. The other bees are small-bodied and do not display buzzing behaviour to release pollen from poricidal anthers but they simply collect residual pollen available around the rim of the apical pore of the anthers, and hence they act as supplementary pollinators only. In this plant, the style length has a positive relationship with pollen deposition and a negative relationship with pollen removal in flowers visited by large carpenter bees of *Xylocopa* genus and hence, pollinator-specific interactions with flower morphology are important in the maintenance and perfect evolution of andromonoecy in this plant species. Florivory by *Mylabris pustulata* could vary with the flower production rate in *S. carolinense* and could favor higher floral-sex ratios biased in favour of higher proportion of female-sterile flowers.

Keywords: Buzz-pollination, female-sterile flowers, florivory, indehiscent berry nectar-less flowers, poricidal anthers.

Editor: Anonymity requested.

Date of publication: 26 February 2023 (online & print)

Citation: Palathoti, S.R. & A.J.S. Raju (2023). Andromonoecy functional through heterostyly and large carpenter bees as principal pollinators in *Solanum carolinense* L. (Solanaceae). *Journal of Threatened Taxa* 15(2): 22686–22694. https://doi.org/10.11609/jott.8287.15.2.22686-22694

Funding: Self-funded.

Competing interests: The authors declare no competing interests.

Author details: Prof. A.J. Solomon Raju is honorary professor, Department of Environmental Sciences, Andhra University, Visakhapatnam, India. Dr. P. Suvarna Raju is assistant professor, Department of Health, Safety and Environmental Management, International College of Engineering and Management, Muscat, Sultanate of Oman, Oman.

Author contributions: Both authors contributed equally.

Acknowledgements: We thank the Andhra University, Visakhapatnam, for providing physical facilities to carry out this research work

INTRODUCTION

The family Solanaceae has about 100 genera consisting of 2,500 species distributed world over with species diversity centered in America, Australia, and Africa (Olmstead et al. 1999, 2008). Species of this family have enormous importance as food plants the world over. Crops such as potato, tomato, and capsicum in Solanaceae family are important staple vegetables although there are many other species which are important as edible products (Samuels 2009). In India, this family is represented by 29 genera with 116 species, two sub-species, three varieties, and one forma (Kumari 2004). Of these, 12 genera with 39 species are distributed in the Eastern Ghats region (Venkatappa 2011). In this family, *Solanum* with about 1,500 species is one of the largest genera distributed throughout the world (Vorontsova et al. 2013). In India, this genus is represented by 49 species which are distributed throughout the country, of which 17 species occur in the Eastern Ghats region (Venkatappa 2011).

Andromonoecy is more common in Solanaceae family and it is well documented in *Solanum* genus (Vorontsova et al. 2013). In *Solanum* genus, a number of species display andromonoecy and dioecy as functional sexual systems. In vast majority of dioecious species, the female flowers produce pollen-bearing anthers but the pollen is inaperturate, viable and does not produce a pollen tube while male flowers produce pistils with ovules (Martine & Anderson 2006). In andromonoecious species, the staminate flowers produce variously or noticeably reduced pistil because the style is short to place the stigma above the staminal column. As a result, the stigma is unable to receive pollen directly from the pollinating bees but there is a possibility for incidental gravitational pollination from pollen puffed into the air in the space between anthers by the sonicating action of probing bees (Vorontsova et al. 2013). Andromonoecism is functional in species pollinated by bats, bees, flies, hummingbirds, and moths (Bawa & Beach 1981). Heithaus et al. (1974) stated that andromonoecy is evolved to selective pressure for increasing cross-fertilization. Zapata & Arroyo (1978) mentioned that andromonoecism is a result of abortion of non-functional pistils in certain flowers that serve as male or attraction functions before their anthesis. These authors suggested three possibilities as to the significance of pistils in bisexual flowers that largely serve as pollen donors. First, the abortion of pistils could structurally perturb the floral morphology, disrupting the pollination mechanism. Second, the abortion of pistils in many bisexual flowers prior to pollination could restrict the efficacy of selection on progeny acting through control over pollen germination, tube growth, and embryo & fruit abortion. Third, the abortion of pistils may not occur in most hermaphroditic species because it is not possible to predict the fate of flowers as pollen donors or pollen recipients before pollination (Lloyd 1980).

