



REVIEW

Pollination Redefined: Non-*Apis* Bees in Greenhouse Tomatoes and Emerging Global Research Trends

J. MALATHI¹, G. PREETHA¹, V. R. SAMINATHAN¹, B. KEERTHANA¹, M. KAVITHA², P. C. PRABU³, S. PRADEEP¹

1 - Department of Agricultural Entomology, Tamil Nadu Agricultural University, Coimbatore, Tamil Nadu, India

2 - Horticultural Research Station, Tamil Nadu Agricultural University, Ooty, The Nilgiris, Tamil Nadu, India

3 - Centre for Water and Geospatial Studies, Tamil Nadu Agricultural University, Coimbatore, Tamil Nadu, India

Article History

Edited by

Evandro Nascimento Silva, Brazil, UEFS
 Received 02 January 2025
 Initial acceptance 16 June 2025
 Final acceptance 19 July 2025
 Publication date 27 August 2025

Keywords

Tomatoes, Bibliometric analysis, Buzz pollination, Bumble bees, Stingless bees, Blue-banded bees.

Corresponding author

Dr. G. Preetha
 Department of Agricultural Entomology, Tamil Nadu Agricultural University, Coimbatore – 641 003, Tamil Nadu, India.
 E-Mail: preethag@tnau.ac.in

Abstract

This review concentrates on the importance of non-*Apis* bees, such as bumble bees, stingless bees, and other bee species, in enhancing tomato (*Solanum lycopersicum* Linnaeus) pollination within greenhouse environments. Due to the limited presence of natural pollinators in controlled environments, non-*Apis* bees significantly improve fruit yield, weight, seed count, and overall fruit quality. Among these, bumble bees are the most effective buzz pollinators, enhancing fruit weight, fruit set, external diameter, and seed production, while stingless bees excel in seed production and fruit weight in tropical regions, and blue-banded bees specialize in fruit weight improvement. Therefore, the advantages of non-*Apis* bees over mechanical and manual pollination methods are well established. Based on a bibliometric analysis of forty-eight peer-reviewed research papers, this review identifies key trends, influential contributors, and significant knowledge gaps. We emphasize the need for further research to improve pollination management, enhance mass-rearing techniques, and study the behavior of non-*Apis* bees in greenhouses. It highlights the important role of these bees in sustainable greenhouse tomato cultivation and their value for commercial pollination services.

Introduction

Tomato (*Solanum lycopersicum* L.), belonging to the family Solanaceae, originated in South and Central America, and its domestication and cultivation can be traced back to the early Aztecs of Mesoamerica by 700 A.D. (Bergougnoux, 2014). In the 16th century, colonizers introduced the tomato to Europe and its European colonies, and from there, it spread to the rest of the world (Smith, 2001; Bergougnoux, 2014). Tomatoes are now found ubiquitously, with more than 7,500 varieties, and a global annual value of US\$10.8 billion (Tridge, 2020). Since 2000, global vegetable production has risen by 71 percent, reaching 1.17 billion tonnes in 2022. In India, vegetable production amounted to 20.69 million tonnes in the same year (Ritchie et al., 2023). Tomatoes were the most produced vegetable, totaling 186 million tonnes in

2022 (FAOSTAT, 2023). It is an annual plant of significant nutritional value due to its content of essential amino acids, vitamin C, vitamin A, lycopene, and β -carotene (Ali et al., 2021).

Tomato flowers, measuring 1.5-2.0 cm in diameter, are actinomorphic and arise terminally, positioned either opposite or between leaves (Naika et al., 2005). Their structure includes a calyx with 5-6 green sepals, a corolla of bright yellow petals fused at the base, an androecium with 5-6 stamens forming a staminal cone supporting bright yellow anthers, and a pistil with 2-9 fused carpels enclosing the ovary. Depending on the cultivar, the style may be found within the staminal cone (brevistyle flower), at the same level as the stamens, or slightly above the staminal cone (longistyle flower) (Ranc, 2010; Petit, 2013). Tomato flowers do not produce nectar; instead, they benefit from nearby nectar-producing plants to attract pollinators (Gaglianone et al., 2015).



