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ORIGINAL RESEARCH ARTICLE

Amegilla violacea (Lepeletier, 1841) (Anthophorini: Apidae) – A native bee, an effective pollinator of eggplant (*Solanum melongena*)

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Eggplant is an important vegetable crop grown worldwide. Eggplant flowers have typical poricidal anthers which need a vibratory motion for effective pollination. This study was conducted to identify the major flower visitors and their effect on eggplant pollination/fruit set. Nine different species of bees visited eggplant flowers. The pollination efficiency index of the buzz pollinating bee, *Amegilla violacea*, was found to be the highest and was the most efficient pollinator of eggplant. The fruit set, fruit weight, and the number of seeds per fruit increased with an increase in the level of anther cone bruising and with a greater number of buzzes made by the native bee. Our study confirmed the distinct role of native sonicating bees and emphasizes the need to conserve the native bee fauna for enhancing fruit and seed set in eggplant.

Keywords: Anther cone; bruising; crop pollination; buzz pollination; foraging behavior; native bee

Introduction

Eggplant, *Solanum melongena* (Solanaceae) is an important vegetable crop grown worldwide and rich in nutrients. Eggplant flowers, like many species of Solanaceae and specifically *Solanum* genus (Buchmann, 1983; Bezerra & Machado, 2003), present typical poricidal anthers. The anther cone needs a vibratory motion (buzz pollination or sonication) to expel the pollen onto the female flower parts (De Luca & Vallejo-Marín, 2013; Shelly & Villalobos, 2000). The pollination starts with the bee's vibratory motion (made by its thoracic wing muscles), the pollen is loosened from the anther locules and is dispersed (Proenca, 1992); bees are rewarded with the pollen which is collected in their branching hairs over their legs and abdomen (Buchmann, 1983). Poricidal anthers in plants were reported to be an evolved morphological feature for 'pollen dispensing' to increase pollination and limit pollen loss as they release pollen based on vibration created by the buzzing bees (Moquet et al., 2017). Buzz pollination, therefore, referred to an adaptive mechanism for pollen release, pollen collection, and deposition in stigma thereby improving self pollination (Arceo-Gómez et al., 2011). Bees belonging to the genus *Hoplonomia*, *Lasioglossum*, *Patellapis*, *Amegilla,* and *Xylocopa* were known to buzz pollinate at the flowers with poricidal anthers in Sri Lanka (Karunaratne et al., 2005). Amala and Shivalingaswamy (2017) recorded major fruit weight and a number of seeds in tomato under open field conditions mediated by the native buzz pollinating bee, *Amegilla zonata*. *Solanum* plants grown in cages with complete exclusion of pollinators were incapable of setting fruits (Kakizaki, 1924). Jayasinghe et al. (2017) reported seven different bee species as floral visitors in eggplant with increased fruit set and seed set in eggplant due to buzz pollinating bees suggesting that beyond cross pollination, vibration by the bee during buzzing activity cause the pollen to dislodge easily and get dropped over the stigma resulting in improved self pollination.

Visitation by the sonicating native bees causes typical bruising or necrotic spots on the anther cone of *Solanum* flowers. For example- tomato flowers handled by bumble bees recorded necrotic spotting or bruising in the anther cone (Bin & Sorressi, 1973). The level of anther cone bruising was used as a monitoring tool to assess the bumble bee visitation level in greenhouse tomatoes and to standardize the bumble bee colony requirement for pollination (Morandin et al., 2001). Unfortunately, the role of native bees in the pollination and fruit set of eggplant in India are scarce. The present study was undertaken to identify the major flower visitors and their effect on pollination and fruit set in eggplant. We recorded the native floral visitors, foraging behaviour of the visitors, effective buzz pollinator, degree of anther cone bruising, and the number of buzzes on the fruit and seed set in eggplant crop.

Materials and methods

Study area

The present study was carried out in the experimental farm of ICAR-National Bureau of Agricultural Insect

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Resources (NBAIR) Bengaluru, Yelahanka Campus (13.096792 N, 77.565976E) from July 2016 to May 2017. The experiment was conducted in a plot size of 0.15 acres in eggplant (cv. Gaurav) crop (Figure 1 and 2). The study area comprised cultivated croplands with various annual crops like cereals and pulses, orchard blocks of mango, sapota, and cherimoya. Also, there were two patches of pollinator gardens of about 1.5 acres with over 100 plant species of diverse plant families. This research campus is situated right in the heart of a rapidly growing high-tech-city and capital of the southern Indian state of Karnataka. The mean maximum and minimum temperature during the flowering period was 27.8 °C and 19 °C, respectively, with rainfall of 51.4 mm.