Different authors reported on the sexual system and pollinators of *Solanum carolinense.* It is an andromonoecious species with hermaphrodite and male flowers on the same individual (Bertin 1982). The anthers in staminate and hermaphroditic flowers are of the same size and produce the same quantity of pollen but they display some specialization in each flower sex (Connolly & Anderson 2003). The long-styled flowers serve primarily as pollen recipients while short-styled flowers as pollen donors (Quesada-Aguilar et al. 2008). It is self-incompatible but it is flexible as a part of stable mixed mating system which permits self-fertilization when cross-pollination limits seed production in situations of establishing new populations as a weed (Kariyat et al. 2011). It is pollinated by different bees in different regions of USA (Hardin et al. 1972; Quesada-Aguilar 2001; Connolly & Anderson 2003; Travers et al. 2004; Vallejo-Marin & Rausher 2007). With this backdrop, the intent of the present study is to evaluate whether only long- and short-styled hermaphrodite flower types occur or other hermaphrodite flower types with variation in style length also occur with different sexual functions in *S. carolinense*. Further, the study also aims at providing additional information on its fruiting aspects and florivory. Since there is not even a single report on the sexual system and pollinators of *S. carolinense* from India, this study is an attempt to provide the details of sexual reproduction and fruiting aspects functional through local pollinators and compare the same with the reports published from outside India.

MATERIALS AND METHODS

Flowering season, floral morphology, and biology

Solanum carolinense population growing in the wild pockets of Madhurawada area of Visakhapatnam city ($17^0$49’20.8992”N & $83^0$21’8.0028”E), Andhra Pradesh, India, was used for the present study during May–December 2021. This plant population was observed for its flowering season, anthesis and anther dehiscence mode, flower visitors and their foraging behavior, pollination, natural fruit, and fruit aspects. The population was followed continuously during the study period for the flowering intensity levels to classify into initial, peak, and fag end of flowering. Twenty-five just open flowers were used to record the floral details. Anthesis schedule and anther dehiscence timing were recorded by tagging and following 25 marked mature buds in the field. Flowers were classified into five types according to style length and the absence of style and stigma. A total of 211 flowers collected randomly from ten plants were used to calculate the percentage of plants producing each flower type and the production rate of each flower type. Morphological aspects of these flower types are briefly described. Twenty undehisced anthers from each flower type on ten plants were used to determine pollen output and study pollen grain characteristics as per the protocols given in Dafni et al. (2005).

Foraging behavior and pollination

Flowers visitors included exclusively bees and they were listed along with forage sought, foraging schedule and the total number of foraging visited made per day. Their foraging activity pattern during day-time was observed in the field. The hourly foraging visits of each bee species were recorded on four different days during peak flowering phase. The average number of foraging visits made by each bee species at each hour was noted to present the foraging activity pattern of bees. The species were identified by tallying with the reference species collected from the study region and identified by Zoological Survey of India, Calcutta. Further, the same data were used to calculate the percentage of foraging visits of each bee species per day in order to understand the relative foraging activity levels of each bee species. The bees were observed carefully for their foraging behavior such as mode of approach, landing, probing behavior employed for pollen collection and contact with essential organs in effecting pollination.

Florivory

The blister beetle *Mylabris pustulata* (Thunberg, 1821) was found feeding on the flowers. Keeping this in view, a sample of 100 flowers was chosen at the initial, peak and fag-end of flowering phase to record the percentage of flowers fed by this beetle. Further, the floral parts fed by this beetle were recorded to know whether the flowers used by them have any role in fruit set.

Natural fruit set and fruiting ecology

Twenty-five fertilized flowers that showed initial growth of fruit development were tagged and followed to record the duration of fruit development and maturation. Fruit set rate was recorded only in long and semi-long flowers since the other flower types did not initiate and develop fruits. Fifty flowers of each flower type were tagged and followed to record fruit set rate in open-pollinations. Fruit characters were also recorded.