Tomato, *S. lycopersicum*, is the best-studied buzz-pollinated crop, and pollination is vital for fruit set and quality (Bailey, 1891). Cultivated tomato plants are usually hermaphrodite and self-pollinated (Cauich et al., 2004) with poricidal anthers, necessitating vibration to release pollen grains through apical pores when the androecium or anther cone is shaken (McGregor, 1976; Buchmann, 1983; de Moura-Moraes et al., 2021). These vibrations are naturally generated by wind or insect activities, especially those of bee species, which exhibit vibratory behavior or buzz-pollination in open fields to induce effective pollination (Free, 1970; Hanna, 1999). In greenhouse conditions, tomato pollination often encounters challenges that lead to poor fruit set due to the scarcity of wind and animal pollination conditions. To achieve adequate fruit formation and quality, special interventions, such as employing pollinating agents or implementing mechanical aids, are essential in these conditions (Neiswander, 1956; Banda & Paxton, 1990; Morandin et al., 2001a; Palma et al., 2008). Therefore, the quality and yield of tomatoes can be improved by utilizing supplementary pollination techniques (McGregor, 1976; Picken, 1984; Free, 1970) such as the mechanically induced vibration and airflow (Bell et al., 2006), watch-glass method (Schneck, 1928), emasculation (Fletcher & Gregg, 1907; Schneck, 1928), the vibration of trellis wires (Short & Bauerle, 1973), acoustically forced vibration (DeTar et al., 1968), air blowers (Stoner, 1971; Hanna, 2004), hand pollination using a pulsating air jet (Nahir et al., 1984), soundwaves (Cawood, 1964), air cylinder vibration (Short & Bauerle, 1974), plant hormone application (Verkerk, 1957), handheld vibrators (Dasgan et al., 2004; Velthuis & Doorn, 2006; Dos Santos et al., 2009) and electric bees have traditionally been employed but are expensive and less efficient than biotic pollinators (Cottrell-Dormer, 1945; Short & Bauerle, 1974). However, this increases production costs and results in losses to commercial value (Picken, 1984; Westerkamp & Gottsberger, 2000), as it requires additional labor and can cause damage to flowers and consequently to fruits (Van Ravestijn & Van der Sande, 1990; Kevan et al., 1991; Cribb et al., 1993; Ilibi & Boztok, 1993; Dogterom et al., 1998; Hanna, 2004).

As a result, the number of studies on managing pollinators in greenhouses has increased steadily over the past few years. Pollination in tomatoes relies on the unique process of buzz pollination, which non-*Apis* bees, such as bumble bees, stingless bees, and blue-banded bees, are particularly adept at due to their specialized physiology. These bees use rapid vibrations generated by their flight muscles to dislodge pollen from the anthers, making this method highly effective for crops like tomatoes that require mechanical pollen release. While many pollinators engage in simple contact pollination, the ability of non-*Apis* bees to produce controlled, high-frequency vibrations gives them an advantage in enhancing fruit quality and yield. The introduction of bees, including honey bee, *Apis mellifera* Linnaeus (Dos Santos et al., 2009),

and non-*Apis* bees like *Amegilla* (*Notomegilla*) *chlorocyanea* Cockerell (Hogendoorn et al., 2006), *A. holmesi* Rayment, *Lestis aeratus* Smith, *L. bombylans* Fabricius (Hogendoorn et al., 2000; Bell et al., 2006; Hogendoorn et al., 2006), *Bombus* spp. Latreille (Morandin et al., 2001a), *Melipona quadrifasciata* Lepeletier (Del Sarto et al., 2005; Dos Santos et al., 2009; Hikawa & Miyanaga, 2009; Santos et al., 2014; Silva-Neto et al., 2018), *Tetragonula pagdeni* Schwarz (Wongsa et al., 2023), *Nannotrigona testaceicornis* Lepeletier, *Partamona helleri* Friese (de Moura-Moraes et al., 2021) and *Nannotrigona perilampoides* Cresson (Cauich et al., 2004; Palma et al., 2008) and *Xylocopa* (*Lestis*) Lepeletier & Serville (Hogendoorn et al., 2000; Velthuis & Doorn, 2006). These non-*Apis* species are often more effective than honey bees because tomato flowers do not attract honey bee visitors due to the lack of nectar, and honey bees cannot produce the vibrations necessary to remove pollen (Dos Santos et al., 2009). This review asserts that non-*Apis* bees are vital in pollinating greenhouse tomatoes, significantly impacting crop yields and overall fruit quality. Their essential contribution cannot be overlooked.

The Unsung Pollinators: A Bibliometric Exploration of Non-*Apis* Bees in Tomato Greenhouse Systems

On June 18th, 2025, an extensive analysis and systematic review were conducted using the Elsevier Scopus (<https://www.scopus.com/>) and Google Scholar (<https://scholar.google.com/>) databases to extract bibliographic data and establish a network of globally published articles related to non-*Apis* bees in greenhouse tomato pollination. The search was performed using the following keywords: *Solanum lycopersicum*, pollination, pollinators, fruit characteristics, managed pollinators, non-*Apis* bees, *Amegilla*, stingless bees, bumble bees, fruit set, and yield. A total of 59 articles were initially identified. These were screened to exclude duplicates, articles lacking full-text access, and those not focused on non-*Apis* bees. Review papers that contained unique data not available elsewhere were also included. Following this screening process, the final list consisted of 49 articles. The bibliometric analysis was performed using various indices, including popular keywords, countries of origin, and leading journals. This analysis was executed and visualized using R Studio software version 4.5.0. The bibliometric analysis spans from 1990 to 2025, encompassing documents sourced from 30 different journals, books, and publications. The analysis identifies 128 distinct Keywords Plus (ID) and 80 author-defined keywords (DE), reflecting a diverse thematic scope (Table 1).

