



MORPHOLOGY AND INSECT VISITORS OF *Solanum torvum* SW. (SOLANACEAE) FLOWERS

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ABSTRACT

Objective: The aim of this paper was to analyze the floral morphology and identify the visitors to the flowers of *Solanum torvum* Sw. (Solanaceae).

Theoretical Framework: The morphological study of flowers and their interaction with visiting or pollinating insects are essential for the preservation, taxonomy and ecology of angiosperm species, particularly for the genus *Solanum* (Solanaceae). In the present study, *Solanum torvum* flowers were investigated and compared with other studied species of the genus.

Method: Flowers of *Solanum torvum* plants from vacant lots in Maringá and Sarandi, Paraná, Brazil, were selected for studies of morphology, anthesis and floral visitors. Insect behavior and identification were performed for 5 days. The temperature of the inflorescences was measured using a FLIR thermal camera.

Results and Discussion: The flowers of *Solanum torvum* have typical morphology of the genus, especially poricidal anthers and long or short style. The flowers are frequently visited by bees, here by *Bombus mori*. Our results were compared with other *Solanum* species, whose flower features, visiting insects and breeding system are shown in a table.

Research Implication/value: The study of the flower and insect visitors of *Solanum torvum*, associated with the survey of floral biology characters of other *Solanum* species, will contribute significantly to the taxonomy and ecology of the genus.

Keywords: Andromonoecy, Anthesis, *Bombus*, Long-styled Flower, Poricidal Anthers, Short-styled Flower.

MORFOLOGIA E INSETOS VISITANTES DE FLORES DE *Solanum torvum* SW. (SOLANACEAE)

RESUMO

Objetivo: O objetivo desse trabalho foi analisar a morfologia floral e identificar os visitantes das flores de *Solanum torvum* Sw. (Solanaceae).

Referencial Teórico: O estudo morfológico de flores e sua interação com insetos visitantes ou polinizadores são essenciais para preservação, taxonomia e ecologia de espécies de angiospermas, particularmente para o gênero *Solanum* (Solanaceae). No presente estudo, as flores de *Solanum torvum* foram investigadas e comparadas com outras espécies estudadas do gênero.

Método: As flores de plantas de *Solanum torvum*, que ocorrem em terrenos baldios de Maringá e Sarandi, Paraná, Brazil, foram selecionadas para estudos da morfologia, da antese e dos visitantes florais. O comportamento e a

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identificação dos insetos foram realizados por 5 dias. A temperatura das inflorescências foi medida mediante câmera termal FLIR.

Resultados e Discussão: As flores de *Solanum torvum* têm morfologia típica do gênero, especialmente as anteras poricidas e estiletes longos ou curtos. As flores são visitadas frequentemente por abelhas, nesse trabalho por *Bombus mori*. Nossos resultados foram comparados com outras espécies de *Solanum*, cujas características florais, insetos visitantes e sistema reprodutivo são mostrados numa tabela.

Implicações da Pesquisa/valor: O estudo da flor e insetos visitantes de *Solanum torvum*, associado com o levantamento de caracteres de biologia floral de outras espécies de *Solanum*, contribuirá significativamente com a taxonomia e ecologia do gênero.

Palavras-chave: Andromonoica, Anteras Poricidas, Antese, *Bombus*, Flor de Estilete Longo, Flor de Estilete Curto.

MORFOLOGÍA E INSECTOS VISITANTES DE LAS FLORES DE *Solanum torvum* SW. (SOLANACEAE)

RESUMEN

Objetivo: El objetivo de este trabajo fue analizar la morfología floral e identificar los visitantes a las flores de *Solanum torvum* Sw. (Solanaceae).

Marco Teórico: El estudio morfológico de las flores y su interacción con los insectos visitantes o polinizadores es esencial para la preservación, taxonomía y ecología de las especies de angiospermas, en particular del género *Solanum* (Solanaceae). En el presente estudio, se investigaron las flores de *Solanum torvum* y se compararon con las de otras especies estudiadas del género.

Método: Se seleccionaron flores de *Solanum torvum* provenientes de terrenos baldíos en Maringá y Sarandi, Paraná, Brasil, para estudios de morfología, antesis y visitantes florales. Se realizó un estudio de comportamiento e identificación de insectos durante cinco días. La temperatura de las inflorescencias se midió con una cámara termográfica FLIR.