RESULTS

Flowering season and floral morphology

It is a small perennial shrubby weed. The stem and underside of larger leaf veins are covered with prickles. Leaves are petiolate, arranged alternately to each other; they are elliptic to oblong, irregularly lobed and the upper and lower surface is covered with fine hairs. The plant propagates by underground rhizome and seed. The plants emerging from the rhizome appear producing new aerial stalks and foliage with the onset of wet season in June and initiate flowering by late July while those emerging from seed produce full-grown plants by late July and begin flowering by second week of August. The flowering continues without a break until late October and gradually ceases by second week of November (Image 1a). In year-long wet locations, plants display vegetative growth, flowering and fruiting simultaneously or alternately throughout the year. The flowers are produced in terminal and axillary cymes (Image 1b). The flowers are medium-sized, non-tubular, white, odorless and actinomorphic. They are morphologically bisexual but functionally either bisexual or female-sterile. The style length varies but the length of stamens remains unchanged in all flowers borne on the same individual. According to style length, the flowers are classified into four types, long-styled (Image 1d), semi-long-styled (Image 1e), medium-styled (Image 1f), and short-styled ones (Image 1g). Further, another flower type with pistil lacking style and stigma (Image 1h) is also produced along with these four types of flowers in the same individual. All individuals produce long-styled flowers but semi-long-styled flowers are produced only in 75%, medium-styled flowers in 83%, short-styled flowers in 75% and flowering lacking style and stigma in 67% of the total monitored plants (Figure 1). Of the total flowers observed in monitored individuals, 59% are long-styled, 11% semi-long-styled, 10% short-styled, 9% short-styled flowers and 11% flowers lacking both style and stigma (Figure 2). In all flower types, the calyx has five green pointed spiny sepals and is quite inconspicuous. The corolla is rotate bearing five spreading lobes with yellow center and is quite conspicuous. The stamens

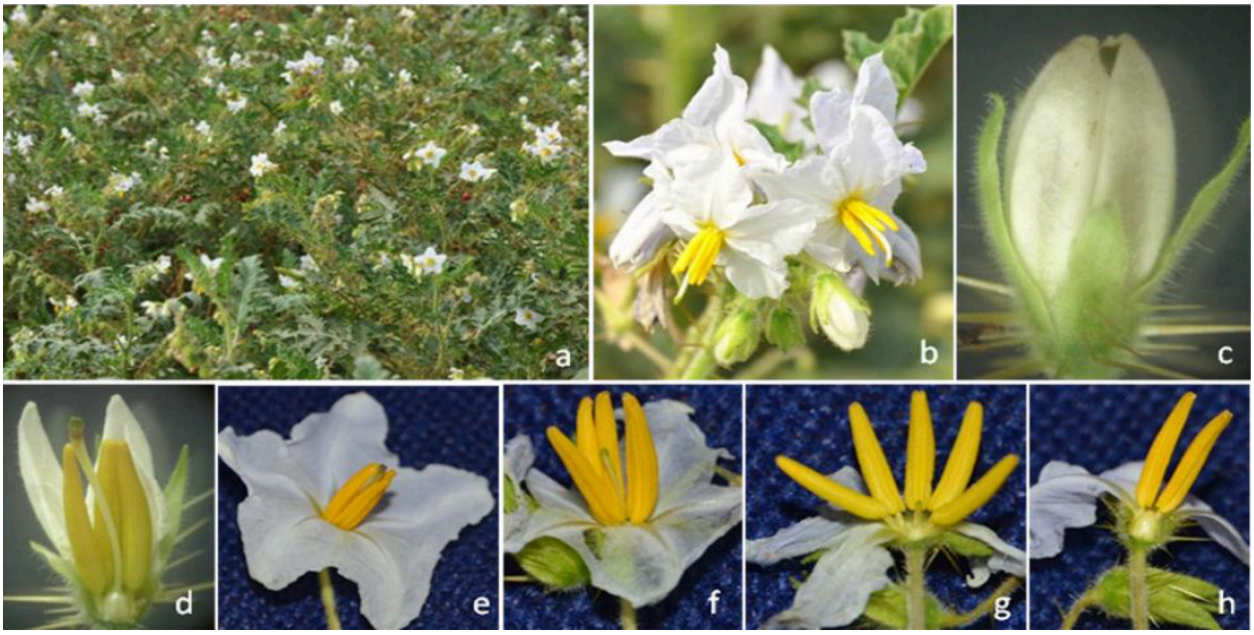

Image 1. *Solanum carolinense*: a—Habit – in flowering phase | b—Flowering inflorescence | c—Anthesing bud | d—Long-styled flower | e—Semi-long styled flower | f—Medium-styled flower | g—Short-styled flower | h—Flower lacking style and stigma. ©. A.J. Solomon Raju.