The bibliometric analysis reveals trends in annual scientific production (Fig 1) on pollination research from 1991 to 2023, characterized by fluctuating patterns with noticeable peaks in the early 2000s and 2013, alongside periods of reduced activity in the mid-1990s and 2015,

resulting in an overall negative annual growth rate of -2.14 percent. However, a recovery has been evident in recent years, with a marked increase in publications since 2019. Key journals contributing to this research (Fig 2) include the *Journal of Economic Entomology* (12 articles), followed by the *Journal of Pollination Ecology* (3) while journals such as the *Sociobiology*, *Acta Horticulturae*, *Applied Entomology*

and *Zoology*, *Journal of Apicultural Research*, *Journal of Horticultural Science and Biotechnology* (2 articles each), *Apidologie*, *Canadian Entomologist* and others each contribute 1 article reflect a mix of specialized and general scientific platforms. Geographically, the field has seen significant contributions from countries such as Canada (28), Brazil (23), Australia (17), Mexico (14), and Pakistan (12), reflecting strong engagement from regions in the Americas and Asia. A moderate representation from Latvia (10), China (9), along with smaller contributions from Egypt and Ghana, indicating the global interest in this area (Fig 3). Keyword analysis highlights *Lycopersicon esculentum* (21 occurrences) and tomato (20 occurrences) as the central focus, underscoring the prominence of tomato crops in pollination studies. These are closely followed by pollination (19 occurrences) and bee (13), indicating a strong emphasis on pollinator roles. Also, terms such as Apoidea, greenhouse, and Hymenoptera (12 each), reflecting a broader interest in bee-mediated pollination (Fig 4). Thematic visualization positions *Lycopersicon esculentum* and tomato as the core node, connected to clusters reveal thematic focuses such as greenhouse ecosystems and plant-pollinator dynamics (green cluster); the pollination biology involving bees like *Bombus terrestris* and stingless bees (red cluster); floral physiology and reproductive biology (purple cluster); broader horticultural and agricultural practices (blue cluster); controlled environments and bumble bee pollination (orange cluster); and the isolated brown cluster hints at niche or emerging topics such as self-pollination and colony traffic (Fig 5). Co-occurrence analysis strengthens this perspective, showing central terms like *Lycopersicon esculentum* and tomato anchoring discussions on crop ecology (green cluster), pollination and bees (red cluster), and pollinator taxonomy and ecology in cultivation systems (blue) (Fig 6).

Table 1. Main information of data by bibliometric analysis.

Main information about data	
Timespan	1991:2023
Sources (Journals, Books, etc)	30
Documents	49
Annual Growth Rate %	-2.14
Document Average Age	16.40
Average citations per doc	31
References	0
Document contents	
Keywords Plus (ID)	128
Author's Keywords (DE)	80
Authors	
Authors	180
Authors of single-authored docs	1
Authors collaboration	
Single-authored docs	1
Co-Authors per doc	4.27
International co-authorships %	12.24
Document types	
Article	31
Review	2