Resultados y Discusión: Las flores de *Solanum torvum* presentan la morfología típica del género, especialmente anteras poricidas y un estilo largo o corto. Las flores son frecuentemente visitadas por abejas, en este caso por *Bombus mori*. Nuestros resultados se compararon con los de otras especies de *Solanum*, cuyas características florales, insectos visitantes y sistema reproductivo se muestran en una tabla.

Implicaciones de la Investigación/Valor: El estudio de los visitantes de flores e insectos de *Solanum torvum*, asociado con el estudio de los caracteres de la biología floral de otras especies de *Solanum*, contribuirá significativamente a la taxonomía y ecología del género.

Palabras clave: Andromonoecia, Anteras Poricidas, Antesis, *Bombus*, Flor Brevistila, Flor Longistila.

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1 INTRODUCTION

Knowledge of flower biology in the widest sense is currently urgent, given the threats to biodiversity (Endress, 1994). Better knowledge of phylogenetic history and of interactions between animals and plants is vital for evaluation of conservation actions (*sensu* Endress,



1994). The study of flower life can provide new insights into the evolutionary ecology of species (Morellato & Leitão Filho, 1992; Kearns & Inouye, 1993).

Among the phanerogamous families that deserve attention is Solanaceae, which has a wide distribution around the globe, with the Neotropical region being the center of its diversity (Souza & Lorenzi, 2008; Powo, 2023). In Brazil, there are 36 genera and 515 species of Solanaceae, distributed throughout the territory, with a concentration of their diversity in the Atlantic Forest, especially in the southeast region, with *Solanum* L., *Cestrum* L. and *Brunfelsia* L. being the most common genera (Flora e Funga do Brazil, 2025).

Solanum is the most representative taxon of the family, which has 191 endemic species in the Brazilian territory (Flora e Funga do Brasil, 2025). The genus is traditionally characterized by the presence of poricidal anthers, and a feature that is considered a specialization of the group is pollination by vibration performed by bees (buzz-pollination) (Buchmann & Hurley, 1978; Storti, 1988; Endress, 1994; Souza & Lorenzi, 2008; Porto, 2015; Santana et al., 2023). In *Solanum*, female bees are considered effective pollinators and use pollen as their main reward (Buchmann, 1983; Judd et al., 2009).

The intensity of floral visitors depends on intrinsic and extrinsic factors of the visitors and the plant group visited (Waddington, 1983; Roubik, 1992). Biotic parameters of flowers such as color, symmetry, shape, floral density, temporal distribution of resources and attractants, and physical parameters, such as environmental conditions of temperature and humidity of the foraging area are important aspects when studying floral visitors and visit intensity (Waddington, 1983).

Temperature differences between flowers and the environment exert an effect on floral visitors (Kevan, 1975; Herrera, 1995). Floral thermogenesis results from the metabolic pathway and is associated with the presence of numerous mitochondria in these organs (Taiz & Zeiger, 2012), characteristics reported for several botanical families (Bernal & Ervik, 1996; Gottsberger & Silberbauer-Gottsberger, 2006; Gottsberger, 2012). The retention of solar heat and accumulation of heat produced in flowers are also associated with floral morphology, with aspects of shape, color, presence and size of trichomes being related to the thermal maintenance of the flower (Van der Kooi et al., 2019).

Research on the floral biology of *Solanum* has been carried out by several authors (Anderson, 1979; Storti, 1988; Forni-Martins et al., 1998; Oyelana & Ogunwenmo, 2012; Porto, 2015; Puthiamadom & Kumari, 2017; Passarelli, 2019; Kanta & Sharma, 2020; Ahmad et al., 2023; Santana et al., 2023), although the percentage of studies is still very low when the number of species is taken into account. In order to contribute to the characterization of the



genus, the aim of this paper was to analyze the floral morphology and identify the visitors to the flowers of *Solanum torvum* Sw., which is an annual and shrubby weed species. Data on floral morphology, visiting insects and possible reproductive system of *Solanum torvum* were compared with other investigated species of the genus (Table 1).