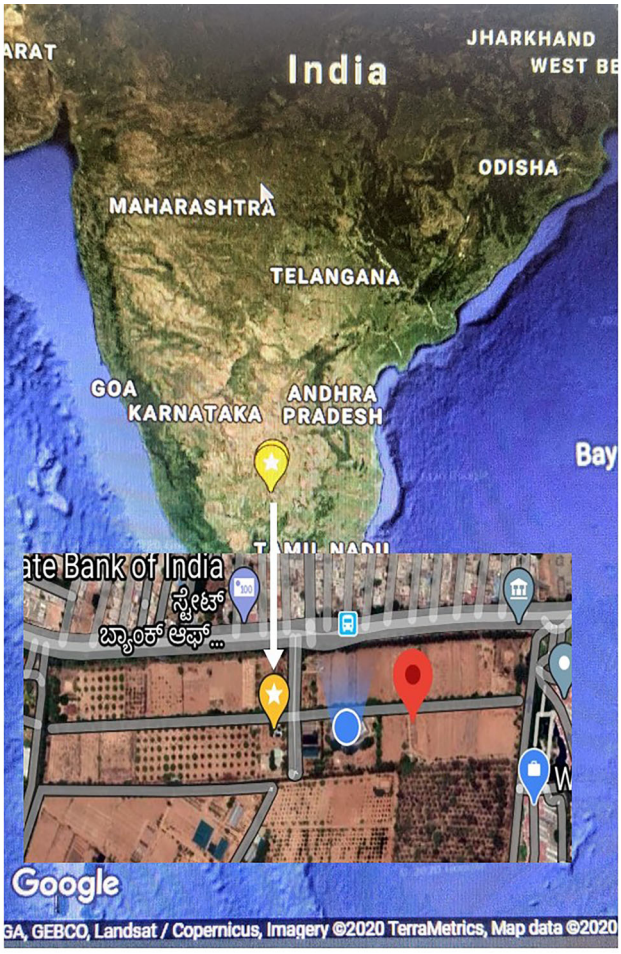

Figure 1. Satellite image of thestudy area (Bengaluru, India).

Bee foraging behaviour

We recorded eggplant floral visitors by direct observation and captured them in yellow pan traps or sweep net. The flower visitors were collected using sweep nets and killed using ethyl acetate, were sorted and dry preserved for taxonomic identification. The behavior of the flower visitors for sonication/scraping the anther cones/robbing were recorded. Further observations were made on the native buzz pollinating bees (*H. westwoodi*, *A. zonata,* and *A. violacea*). The number of flowers visited by the three species of buzz pollinating bees was recorded at three different time points viz. 7–8 am, 12–1 pm, and 3–4 pm. The time spent by the bees per flower was recorded. The number of flowers per unit time by the bees was also recorded. The peak time of activity of the three species of bees was also recorded right from the time of anthesis (6.30 am to 6.30 pm).

Pollination efficiency index of buzz pollinators

The comparative pollination efficiency of the three buzz pollinating bees, *A. violacea*, *A. zonata,* and *H. westwoodi* was studied in eggplant by recording various parameters *viz*. the number of loose pollen grains on their body, rate of foraging, and abundance of other insect

Figure 2. Experimental Plot.

Figure 3. Bruising level categories of eggplant flowers based on levels of necrotic discoloration on the anther as a result of *Amegilla violacea* buzz pollination.

pollinators in the flowers (Balina et al., 2012). The pollination index was estimated by:

$$P\ index = pollen \times FR \times A$$

where Pollen corresponds to the number of pollen grains on the buzz body of the bee, FR is the number of flowers visited by the bee, per/minute and A is the number of bees/m^2 observed during five minutes.