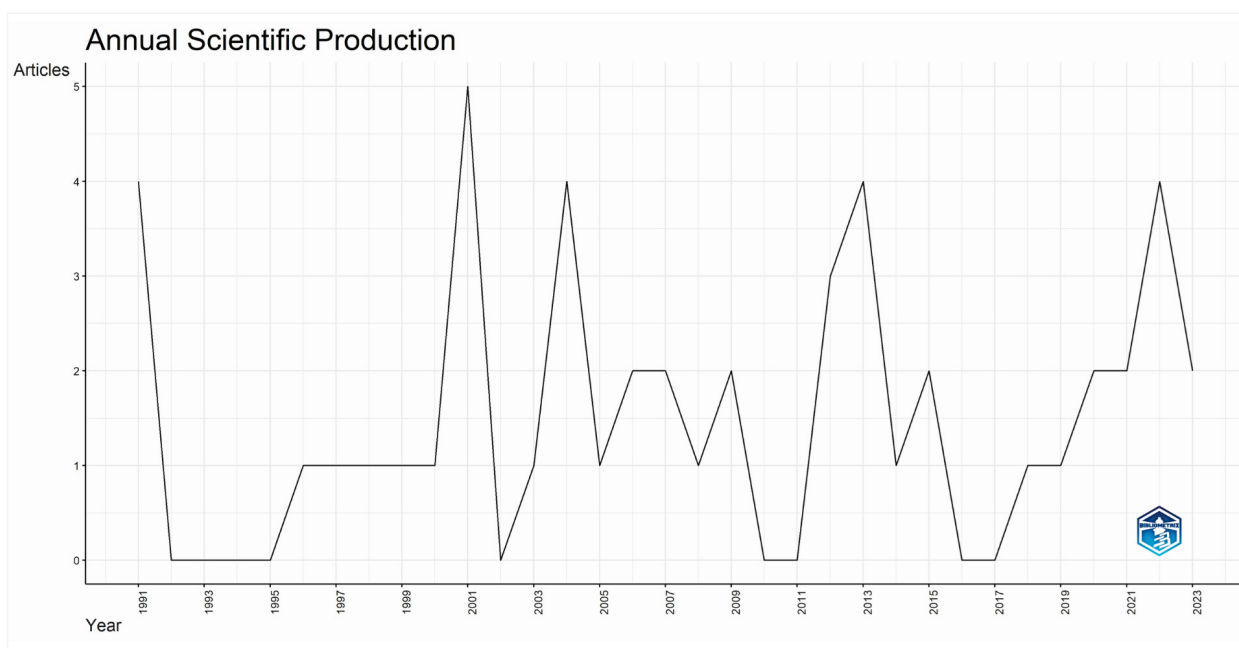


Fig 1. Annual Scientific Production.

Collaboration analysis identifies prominent contributors such as Kevan PG as the central author with strong collaborations, especially with Shipp L and Plowright RC and followed by Quezada-Euán JJG and Alamri S, who lead smaller, dispersed networks offering insights into key contributors and foundational studies shaping this field (Fig 7). The analysis underscores the dynamic and evolving nature of pollination research, with a central focus on *Lycopersicon esculentum* and bee interactions, supported by diverse contributions across journals, regions, and authors. While historical trends reveal periods of decline, recent years show a strong recovery, highlighting growing global significance of pollination in agriculture.

Pollination Efficiency by Non-*Apis* Bees

Pollination efficacy is the contribution of each pollinator to a plant's reproductive success after pollination. In contrast, pollination effectiveness is the total contribution of a specific pollinator to both male and female reproductive success (Freitas, 2013). Pollinator efficiency is the relationship between efficacy and the consumption of floral resources and pollen wastage. Several studies investigated the efficiency, effectiveness, and efficacy of native and exotic pollinators in greenhouse conditions. The studies collectively emphasize the substantial role that pollinators, primarily bumble bees, stingless bees, and blue-banded bees, play in improving the yield and quality of greenhouse tomato crops.

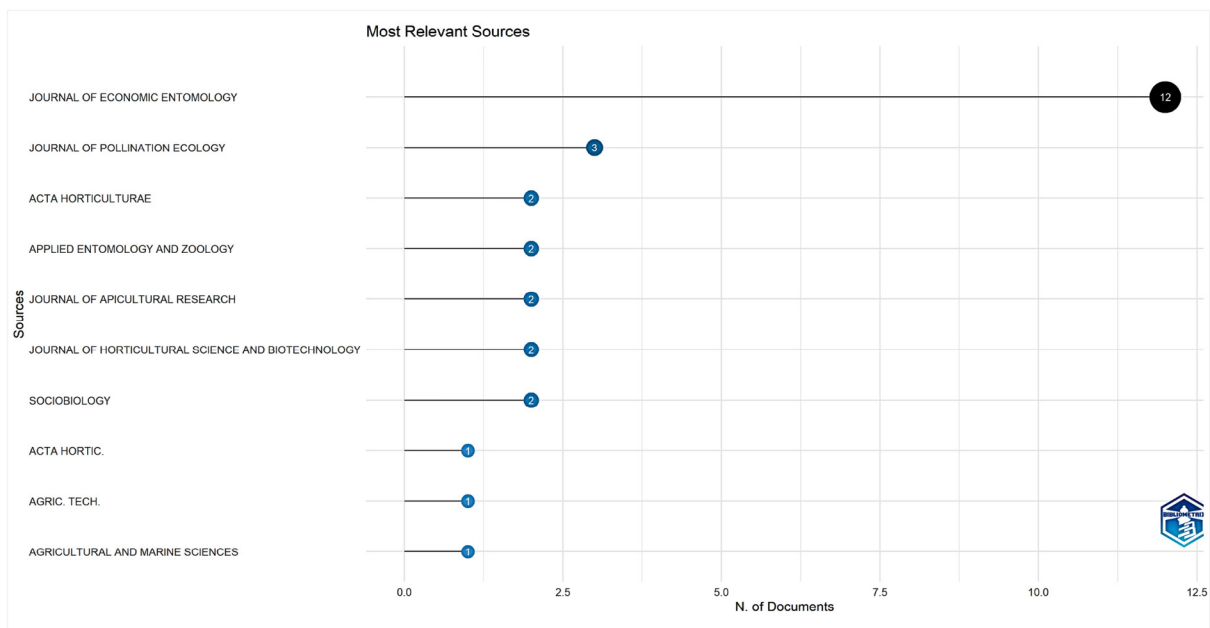


Fig 2. Most Relevant Sources.