2 MATERIAL AND METHODS

Study location and samples – Floral buds and flowers were analyzed and collected from vacant lots on the campus of the State University of Maringa and in the city of Sarandi, Paraná, Brazil. For morphological analysis, five flowers from inflorescences of different plants were collected. For the study of insect visitors, some plants from both environments were used.

Flower morphology - The flowers were described morphologically according to the basic literature on flower terminology (e.g., Hickey & King, 2000, Beentje et al., 2010, and Souza et al., 2019). Morphometric data of the flowers were obtained using a digital pachymeter, taking measurements of the height and width of the floral pieces.

Morphological observations and photographic illustrations were performed using a Leica EZ4D stereoscopic microscope with a digital camera. Printed pictures were created using Inkscape 1.0.2 software, with the scales inserted using ImageJ software; the images were processed using GIMP 2.10.30 software.

Inflorescence temperature - The temperature of the inflorescences was measured using a FLIR thermal camera. The camera was previously calibrated to capture images in rainbow color, an option in which locations with higher temperatures have colors ranging from red to orange and cooler ones in shades of green and blue. In addition, the Thermal MSX (Multi Spectral Dynamic Imaging) mode was used to capture enhanced infrared images. The temperature of the inflorescences was measured in the morning and afternoon on three days in May 2023.

The images obtained by the camera were transferred to the FLIR Tools 3.15 software. In this software, some regions of the inflorescence were measured using a spot meter. At least two measurements were established per inflorescence. For statistical purposes, the average and maximum and minimum values of the inflorescence temperature were calculated per day, as well as the difference between the inflorescence and ambient temperatures. The images were organized into printing pictures using the Inkscape 1.0.2 software.



Insect visitors - For the observation, recording and behavior of floral-visiting insects, the inflorescences of the sampled population were inspected for 5 days in the morning, early afternoon and late afternoon, in visits of 5 minutes each, totaling 15 minutes per day and 1 hour and 15 minutes of total observation. The visiting insects, their behavior, the floral region visited and the possible resource collected were recorded. The behavior of the visitors was determined by direct observations and by photographic records and filming with a cell phone, during the visits to the inflorescences.