The pollen grains on the body of the three buzz pollinating bees were counted by randomly collecting ten individuals of the bees during their peak time of activity (morning hours). The collected pollen laden bees were shaken vigorously in 70% ethanol to remove the entire pollen from the body of the bee. The volume of ethanol was made up to 5 ml and 1 ml of aliquot was taken and the number of pollen grains was counted using the hemocytometer. The pollen structure of the eggplant was compared with the reference pollen slides maintained in our laboratory.

Effect of different levels of bruising by native bee, A. violacea on pollination

The flowers attended by an efficient pollinating native bee *A. violacea* were observed to contain bruise marks after flower handling. Different levels of bruising were observed over the flowers depending upon the number of visits made by *A. violacea*. The bruising was categorized into four different levels as reported by Morandin et al. (2001). The levels of bruising were categorized as Level 0 - no bruising; Level 1 - One or two small areas of discoloration; Level 2 - Two to three small to medium size discolorations; Level 3 - One or more large, or greater than 3 medium discolorations; Level 4 - Entire anther cone bruised, and anthers coming apart (Figure 3). Ten flowers in each category level of bruising were observed and bagged using a mesh cover to avoid further visits by *A. violacea* and set aside till fruit set. The percent fruit set and the number of seeds set per fruit in each level of bruising was recorded. The relation between the number of visits made by *A. violacea* and the percent fruit set was studied. The set fruits were allowed for ripening under the field conditions and brought to the laboratory for extraction of the seeds. The extracted seeds were dried and counted.

Effect of number of buzzes made by A. violacea on fruit set

To study the effect of the number of buzzes of *A. violacea* on flowers, 50 flowers of eggplant were selected. The visits by *A. violacea* were observed, the newly opened fresh flowers visited were covered after two buzzes (25 flowers, two per plant) or multiple buzzes (preferably 3–6 buzzes; 25 flowers, two per plant) using a mesh bag to prevent further visits by *A. violacea* or other species of bees and were observed till fruit set. The percent fruit set in both the treatments were recorded. The fruits after attaining physiological maturity were harvested; fruit weight was recorded, and then allowed for complete ripening. The seeds were extracted from the ripened fruit and counted.

Results

Foraging behaviour of bees in eggplant

Nine different species of bees were observed to visit the flowers of eggplant (Table 1) during the flowering period. O nine species, three are honey bees viz., *A. cerana*, *A. dorsata,* and *A. florea* were observed to rest on the anther cone and to scrape the anther cone. Two species of digger bees viz. *A. zonata* and *A. violacea* were seen buzz pollinating the flowers soon after anthesis. *A. violacea* was found to visit newly opened flowers rather than old flowers. Two species of large carpenter bees viz. *X. fenestrata* and *X. ruficornis* were also noticed attending to the flowers. Pearl banded bee *H. westwoodi* (Nomiinae) was observed to sonicate the flowers and *Lasioglossum* sp (Halictinae). Foraging of *A. violacea* was uniformly distributed across the three time-points whereas *A. zonata* and *H. westwoodi* were found abundantly only during the morning hours. Another three species of bees, *Lasioglossum* sp, *X. fenestrata,* and *X. ruficornis* though found to be less abundant were observed to forage uniformly throughout the day. The time spent per flower by the sonicating bees was 18, 18.33, and 32 seconds by *A. violacea*, *A. zonata* and *H. westwoodi,* respectively. Two species of the large carpenter bee, *X. fenestrata and X. ruficornis* spent 50.07 and 42.18 seconds per flower n eggplant. *Lasioglossum* sp spent maximum time per flower (80 seconds).

Soon after the onset of anthesis during the early morning hours, the flowers were observed to be attended by the three buzz pollinating bees, *A. violacea, A. zonata and H. westwoodi.* Uniform visitation pattern was observed by the three flower visitors although the abundance varied between the species across different time points of observation. Among the three buzz pollinators, *A. violacea* was observed to be most abundant during morning hours (3.47–4 bees/5 minutes) followed by *A. zonata* (3.33–2 bees/5 minutes) and *H. westwoodi* (1.66 bees/5 minutes). The descending order of the number of flowers visited by the buzz pollinating bees in eggplant was *A. violacea* > *A. zonata* > *H. westwoodi*. The mean number of flowers visited by *A. violacea*, *A. zonata* and *H. westwoodi* was 6.0, 4.2, and 2.1 flowers/minute, respectively.