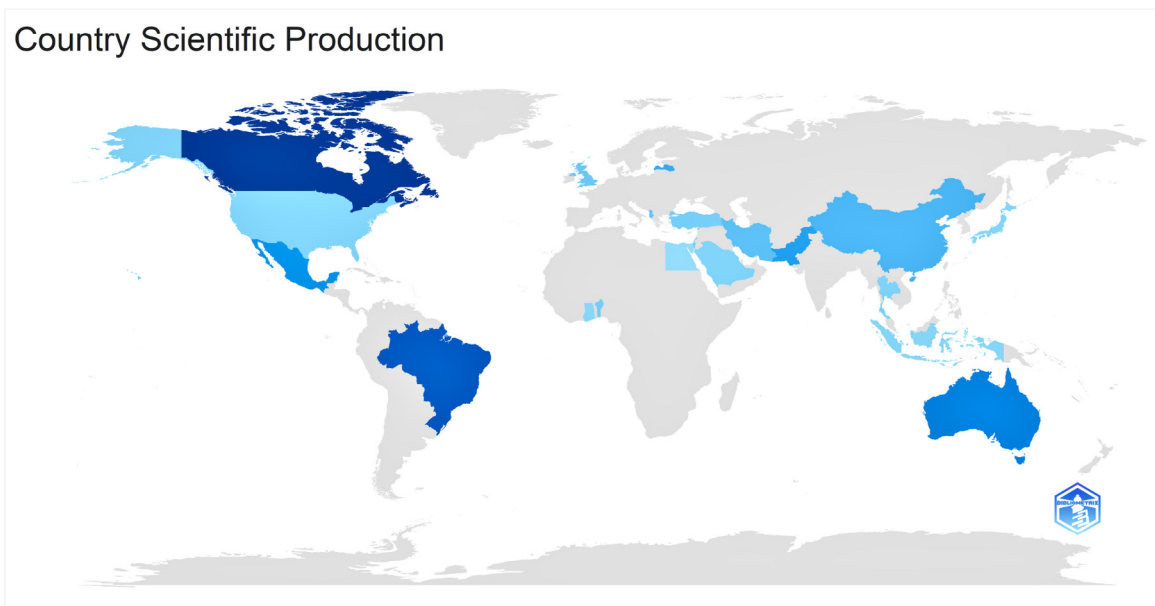


Fig 3. Country Scientific Production.

Native and commercial bumble bee efficiency

Globally, bumble bees (*Bombus* spp.) are crucial pollinators for greenhouse tomatoes, boosting fruit weight and reducing harvest time compared to non-pollinated plants. Over a million colonies are sold annually to meet the demand for pollination. Studies now focus on native western North American species, such as *Bombus huntii* Greene and *Bombus vosnesenskii* Radoszkowski, to mitigate the risks associated with transporting non-native bees. Bee-pollinated tomatoes showed an average increase in fruit weight of 25.2g and a nearly three-day reduction in harvest time. Fruit weight was strongly correlated with fruit diameter and seed production, making it a reliable metric for assessing pollination in future studies. These findings suggest that commercializing western bumble bees is a viable alternative to non-native bees for tomato pollination in western North America (Strange, 2015).

The native *Bombus atratus* in greenhouse conditions increased fruit set by 13–47 percent in Lapatia and Elpida tomato varieties compared to unvisited flowers. Additionally, fruit weight, size, and seed number were significantly higher in bumble bees bee-pollinated flowers (Salvarrey et al., 2020).

In Mexico, experiments using two colonies of native *Bombus ephippiatus* Say, reared in the laboratory, demonstrated their effectiveness in pollinating Mallory (Hazera ®) tomato varieties, the commercial and practical alternative to using imported bumble bees for pollination. Bumble bee-pollinated flowers produced fruits with greater weight, higher sugar content, and more seeds than manual or no pollination (Vergara & Fonseca-Buendía, 2012). Similarly, *B. vosnesenskii* was found to increase fruit size and seed content in greenhouse-grown tomatoes, further confirming its efficiency as a pollinator (Dogterom et al., 1998).

Furthermore, studies on bumble bee pollination of greenhouse-grown tomatoes have compared the foraging efficiency of two species: *Bombus impatiens* Cresson, native to northeastern North America, and *B. ephippiatus*, native to Mexico and Central America. Both species were found to be similarly effective in enhancing fruit quality, as evidenced by improvements in fruit weight, seed count, and maximum fruit diameter. Their foraging behaviors and responses to temperature changes were also alike, with pollination rates nearing 100 percent throughout the study period. Notably, *B. impatiens* showed higher foraging activity during the first half of the 27-day study, while *B. ephippiatus* increased its activity in the latter half. These findings suggest that *B. ephippiatus* is a viable alternative as a managed pollinator. However, developing reliable mass-rearing techniques is crucial to ensure sustainable use and minimize the ecological impacts of unregulated queen collection (Torres-Ruiz & Jones, 2012).

Behavioural and climatic considerations

Environmental factors such as temperature, humidity, and light play a pivotal role in the activity of non-*Apis* bees

within controlled greenhouse systems. Bumble bees, for instance, exhibit peak efficiency at moderate temperatures, typically between 20 and 25 °C (Morandin et al., 2001b). However, as temperatures rise above this range, their foraging activity may decrease due to heat stress, which can impact pollen transfer and fruit set (Pressman et al., 1999).