Figure 1. Percentage of plants producing each flower type in *Solanum carolinense*.

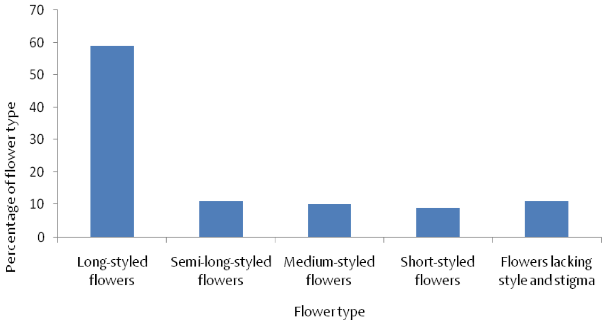

Figure 2. Percentage of flower types produced in *Solanum carolinense*.

are five with short filaments and large, non-adherent yellow anthers inserted on the corolla and form a cone around the pistil; there is no variation in the length of filament and anthers in all flower types. The style is long, extends beyond the length of stamens, it is strikingly sub-capitate. The ovary is bulbous and bears numerous ovules (Image 2b).

Floral biology

The flowers are open daily during 0600-0830 h (Image 1c). The corolla expands and its lobes become flat exposing the anthers as a single unit. All anthers in individual flowers dehisce simultaneously by apical pores. All five flower types produce the same amount of pollen; it is 19,246 ± 346.4 per anther. The pollen grains are dry, powdery, yellow, spheroidal to sub-prolate, tricolporate and 27.39 ± 4 µm in size (Image 2a). The pollen release occurs through apical pores of the anthers when flower foragers exhibit buzzing behavior to collect pollen and in the absence of flower foragers, the pollen remain inside the anthers and is not self-exposed or released. The nectar disc is absent and hence nectar is not produced. As a result, the flowers offer pollen as exclusive reward for the probing insects.

Foraging behavior and pollination

The flowers were visited by five bee species, namely, *Apis cerana*, *Trigona iridipennis*, *Xylocopa latipes, X. pubescens*, and *Nomia* sp. during day time from 0700 to 1700 h (Table 1). These bees showed a gradual increase in foraging activity from morning and until noon and then a gradual decrease towards evening hours (Figure 3). Of these bees, *Xylocopa* bees exhibited buzzing