Pollination efficiency index of native buzz pollinating bees

A. violacea had entrapped a greater number of pollen grains on its body (29,15,696) followed by *A. zonata* (6,63,872) and *H. westwoodi* (3,89,392). The reason for the relatively larger number of pollen grains trapped by *A. violacea* might be due to its larger body size than *H. westwoodi* and *A. zonata*. De Luca et al. (2019) reported that larger sized bees generated increased buzz ratio causing greater floral vibrations to liberate more pollen from the poricidal stamens. The foraging rate (6.10 number of flower visited/minute) and abundance of *A. violacea* (3.80 bees/m^2/5 minutes) was the highest. The pollination index of *A. violacea* was the highest (29,15,696) followed by *A. zonata* (6,63,872) and *H. westwoodi* (3,89,392) (Table 2). A positive correlation (R-value = +0.96) between the number of visits made by *A. violacea* and the percent fruit set was observed in eggplant (Figure 4).

Table 1. Flower visitors of eggplant.

Bee species	Family	Buzz pollination
Apis dorsata	Apidae	X
A. florea	Apidae	X
Apis cerana indica	Apidae	X
Amegilla violacea	Apidae: Anthophorini	✓
A. zonata		✓
Xylocopa fenestrata	Apidae: Xylocopini	✓
X. ruficornis	Apidae: Xylocopini	✓
Hoplonomia westwoodi	Halictidae: Nomiinae	✓
Lassioglossum sp.	Halictidae: Halictinae	X

X indicates no Buzz pollination; ✓ indicates Buzz pollination.

Effect of levels of bruising and multiple buzzes on fruit set in eggplant

There was a steady increase in the percent fruit and number of seeds/fruit eggplant with the increase in the level of bruising (Figure 5). The highest fruit set and the number of seeds/fruit was observed in Level 4 bruising and were 94.20% and 99.19 seeds/fruit, respectively. The percent fruit set and fruit weight were significantly higher in the flowers that received 3–6 buzzes (72.30% and 23.35 g/fruit) than in 1–2 buzzes (58.5% and 18.85 g/fruit) by *A. violacea* (Figure 6).

Discussion

We documented the native floral visitors, their foraging behavior, identified an effective buzz pollinator, the degree of anther cone bruising, and the number of buzzes on the fruit and seed set in eggplant. The plant was visited by nine different species of bees viz. *A. dorsata*, *A. florea*, *A. cerana*, *A. violacea*, *A. zonata*, *X. fenestrata*, *X. ruficornis*, *H. westwoodi,* and *Lasioglossum* sp. *A. violacea* was the main pollinator of the eggplant in terms of pollination index. Other species were also important pollinators because they actively buzz pollinate the flowers of eggplant. The buzzing bees were found to visit the flowers immediately after the onset of anthesis followed by honey bees. Similar observations were recorded by Wanigasekara and Karunaratne (2012) who reported the maximum activity of buzzing bees, *H. westwoodi*, *A. comberi*, *Patellapis kaluterae* and *X. tenuiscapa* on the flowers of *Solanum violaceum* – a wild relative of eggplant after anthesis. Honey bees were observed to scrape the pollen and spread it over the anther cone and other floral parts soon after the visitation by the buzzing bees. Honey bees lack the ability to buzz pollinate hence they are poor pollinators of *Solanum* flowers (King & Buchmann, 2003). Flowers that demands buzz pollination generally are not capable of producing nectar reward (Moquet et al., 2017). Fenster et al.,(2004) referred it to be 'pollination syndrome' where floral traits (poricidal anthers) and rewards were closely related to the attraction and utilization by specific groups of pollinators. In the present study, poricidal anthers of eggplant were suited for the buzzing activity by native bees to effect pollination.

Under open field conditions, tomato flowers were reported to be pollinated by *Oxaea flavescens*, *Exomalopsis analis*, *Exomalopsis fulvofasciata*, *Thygater analis*, *Trigona spinipes*, *Augochloropsis callichroa* and *Pseudaugochlora erythrogaster* (Santos et al., 2014; Silva et al., 2017). Inoka et al. (2006) reported five species of

Table 2. Pollination efficiency of three different bee species visiting eggplant.