Research in Ontario, Canada, has demonstrated that buzz pollination by bumble bees enhances pollen transfer to tomato flowers. The fruit set was highest (100 percent) when flowers were pollinated at higher levels of anther cone bruising. However, beyond one to two bee visits, further increases in quality metrics such as fruit weight, diameter, or seed count were negligible (Morandin et al., 2001b). Under extreme winter conditions, bumble bees were more efficient than electric vibrators, which required daily operation to achieve comparable pollination outcomes. Bumble bee colonies ensured a consistent fruit set, even under low pollen availability (Pressman et al., 1999). Similarly, in the Mediterranean Basin, bumble bee pollination increased the yield by 90% and 61% compared to vibration and growth regulator applications, respectively. Bumble bee-pollinated fruits were 41% heavier than those vibrated and nine percent heavier than those treated with growth regulators, underscoring their efficiency, especially during winter (Dasgan et al., 2004).

Stingless bee pollination

In recent years, the management of stingless bees for crop pollination has significantly increased. This growth can be attributed to the high diversity of species, their non-aggressive behavior, and ease of handling and colony multiplication (Nogueira-Neto, 1997).

In greenhouse experiments, Neotropical Stingless Bee (*M. quadrifasciata*) demonstrated promising results for tomatoes with different growth habits. The pollen loads for creeping tomatoes were 433 percent larger in closed environments with bees than in greenhouses without bees. Additionally, fruits that were pollinated by bees weighed 15 percent more and contained 41.1 percent more seeds than those grown in open fields. For indeterminate tomatoes, seed production increased by 33 percent, while fruit mass increased by 16 percent (Silva-Neto et al., 2018). Similarly, tomatoes pollinated by *M. quadrifasciata* workers produced 47% more seeds and had 14% higher sugar content than those pollinated mechanically. This highlights its potential for improving both productivity and fruit quality (Bartelli & Nogueira-Ferreira, 2014).

However, the foraging period of *M. quadrifasciata* (08:00–11:00 h) did not align with the tomato stigma receptivity (10:30–15:30 h), limiting its efficiency. Despite this, fruits pollinated by *M. quadrifasciata* exhibited improved quality and reduced mechanical injury compared to those pollinated manually (Del Sarto et al., 2005). Additionally, *M. quadrifasciata* and bumble bees exhibited similar pollination efficiency when pollen was abundant. However, during high-temperature periods (>28 °C), tomato pollen production

decreased, resulting in reduced fruit set, seed numbers, and yield for *M. quadrifasciata* compared to bumble bees. This finding suggests that *M. quadrifasciata* is suitable only under optimal pollen availability (Hikawa & Miyanaga, 2009).

Another stingless bee species, *Tetragonula pagdeni* Schwarz, is widely used in Southeast Asia for greenhouse pollination. In experiments, greenhouses with *T. pagdeni* achieved higher fruit sets (85 ± 4.24 fruits/100 flowers) than those using mechanical vibration (79.5 ± 2.12 fruits/100 flowers) or without pollinators (15 ± 0.00 fruits/100 flowers). Fruit weight and seed numbers were also significantly higher, with *T. pagdeni* indicating its potential in tropical regions unsuitable for honeybees or bumble bees (Wongsa et al., 2023).

Similarly, three stingless bee species were tested on cherry tomatoes: *Melipona bicolor* Lepeletier, *Nannotrigona testaceicornis*, and *Partamona helleri*. *M. bicolor* and *N. testaceicornis* improve fruit weight, seed count, and pericarp thickness. However, *P. helleri* did not collect pollen under experimental conditions. While *N. testaceicornis* did not buzz-pollinate, its pollination effects were comparable to *M. bicolor* (de Moura-Moraes et al., 2021). Also, *N. perilampoides* was evaluated in greenhouses with treatments of bee pollination, mechanical vibration, and no pollination. Greenhouses with bees showed higher fruit set percentages, individual fruit weights, and seed counts. This study supports *N. testaceicornis* as a viable alternative to Africanized honeybees or non-native bumble bees in tropical climates (Cauch et al., 2004).

Blue-banded bee pollination

Amegilla chlorocyanea showed that a single buzz by a female increased tomato weight by 11 percent compared to pollination using an industrial pollination wand. Multiple buzzes further increased tomato weight, while unlimited flower visits resulted in a 21 percent increase in fruit weight compared to wand pollination. These results, comparable to bumble bee pollination, validate *A. chlorocyanea* as an effective alternative for greenhouse tomato pollination in Australia (Hogendoorn et al., 2006). Similarly, *Anthophora holmesi* pollinated greenhouse tomatoes significantly improved fruit set, size, roundness, and seed numbers compared to no supplementary pollination (Bell et al., 2006).