3 RESULTS

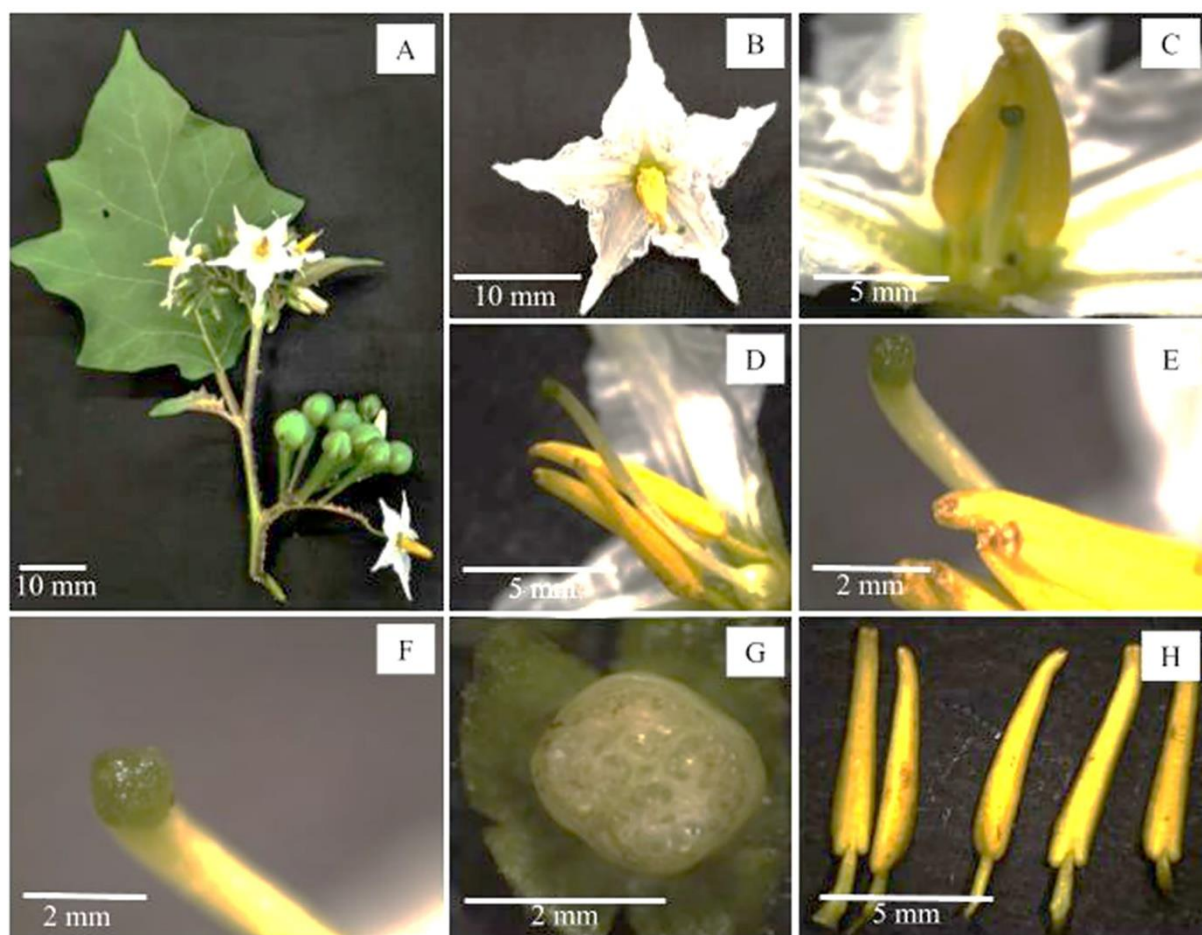
Flower morphology - The inflorescences (Figure 1A) are dichasium with around 30 flowers. The flowers (Figure 1A) are pedicellate, and have approximately 12 millimeters in size. Flowers and fruits at different stages of maturation were observed in the inflorescences (Figure 1A). The flowers (Figure 1A,B) are pentamerous, actinomorphic, dichlamydeous and heterochlamydeous, with a greenish hairy calyx and a cream-colored corolla. Calyx and corolla (Figure 1B) have fused sepals and petals. The corolla (Figure 1B) exhibits emerald green coloration at the base, around the stamens.

The flowers (Figure 1B,D,E) are staminate and pistillate. The androecium (Figure 1B,H) is isostemone, has stamens of the same height, and they measure approximately 5 millimeters. The anthers are poricidal and yellow in color (Figure 1B,D-F,H). The gynoecium (Figure 1B,D-F,G) is unipistillate, with a little more than 13 millimeters in length, and exhibits a moist capitate stigma, style, and bicarpellary, bilocular, pluriovulate, superior ovary, with axile placentation. Most of the flowers investigated have part of the style and stigma elevated in relation to the stamens (Figure 1B), but a flower with a short style with anthers above the stigma was found (Figure 1C).



Figure 1

Flower morphology of Solanum torvum. A - Branch with flowers and fruits. B - Flower showing corolla and stamens surrounding the gynoecium. C - Flower with stamens/anthers located above the pistil. D - Detail of the stamens and gynoecium with superior ovary. E - Stigma/style and poricidal anthers. F – Detail of the stigma and style. G - Ovary cross-sectioned with 2 carpels and axial placentation. H - Detail of the stamens that have the same height.