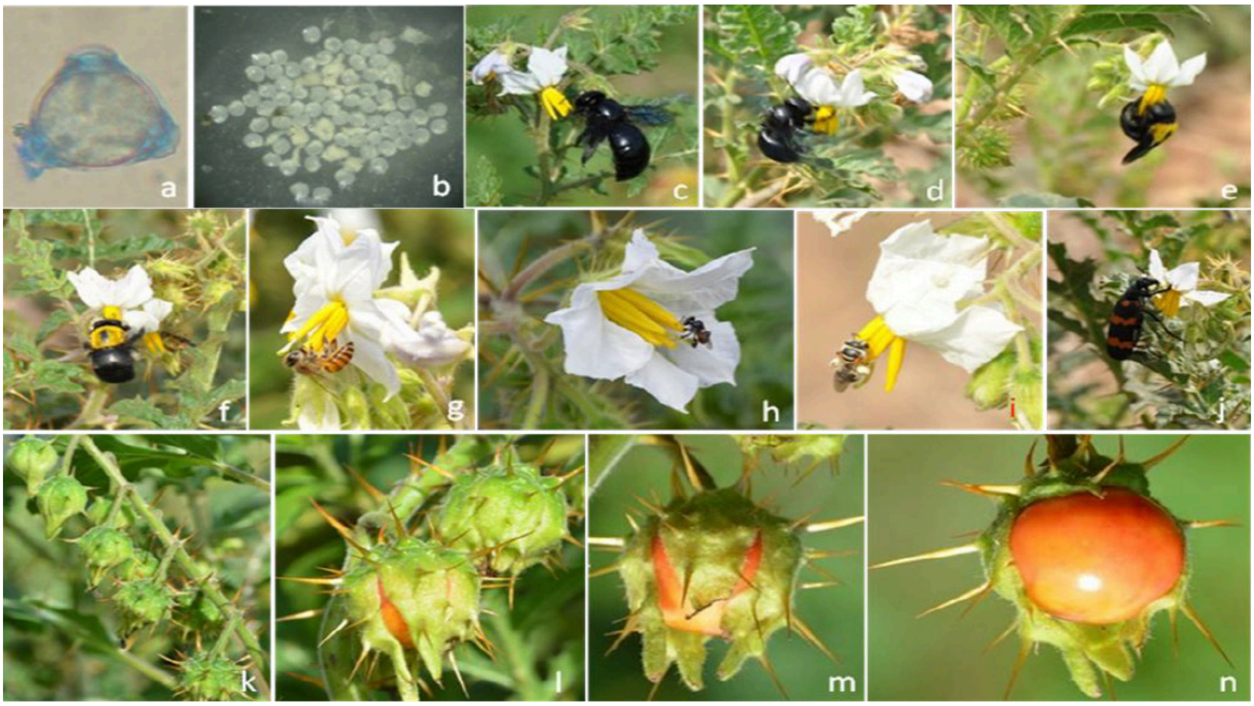

Image 2. *Solanum carolinense*: a—Pollen grain | b—Ovules | c—*Xylocopa latipes* approaching the flower for pollen collection | d—*X. latipes* vibrating the base of anthers for pollen collection | e & f—*Xylocopa pubescens* vibrating the anthers for pollen collection | g—*Apis cerana* collecting pollen from poricial anthers | h—*Trigona iridipennis* collecting pollen from poricial anthers | i—*Nomia* sp. collecting pollen from poricidal anthers | j—*Mylabris phalerata* feeding on the flowers | k—Fruiting branch | l–n—Fruit developmental stages. ©. A.J. Solomon Raju.

behavior to collect pollen from the poricidal anthers (Image 2c–f). The buzzing length was relatively very less at the fresh flowers and its length increased gradually with a gradual decrease in the amount of pollen in the anthers. Accordingly, the pollen quantity in anthers gradually decreased from morning to evening. These bees upon landing on the anthers, grasped the latter with their hind legs, rotated on the flower to handle each anther separately to collect pollen. In this process, they performed vibrations with their wings by producing audible buzzes. Then, the pollen was released as puffs from the apical pores of the anthers and it is dispersed into the air surrounding the stigma in case of long- and semi-long-styled flowers. Sometimes, the pollen-laden ventral side of the bee body came into contact with the stigma resulting in pollination. Some pollen gradually descended through narrow spaces between the anthers in all other flower types. The flowers that were visited by these bees showed bruise marks on the anthers and these marks were taken as indicators of bee visits that buzz the flowers. Large mass of pollen was visible on the hind legs of the bees visiting the flowers. The other bees, *Apis cerana, Trigiona iridipennis*, and *Nomia* sp. did not show buzzing behavior to handle anthers to collect pollen from apical pores but they simply gathered pollen on and around the rim of the apical pores and in this process, they were able to come in contact with the stigma in long- and semi-long-styled flower types effecting pollination (Image 2g–i). But the contact between the ventral side of the bee body and the stigma in these two flower types was found to be dependent on the posture used by the bees while gathering pollen. All bees were consistent and regular in utilizing the pollen from this plant during its peak flowering season. Only *Xylocopa* bees displayed fidelity to the flowers of this plant throughout its flowering season while all other bees paid visits to its flowers occasionally only. Of the total foraging visits made by bees, *Xylocopa* bees accounted for 54% and all other bees 46% during peak flowering period (Figure 4). Therefore, *Xylocopa* bees were found to be appropriate foragers and hence are the principal pollinators while other bees are only supplementary pollinators for the plant.