Bee species	Abundance (bees/m^2/5 minutes)	Foraging rate (number of flowers visited/minute)	Number of pollen grains on the body of a bee	Pollination index (abundance × foraging rate × pollen grains)	Pollination efficiency (Rank)
A. violacea	3.80	6.10	125785	29,15,696	1st
A. zonata	2.33	4.20	67839	6,63,872	2nd
H. westwoodi	2.06	2.10	90012	3,89,392	3rd

buzzing bees, *A. comberi*, *Amegilla* sp., *Gnathonomia nasicana*, *Leuconomia* sp., and *H. westwoodi* from the eggplant. *A. violacea* was observed to spend less time in the flowers of eggplant followed by *A. zonata* and *H. westwoodi*. Bees of the genus *Amegilla* spent the least time in flowers of eggplant followed by *Hoplonomia* and *Pachynomia* sp. (Anderson & Symon, 1988).

A. violacea was more abundant and visited more flowers of eggplant per minute compared to the other two buzz pollinating bees, *H. westwoodi* and *A. zonata*. This bee is bigger in size compared to the other two species and carried a greater number of pollen grains on its body surface. The foraging behavior of bees is a vital factor that determines the pollination efficiency (Singh et al., 2006). Based on the pollination index, it was evident that *A. violacea* was the most efficient pollinator of eggplant followed by *A. zonata* and *H. westwoodi*. Devkota and Thapa (2005) reported a significant difference between the number of broccoli flowers visited per minute between two different species of honey bees, *A. cerana, A. mellifera* and *A. cerana* showed higher flower visiting efficiency compared to *A. mellifera* resulting *A. cerana* as an efficient pollinator of broccoli compared to *A. mellifera*. There was a steady increase in percent fruit set and the number of seeds per fruit with an increase in the level of bruising. The intensity of bruise on the anther cone of tomatoes was considered as a sign of successful visitation and pollination by the bumble bees (Silva et al., 2013). The number of flowers visited and pollinated by bumble bees was assured by the brown discoloration of the anthers (Ravestijn & Sande, 1991). Aizen et al. (2002) found that a large number of seeds were produced due to cross pollination by bees compared to artificial pollination which resulted in fewer seeds in *S. melongena*. Buzz pollination by bees is an essential factor for pollination in *Solanum* crops and also improves the yield and quality of fruits produced. An increase in fruit mass of tomatoes by buzz pollinating bee, *Exomalopsis analis* (Apidae) compared to self pollinated flowers was observed (Barbosa et al., 2019). An increase in richness and functional diversity of wild bees increased the seed set and reduced the pollen limitation in apples (Blitzer et al., 2016). Diverse bee species in an ecosystem might increase pollination services through increased richness through the concept of niche partitioning (Fontaine et al., 2006; Hoehn et al., 2008; Tylianakis et al., 2008). Seed production of eggplant under polyhouse conditions

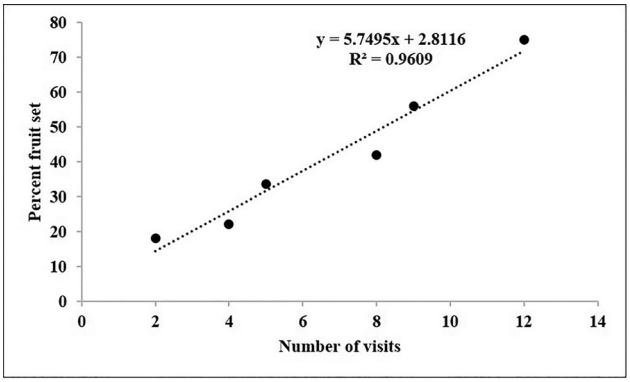

Figure 4. Relationship between the number of visits made by *A. violacea* per flower and percent fruit set in eggplant.

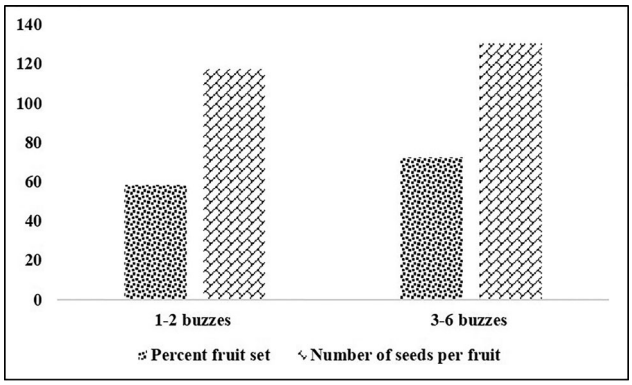

Figure 6. Effect of multiple buzzes made by *Amegilla violacea* on fruit set and seed set in eggplant.