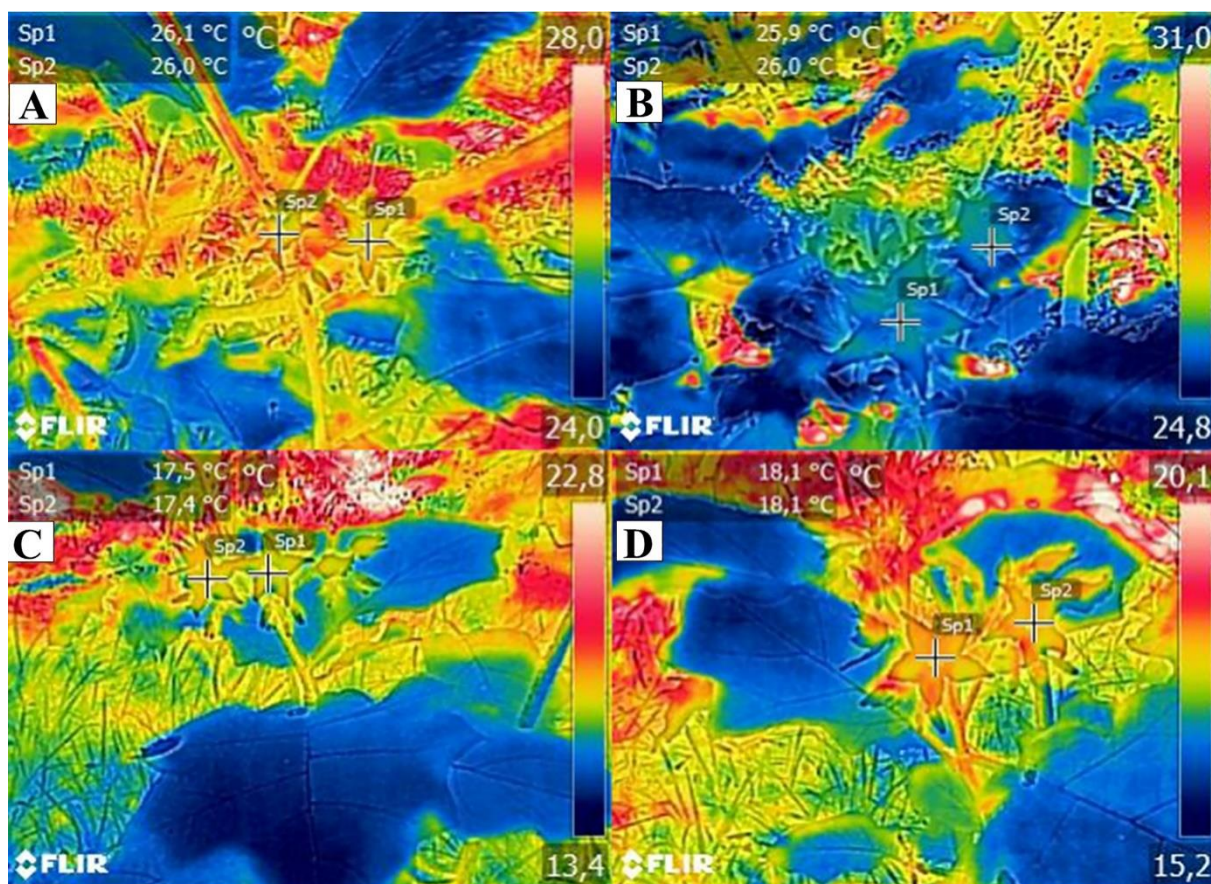
Source: Produced by the author Patrícia Viviane Zorzetto.

Inflorescence temperature - It was observed that all flowers were exposed to shade in the morning and afternoon periods. During the morning, inflorescence temperatures ranged from 25.9°C to 26.1°C when the ambient temperature was 25°C (Figure 2A). The inflorescences also presented temperatures of 17.4°C, 17.5°C and 18.1°C when the ambient temperature was 16°C (Figure 2C-D). It can be stated, therefore, that the temperature of the inflorescences/flowers was higher than that of the ambient, showing an increase of up to 2.1°C.



Figure 2

Thermal photos of Solanum torvum in the morning, 09/05/2023 (A-B) and 11/05/2023 (C-D).