Florivory

The common blister beetle, *Mylabris pustulata* (Image 2j) was found feeding on the corolla, stamens, style and stigma (Table 1). Florivory by this beetle stood at 31% during peak flowering phase and at 8–9% in the initial and fag-end of flowering season. This phenomenon

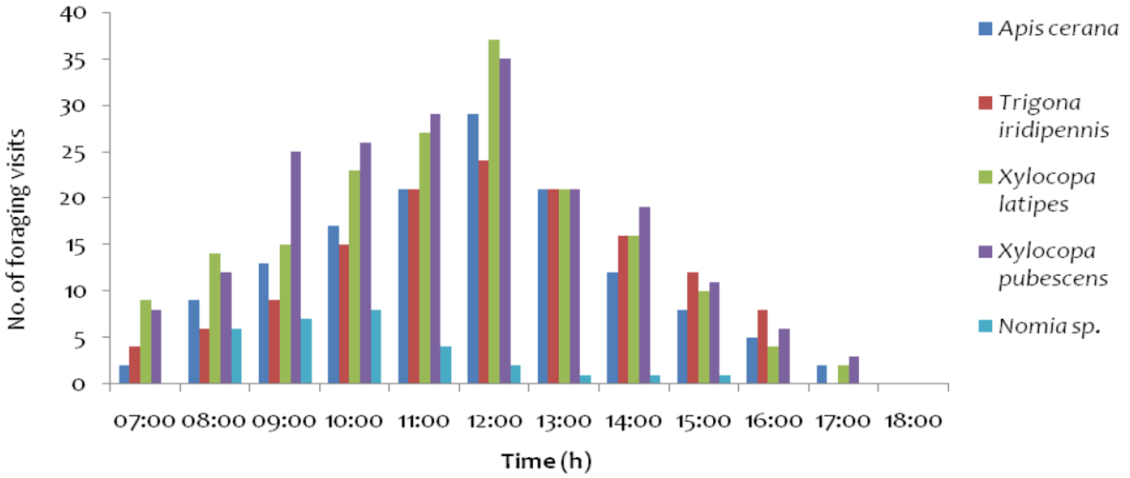

Figure 3. Hourly foraging activity of bees on *Solanum carolinense*.

Table 1. List of flower visitors on *Solanum carolinense*.

Order/ Family	Insect species	Forage sought	Foraging schedule (h)	Total No. of foraging visits/day*
Hymenoptera				
Apidae	*Apis cerana* F.	Pollen	0700-1700	139
	Trigona iridipennis Smith	Pollen	0700-1600	136
	Xylocopa latipes Drury	Pollen	0700-1700	178
	Xylocopa pubescens Spinola	Pollen	0700-1700	195
Halictidae	*Nomia* sp.	Pollen	0800-1500	30
Coleoptera				
Meloidae	*Mylabris phalerata* Pallas	Corolla, stamens, style and stigma	0800-1700	Resident flower feeder

*Approximately 300 flowers on closely spaced plants were used to record foraging visits/day by each pollen- collecting species. The foraging visits indicate mean number of foraging visits made on four clear sunny days during peak flowering days.

appears to have a detrimental effect in the plant for the success of its sexual reproduction.

Natural fruit set and fruiting ecology

Initiation of fruit development occurs as soon as flowers are fertilized and mature and ripe fruits form within a month (Image 2k–n). In open-pollinations, fruit set occurs only in long- and semi-long-styled flower types only. Fruit set is 88% in long-style flower type and 45% in semi-long-styled flower type (Table 2). Fruit is an indehiscent, many-seeded berry; it is dark green when immature and scarlet-orange when mature. The calyx encloses the berry completely throughout the course of its development and maturation. But, the calyx lobes gradually separate and partially unfold exposing the ripe berry.