Challenges and Considerations

Despite their advantages, using non-*Apis* bees poses challenges that require innovative solutions. One major obstacle is the scalability of mass-rearing techniques, which can be complex and resource-intensive (Velthuis & Doorn, 2006). The development of semi-automated breeding facilities that mimic the bees' natural habitat is one way to address these challenges. Additionally, non-*Apis* bees can face reduced efficacy during off-peak seasons or extreme environmental changes (Dogterom et al., 1998). Research into bee species' genetic resilience could aid in breeding bees that are more adaptable to changing conditions (Nino & Cameron Jasper, 2015).

Ensuring genetic diversity in managed colonies can prevent inbreeding and support robust bee populations capable of maintaining pollination efficiency.

Conclusion and Future Perspective

Non-*Apis* bees, including bumble bees, stingless bees, and blue-banded bees, are recognized for their significant contributions to the pollination of greenhouse tomatoes, often outperforming traditional methods in terms of fruit yield, weight, and seed production (Dogterom et al., 1998; Hatami et al., 2013). Their ability to perform buzz pollination by vibrating flowers to release pollen is particularly beneficial for crops like tomatoes, which require specialized pollination for optimal productivity (Buchmann, 1983). While honey bees have traditionally been the standard for pollination in controlled environments, concerns over their adverse effects on wild bee populations highlight the importance of prioritizing native non-*Apis* species to ensure sustainable pollination practices (Kevan & Phillips, 2001).

A stronger focus is needed on expanding our knowledge and application of non-*Apis* bees to advance the future of greenhouse tomato pollination. This agenda includes efforts to optimize mass rearing and commercial use of these species, particularly native ones, to bolster effective and ecologically sound pollination services (Velthuis & Doorn, 2006). Conservation of habitats and promoting floral diversity within greenhouses and their surrounding areas are vital for supporting stable wild bee populations (Nogueira-Neto, 1997).

Research should also delve into the behavioral ecology, foraging habits, and colony management of non-*Apis* bees to enhance their efficiency in controlled environments. Given the challenges of climate change and intensified agricultural practices, integrating non-*Apis* bees into integrated pollination and pest management strategies will be critical for ensuring food security. The selection of appropriate pollinators based on crop needs, environmental conditions, and regional availability is essential. While bumble bees remain the primary choice for greenhouse tomato pollination, stingless and blue-banded bees can provide effective alternatives under specific conditions (Bell et al., 2006; Hogendoorn et al., 2006). Future studies should focus on refining mass-rearing techniques, examining pollinator behavior under diverse climate scenarios, and evaluating the long-term ecological impacts of these practices.

The integration of technology into pollination strategies is poised to redefine sustainable practices. Automated systems such as drones that mimic pollinator movements or sensor-equipped drones for monitoring bee activity can complement natural pollination efforts. Using AI and machine learning algorithms to track bee behavior and optimize greenhouse conditions in real time offers promising potential. Advanced imaging technologies can be utilized to map pollinator movement patterns and interaction rates, identifying high-activity areas and inefficiencies.

For example, a lightweight, solar-powered flight recorder with an application-specific integrated circuit (ASIC) and Angle-Sensitive Pixels (ASPs) can be safely mounted on the thorax of honey bees without disrupting their natural behavior. These devices track the bees flight direction relative to the sun and store data for wireless retrieval at the hive (Abdel-Raziq et al., 2021). Also, a markerless Computer Vision (CV) based system enables real-time, multi-species insect tracking and pollination prediction over large farms. It supports scalable, data-driven decisions in crop yield optimization, hive management, pesticide planning, and precision agriculture (Ratnayake et al., 2023). An AI-driven, drone-based pollination system will be a sustainable alternative to bees and other pollination methods, which integrates autonomous flight, AI-powered flower recognition, and precision vibration tools to identify and pollinate flowers efficiently (Hiraguri et al., 2023).

Additionally, applying micro-sensors to bees allows researchers to gather data on individual performance, enhancing the understanding of foraging preferences and behavioral responses to varying environmental conditions (Bell et al., 2006). This data can inform targeted management strategies and contribute to developing predictive models for greenhouse optimization.

Sustainable pollination extends beyond the selection of pollinators to include comprehensive approaches that prioritize habitat health and biodiversity. The role of non-*Apis* bees is particularly significant, as their presence contributes to ecosystem resilience when native species are utilized (Kevan & Phillips, 2001). Establishing wildflower strips near greenhouses and implementing agroforestry techniques can create habitats that sustain wild pollinators year-round, reducing the dependency on imported colonies (Nogueira-Neto, 1997). Advanced biocontrol strategies, such as incorporating flowering plants that attract non-*Apis* bees, further bolster pollinator populations and promote pollinator health and productivity (Kevan & Phillips, 2001). These sustainable approaches align with agricultural practices that balance productivity with ecological stewardship.

Using climate-controlled systems integrated with real-time data analytics represents a cutting-edge approach to ensuring optimal conditions for pollinator activity. Such systems can monitor environmental shifts and trigger automated interventions, such as precise temperature regulation and humidity control, to create supporting conditions. This adaptive management strategy promotes higher pollination success and allows for adjustments in response to changing climate conditions, ensuring the sustainability of pollination services in greenhouse environments.