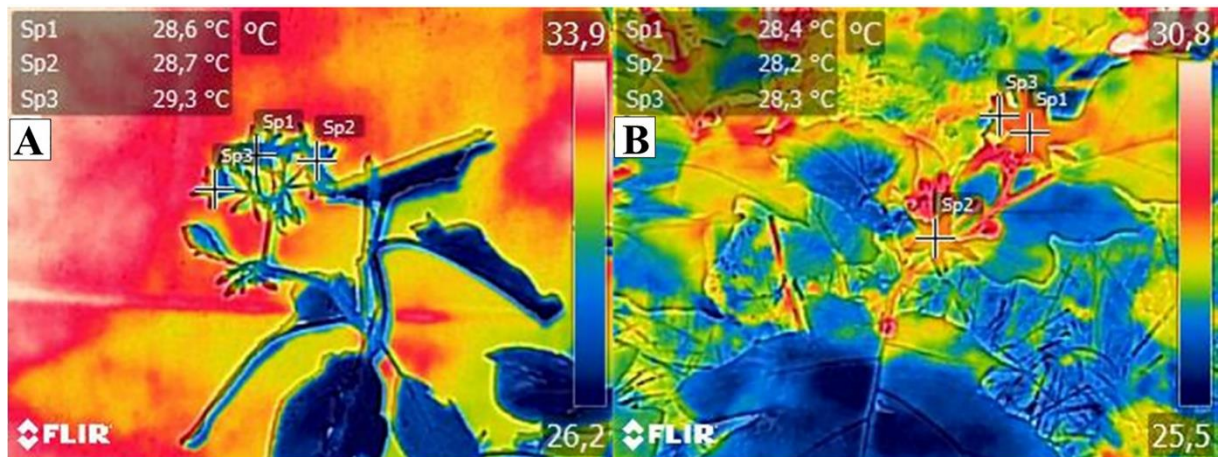
Source: Produced by the author Patrícia Viviane Zorzetto.

In the afternoon, the following temperatures were recorded for the inflorescences: 28.6°C, 28.7°C and 29.3°C, when the ambient temperature was 26°C (Figure 3A). The inflorescences presented temperatures of 28.2°C, 28.3°C and 28.4°C when the ambient temperature was 27°C (Figure 3B). As observed for the morning period, the inflorescences/flowers presented a higher temperature in the afternoon than the ambient temperature, and the greatest difference between the temperatures was 3.3°C in this period.



Figure 3

Thermal photos of Solanum torvum in the afternoon, 03/05/2023 (A) and 09/05/2023 (B).



Source: Produced by the author Patrícia Viviane Zorzetto.

Insect visitors - Anthesis occurs in the morning, when insects begin visiting the flowers. Bees belonging to the genus *Bombus*, popularly known as “bumblebees”, were frequent visitors (Figure 4A-C). The visits occurred in the morning. It was possible to identify one species of this genus, *Bombus morio*, which is commonly found in the region of Maringá, state of Paraná. These bees have corbiculae for transporting pollen. The bees (Figure 4B) positioned themselves on the anthers and made vibrating movements. Other insects, such as bedbugs and beetles, also visited the flowers, but less frequently.

Figure 4

Flower visitors (bees) of Solanum torvum, belonging to the genus Bombus.



Source: Produced by the author Patrícia Viviane Zorzetto.



4 DISCUSSION

Flower morphology - Anthesis of *Solanum torvum* occurred in the morning, when the anthers open and the stigma must become receptive. *Solanum caavurana* Vell., which is a frequent species in forest remnants of Maringá, Brazil, also has morning anthesis, in which the flowers were completely open between 8:00 a.m. and 8:30 a.m. (Santana et al., 2023). Other species of *Solanum* also have anthesis that occurs in the morning (Oyelana & Ogunwenmo, 2012; Falcão, 2015; Passarelli, 2019).

There is a correlation between the morphology of the stamens and the visiting insects in *Solanum torvum*. Endress (1994) calls this type of correlation the bee-flower type, which exhibits anthers with long and narrow thecae with a terminal pore. In the case of the unipistillate gynoecium of *Solanum torvum*, it was found that most flowers have a raised stigma in relation to the height of the stamens. However, there are flowers with stamens located above the stigma, indicating that there is heteranthery in this species.

Puthiamadom & Kumari (2017) found the same characters of the androecium and gynoecium of *Solanum torvum* for some *Solanum* species, but the authors considered them as having zygomorphic flowers, because the ovary is oblique in position with respect to the floral axis. As observed in *Solanum torvum*, Porto (2015) and Passarelli (2019) report that flowers of *Solanum glaucophyllum* Desf. and *Solanum rhytidoandrum* Sendtn., respectively, have styles of different length, some with long styles that protrude from the cone of the androecium and others with short styles that are entirely enclosed by it. Forni-Martins et al. (1998) and Knapp et al. (2025) also found long- and short-styled flowers in *Solanum paniculatum* L. and *Solanum hexandrum* group, respectively.