DISCUSSION

In this species, the role of androecium is different in hermaphrodite and male flowers. In both flower sexes, the anthers are of the same size and produce the same quantity of pollen but display some form of specialization in each flower sex. The anthers of male flowers act primarily as possible near-distance attractors and as pollen donors while hermaphrodite flowers act primarily as pollen recipients and as pollen donors (Connolly & Anderson 2003). In another report, *S. carolinense* is stated to be andromonoecious and functional through long-styled and short-styled flowers; the former type serves primarily as pollen recipient while the latter type as pollen donor (Quesada-Aguilar et al. 2008). *S. carolinense* is self-incompatible but it is flexible as a part of stable mixed mating system which permits self-fertilization when cross-pollination limits seed production

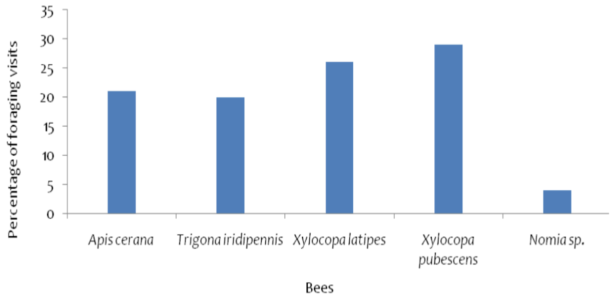

Figure 4. Percentage of foraging visits of bees on *Solanum carolinense*.

Table 2. Fruit set rate in different flower types of *Solanum carolinense*.

Flower type	No. of flowers tagged	No. of flowers set fruit	Fruit set (%)
Long styled	26	23	88
Semi-long-styled	20	9	45
Medium-styled	15	0	0
Short-styled	15	0	0
Ovary lacking style and stigma	10	0	0

in situations of establishing new populations (Kariyat et al. 2011). In the present study also, *S. carolinense* is found to be andromonoecious but this sexual system is functional through heterostyly involving long, semi-long, medium, & short-styled flower types and also another flower type lacking style & stigma completely. All these flower types are present together on the same plant. All individuals produce long-styled flower type while other flower types are not produced by all individuals. The long- and semi- long-styled flowers are functionally co-sexual and produce fruit while the other flower types are functionally male or female-sterile and do not product fruit. The style is placed slightly above the anthers in semi long-styled flowers while it is placed comparatively far above the anthers in long-styled flowers. Such a placement of the style in these flower types facilitates and ensures the occurrence of pollination by specialized pollen collecting bees. In medium- and short-styled flower types, the style is not exposed and enclosed by conical-shaped anthers; there is no scope for contact between the style and pollen collecting bees in these flowers. In flowers lacking style and stigma, the question of pollinator contact with these sex organs does not arise at all. The heterostyly condition functional through andromonoecy appears to have evolved in response to the limitation of nutrients and the production of extra functionally male flowers against functional co-sexual flower types appears to be an indication of resource constraints under which fruit production is most unlikely (Whalen & Costich 1986; Diggle 1991; Meagher 1992). The production of female-sterile flowers is cheaper to produce than perfect flowers and the resources saved by them are not re-allocated to other fitness enhancing functions. The principal morphological trait of female-sterile flowers is pistil reduction which does not increase either pollinator visitation or siring success of open-pollinated flowers (Vallejo-Marin & Rausher 2007). The production of female-sterile flower type completely lacking style and stigma is a functional step in the evolution of perfect male flowers and also an indication of resource constraints for enhancing fruit production. Therefore, the flowers that present style above anthers are functionally co-sexual and fruit producing while the flowers that present style within the anthers or that lack style and stigma are functionally female sterile or male.