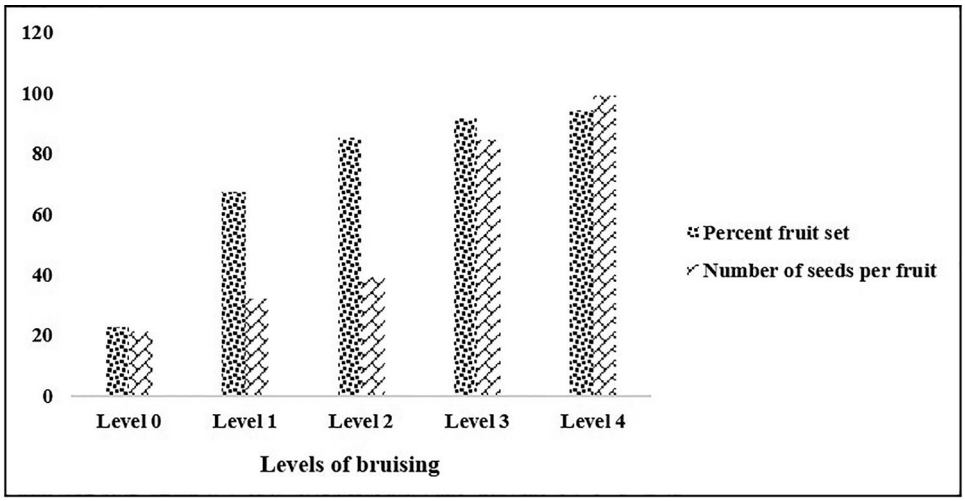

Figure 5. Effect of different levels of anther cone bruising made by *Amegilla violacea* on fruit weight and seed set in eggplant.

warrants the need of buzz pollinating bees for enhanced seed set. A significant difference in the fruit set and fruit weight was observed with respect to the number of buzzes made by *A. violacea*. Similar observations were made by Belavadi (2012) who reported a positive correlation between the number of visits made by a long tongued bee, *Amegilla* sp. with the percent capsule set in cardamom. More buzzes might have resulted in increased levels of bruising by *A. violacea* that resulted in enhanced fruit set, seed set, and fruit weight of eggplant. Buzz density was reported to be positively correlated with the bumble bee density as well as seed set in two alpine forbs, *Trifolium dasyphyllum* and *Trifolium parryi* (Miller-Struttmann et al., 2017).

Conclusions

Native bees were reported to help in effective pollination of crop plants with unique floral morphology and these bees are very diverse and abundant near natural ecosystems (Kremen et al., 2004, Ricketts et al., 2008). Garibaldi et al. (2013) reported that flower visitation by wild insects increased the fruit set by twice as much as an equivalent increase in managed honey bee visitation. In the case of eggplant, as other *Solanum* flowers seldom produce nectar and honey bees that lack the ability buzz pollinate have an insignificant role in pollination. Semi-natural habitats adjacent to sweet cherry orchards were reported to support pollinator species richness and wild pollinator abundance was clearly linked to fruit set in sweet cherry (Eeraerts et al., 2019; Nicholls & Altieri, 2013). Agriculturally dominated landscapes negatively impact the diversity of bee pollinators and pollination and ecosystem services provided by bees (Grab et al., 2019). The persistence of wild bees in an ecosystem relies upon the maintenance of high-quality semi-natural habitats around the farms and on crop management practices that may buffer the impacts of intensive monoculture (Kennedy et al, 2013). Our present study confirmed the distinct role of native sonicating bees in the fruit and seed set of eggplant. Also, the results emphasize the need to conserve the native bee fauna for enhancing fruit and seed set in eggplant. Our study area comprising of diverse non-crop plants along the farm avenues and pollinator gardens in the vicinity of the experimental area served as a pollinator reservoir. This helped in attracting wild bees especially *A. violacea* to eggplant and enhancing the pollination and fruit set under open field conditions.

Disclosure statement

No potential conflict of interest was reported by the authors.

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