Solanum torvum may have an increase in inflorescence temperature related to thermogenesis, due to the size of its flowers, the presence of pollinators and odor production. It is known that thermogenesis (Herrera, 1995) is a metabolic mechanism that promotes the heating of the organism, which can be associated with the volatilization of odorous substances and the creation of a microclimate favorable to the formation of dormitories or mating of floral visitors. *Solanum torvum* showed an increase of 2°C in relation to the environment on a cold day in the morning, coinciding with the pollination period.

Insect visitors - The flowers of *Solanum torvum* are frequently visited by bees belonging to the genus *Bombus*, particularly the species *Bombus morio*. These bees harvest pollen by vibrating movements that are performed on the anthers that release pollen through pores (buzz-pollination). Endress (1994) considers that the most fascinating evolutionary



response of flowers to pollen collection by vibration (buzz-pollination) is a reduction of anther dehiscence to apical pores and at the same time elongation of the anthers. Plants with flowers typical of the buzz-pollination syndrome are found in at least 64 plant families, many of which may contain plants from which humans derive useful products, materials, or foods (Cooley & Vallejo-Marín, 2021). Prominent among these taxa are the *Solanum* species in which buzz-pollination is well known (Storti, 1988; Endress, 1994; Forni-Martins et al., 1998; Anderson et al., 2015; Porto, 2015; Passarelli, 2019; Cooley & Vallejo-Marin, 2021; Santana et al., 2023; Moore et al., 2024).

During observations of *Solanum torvum* flower visitors, other insects were identified, such as bugs and beetles, which searched the flowers for pollen as food. It is very likely that these insects did not play an active role in the pollination of the species, but rather acted as pollen plunderers.

Data on reproduction of *Solanum torvum* and other species of the genus (Table 1) - In the present study, no experimental studies were carried out on the breeding system of *Solanum torvum*. However, our observations on the flowers of *Solanum torvum*, such as buzz-pollination, style/stigma above the anthers and frequent bee visitors of the genus *Bombus*, and comparatively associated with data from the literature (Table 1), indicate that the species under study is allogamous.

The data shown in Table 1 indicate that *Solanum* species are primarily allogamous, but low-grade autogamy may occur, particularly in species subjected to self-compatibility experiments. The occurrence of long-styled and short-styled flowers appears to be common in the genus (Table 1). It is also noted that the flowers are generally melitophilous, and have pollen as a reward for floral visitors. It must be pointed out here that Falcão (2015) found secretory tissue in the connective of poricidal anthers of *Solanum luridifuscescens* (Table 1), probably secreting floral scent. Moore et al. (2024), on the other hand, investigated seven taxa of buzz-pollinated *Solanum*, and suggested that buzz-pollinated plants rarely use scent as an honest cue for foraging pollinators.


Table 1

Floral features and visitors, and data on reproduction of *Solanum* species, with indication of bibliographical references.