In flowering plants, most of the species exhibit longitudinal and poricidal mode of anther dehiscence; in the former mode, pollen is presented along the line of dehiscence and its collection does not require special skills from pollinators while in the latter mode, pollinators require special skills to squeeze the anthers by special buzzes or vibrations in order to collect pollen from the apical pore. In flowers with poricidal anthers present only pollen as the reward and hence pollen collecting insects that exhibit buzzing behavior can only collect this reward while other foragers either visit and subsequently depart from such flowers or do not visit such flowers at all (Buchmann 1983). Different authors (Hardin et al. 1972; Quesada-Aguilar 2001; Connolly & Anderson 2003; Travers et al. 2004; Vallejo-Marin & Rausher 2007; Quesada-Aguilar et al. 2008) reported that *S. carolinense* is pollinated by bees in USA. It is pollinated by pollen-gathering bees which display buzzing behavior, *Lasioglossum* spp., *Augochloropsis metallica*, and *Bombus impatiens.* In the present study, *S. carolinense* flowers display poricidal mode of anther dehiscence and pollen production is copious in poricidal flowers. The carpenter bees employ buzzing or vibration behavior to extract pollen from poricidal anthers by means of vibrations of the wing muscles. Since the pollen is dry and powdery, the carpenter bees collect it with great ease (Buchmann et al. 1989). All other bees recorded on *S. carolinense* do not exhibit buzzing behavior but simply gather pollen from the rim of the apical pores of the anthers. The study shows that there appears to be a positive relationship between the style length and pollen deposition and a negative relationship between the style length and pollen removal in flowers visited by carpenter bees. The study shows that the style length has a positive relationship with pollen deposition and a negative relationship with pollen removal in flowers visited by carpenter bees. But in flowers visited by other bees, their morphological or behavioral traits do not determine pollen deposition or removal. Quesada-Aguilar et al. (2008) reported similar situation in *S. carolinense* in which the style length has a positive relationship with pollen deposition and a negative relationship with pollen removal in flowers visited by bumble bees. The morphological or behavioral traits of small halictid bees that visit the flowers of *S. carolinense* do not determine pollen deposition or removal. The study indicates that pollinator-specific interactions with flower morphology are important in the maintenance and perfect evolution of andromonoecy in this plant species.

Michael & Christopher (1996) reported that the caterpillars of the moths, *Synanthedon rileyana* Edwards, 1881 and *Manduca sexta* Linnaeus, 1763*,* and the beetles, *Leptinotarsa junca* Germar, 1824 and *Epitrix fuscula* Crotch, 1873 feed on *S. carolinense*. The beetles reduce fruit production to the extent of 75%. Michael (2007) reported that the weevils, *Trichobaris trinotata* Say, 1832 and *Anthonomus nigrinus* Boheman, 1843 affect or reduce plant growth and fruit set rate, the former bores into the stems while the latter feeds on the flowers. Wise & Hebert (2010) reported that higher levels of florivory and frugivory would favour lower floral-sex ratios biased in favour of lower proportion of male flowers while lower levels of herbivory would favor higher floral sex ratios biased in favour of optimum percentage of male flowers *S. carolinense*. In the present study, florivory by a common blister beetle *Mylabris pustulata* is found to vary with the flowering intensity in *S. carolinense*. However, florivory levels are not high and this situation would favor higher floral-sex ratios biased in favour of higher proportion of female sterile flowers. But, florivory by this beetle could influence the success rate of sexual reproduction.

CONCLUSIONS

In Solanum carolinense, andromonoecious sexual system is functional through heterostyly involving long, semi-long, medium and short-styled flower types, and also through another flower type lacking style and stigma completely. All plants produce long-styled flowers while other flower types are not produced by all individuals. The long- and semi- long-styled flowers are functionally co-sexual and produce fruit while the other flower types are functionally female-sterile and do not product fruit. The position of style in long- and semi-long-styled flowers the style facilities the occurrence of pollination by pollinator bees. *Xylocopa* bees are large-bodied specialist bees which collect pollen from poricidal anthers in this plant species by displaying buzzing behaviour and hence are treated as principal pollinators. The other bees are small-bodied and do not display buzzing behaviour to release pollen from poricidal anthers but they simply collect residual pollen that is available around the rim of the apical pore of the anthers, and hence they act as supplementary pollinators only. The study shows that in *S. carolinense* the style length has a positive relationship with pollen deposition and a negative relationship with pollen removal in flowers visited by *Xylocopa* bees and hence, pollinator-specific interactions with flower morphology are important in the maintenance and perfect evolution of andromonoecy in this plant species. Florivory by *Mylabris pustulata* could vary with the flower production rate in *S. carolinense* during its flowering season and it could favor higher floral-sex ratios biased in favour of higher proportion of female-sterile flowers if there is persistence of florivory.

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NAAS rating (India) 5.64

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OPEN ACCESS

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

February 2023 | Vol. 15 | No. 2 | Pages: 22559–22770
Date of Publication: 26 February 2023 (Online & Print)
DOI: 10.11609/jott.2023.15.2.22559-22770

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Short Communications

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