Species	Flower visitors/ pollinators	Flower features	Breeding system/ notes	References
<i>Solanum torvum</i>	<i>Bombus</i> (<i>Bombus morio</i>) Bugs and beetles (pollen plunderers)	Poricidal anthers, heteranthery, flowers with long and short pistils, multi-ovulated ovary, anthesis in the morning	Probably allogamy	Own observations
<i>Solanum aethiopicum</i> L.; <i>Solanum anguivi</i> Lam. <i>Solanum erianthum</i> D. Don <i>Solanum gilo</i> Raddi <i>Solanum melongena</i> (Mill.) Dunal <i>Solanum scabrum</i> Mill. <i>Solanum torvum</i>	<i>Megachile latimanus</i> , <i>Diplolepis rosae</i> , <i>Bombus pennsylvanicus</i>	Foliaceous sepals, pink-purple or white corolla, poricidal anthers, multi-ovulated ovary, anthesis in the morning	Most species primary inbreeders (100% selfed) but facultatively outbreeding (12.5 to 75%)	Oyelana & Ogunwenmo (2012)
<i>Solanum caavurana</i>	Hymenoptera and Diptera Bee <i>Augochloropsis</i> (most frequent)	Flowers pendent, umbellate inflorescences, white calyx and corolla, poricidal anthers, multi-ovulated ovary, anthesis in the morning	Not registered/bee visitors	Santana et al. (2023)
<i>Solanum confusum</i> Morton <i>Solanum glaucophyllum</i> Desf. <i>Solanum stuckertii</i> Bitter	<i>Bombus atratus</i> , <i>Bombus belicosus</i> , <i>Xylocopa augusti</i> , <i>Augochlora</i> sp., <i>Augochloropsis</i> sp., <i>Exomalopsis</i> sp.	Pendulous inflorescence, mild or lobed corolla, poricidal anthers, multi-ovulated ovary, long or short styles	Andromonoecy, self-incompatible pollen tubes (self-sterile)	Passarelli (2019)
<i>Solanum luridifuscescens</i> Bitter	<i>Augochlora</i> sp. <i>Augochloropsis</i> sp. <i>Bombus brasiliensis</i> <i>Eucerini</i> sp. <i>Melipona bicolor</i> <i>Melipona quadrifasciata</i>	Inflorescences of scorpion-like monochasium type, hermaphrodite, actinomorphic and pentamerous flowers, purple corolla, poricidal anthers, secretory connective, anthesis in the morning	Allogamy Self-incompatible	Falcão (2015)
<i>Solanum hexandrum</i> group	<i>Bombus morio</i> <i>Eulaema cingulata</i>	Terminal inflorescences, flowers with robust pedicels, corollas with various shades of	Breeding systems no studied,	Knapp et al. (2025)



	<i>Oxaea flavesces</i> <i>Augochloropsis</i> sp. <i>Pseudaugochloropsis graminea</i> <i>Megachile</i> sp.	purple, poricidal anthers, 2-4 locular ovary, long- and short styled flowers	andromonoecy	
<i>Solanum melissarum</i> Bohs	<i>Euglossa cordata</i>	Pendulous flowers, arranged into simple cyme inflorescences, poricidal anthers, anther thecae membranous with osmophores	Self-incompatible, low levels of natural pollination	Coelho et al. (2017)
<i>Solanum melongena</i> L. and variant species of <i>Solanum</i> (<i>S. viarum</i>, <i>S. gilo</i>, <i>S. incanum</i>)	Not registered	Pedicellate, zygomorphic, bisexual, poricidal anthers, hypogynous and complete, present heterostyly	Not registered	Puthiamadom & Kumari (2017)
<i>Solanum orbiculatum</i> Dunal (subsp. <i>orbiculatum</i>)	Not registered	Protogynous flowers, variation in petal colour and shape, poricidal anthers, long or short styles	Self-compatible, unable to carry out spontaneous autogamy or agamospermy	Ahmad et al. (2023)
<i>Solanum paniculatum</i> L.	<i>Oxaea flavesces</i> <i>Bombus morio</i> <i>Xylocopa frontalis</i>	Panicle-like inflorescence, pale violet corolla, long and short style, poricidal anthers	Allogamy	Forni-Martins et al. (1998)
<i>Solanum rhytidoandrum</i> Sendtn.	<i>Trigona</i> sp., <i>Lepidoptera</i> sp., Hymenoptera (<i>Kapala</i> and others)	Two morphs: flowers with long pistil, greater than the anthers, hermaphrodites; and flowers with short pistil, below the level of the anthers (do not form fruit)	Self-incompatible, allogamy	Porto (2015)
<i>Solanum sessiliflorum</i> Dun. (var. <i>sessiliflorum</i>)	<i>Eulaema (Apeulaema) nigrita</i> (most frequent), <i>Euglossa</i> sp., <i>Paratrigona</i> sp., <i>Exomalopsis</i> sp.	Hermaphrodite and staminate flowers, green sepals and greenish-white petals, poricidal anthers, anthesis in the morning	Allogamy (geitonogamy or xenogamy)	Storti (1988)
<i>Solanum vespertilio</i> Aiton	<i>Amegilla quadrifasciata</i> <i>Bombus canariensis</i>	Flowers tetramerous, zygomorphic, heterantherous and enantiostylous, style in male flowers short to vestigial; in hermaphrodites it is strongly up turned, longer than the anthers	Weakly self-compatible, allogamy (geitonogamy or xenogamy)	Anderson et al. (2015)



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