In conclusion, integrating non-*Apis* bees and technological advancements offers promising pathways for advancing greenhouse tomato pollination. Future research should prioritize developing mass-rearing techniques, understanding pollinator behavior in diverse conditions, and assessing the ecological impact of these practices.

The convergence of biological research and technological innovation is essential for redefining sustainable pollination strategies and ensuring long-term food security.

Acknowledgement

The authors gratefully acknowledge the support provided by the Department of Agricultural Entomology, Tamil Nadu Agricultural University.

Authors' Contributions

JM: literature collection, conceptualisation, methodology, writing-original draft, writing-review & editing.

GP: supervision, conceptualisation, methodology, writing-review & editing.

VRS and BK: conceptualisation, writing-review and editing.

MK, PCP and SP: writing-review & editing. All authors read and approved the final manuscript.

References

- Ahmad, M., Bodlah, I., Mehmood, K., Sheikh, U. A. A. & Aziz, M. A. (2015). Pollination and foraging potential of European bumblebee, *Bombus terrestris* (Hymenoptera: Apidae) on tomato crop under greenhouse system. *Pakistan Journal of Zoology*, 47: 1279-1285.
- Abdel-Raziq, H.M., Palmer, D.M., Koenig, P.A. et al. (2021). System design for inferring colony-level pollination activity through miniature bee-mounted sensors. *Scientific Reports*, 11: 4239. <https://doi.org/10.1038/s41598-021-82537-1>
- Ali, M.Y., Sina, A.A.I., Khandker, S.S., Neesa, L., Tanvir, E.M., Kabir, A., Khalil, M.I. & Gan, S.H. (2021). Nutritional composition and bioactive compounds in tomatoes and their impact on human health and disease: A review. *Foods*, 10: 45. <https://doi.org/10.3390/foods10010045>
- Bailey, L.H. (1891). *Experiments in the forcing of tomatoes*. Ithaca, N.Y.: Cornell University Agricultural Experiment Station, 28: 45-61.
- Banda, H. & Paxton, R. (1990). Pollination of greenhouse tomatoes by bees. *Acta Horticulturae*, 288: 194-198. <https://doi.org/10.17660/ActaHortic.1991.288.28>
- Bartelli, B. F. & Nogueira-Ferreira, F. H. (2014). Pollination services provided by *Melipona quadrfasciata* Lepelletier (Hymenoptera: Meliponini) in greenhouses with *Solanum lycopersicum* L. (Solanaceae). *Sociobiology*, 61: 510-516. <https://doi.org/10.13102/sociobiology.v61i4.510-516>
- Bell, M. C., Spooner-Hart, R. N. & Haigh, A. M. (2006). Pollination of greenhouse tomatoes by the Australian bluebanded bee *Amegilla (Zonamegilla) holmesi* (Hym.: Apidae). *Journal of Economic Entomology*, 99: 437-442. <https://doi.org/10.1603/0022-0493-99.2.437>

- Bergougnoux, V. (2014). The history of tomato: from domestication to biopharming. *Biotechnology Advances*, 32: 170-189. <https://doi.org/10.1016/j.biotechadv.2013.11.003>
- Buchmann, S. L. (1983). Buzz pollination in angiosperms. *Bo. Paper* (266). https://digitalcommons.usu.edu/bee_lab_bo/266
- Cauch, O., Quezada-Euán, J. J. G., Macias-Macias, J. O., Reyes-Oregel, V., Medina-Peralta, S. & Parra-Tabla, V. (2004). Behavior and pollination efficiency of *Nannotrigona perilampoides* (Hymenoptera: Meliponini) on greenhouse tomatoes (*Lycopersicon esculentum*) in subtropical Mexico. *Journal of Economic Entomology*, 97: 475-481. <https://doi.org/10.1093/jee/97.2.475>
- Cawood, M. (1964). The effect of sound waves on pollination of tomato flowers. *Stockbridge House Exp. Stn. Rep.*, 1963: 95-96.
- Cottrell-Dormer, W. (1945). An electric pollinator for tomatoes. *Queensland Journal of Agricultural Science*, 2: 157-169.
- Cribb, D., Hand, D. & Edmondson, R. (1993). A comparative study of the effects of using the honeybee as a pollinating agent of glasshouse tomato. *Journal of horticultural science*, 68: 79-88. <https://doi.org/10.1080/00221589.1993.11516331>
- Dasgan, H. Y., Ozdogan, A., Kaftanoglu, O. & Abak, K. (2004). Effectiveness of bumble bee pollination in anti-frost heated tomato greenhouses in the Mediterranean basin. *Turkish Journal of Agriculture and Forestry*, 28: 73-82.
- de Moura-Moraes, M. C., Frantine-Silva, W., Gaglianone, M. C. & de Oliveira Campos, L. A. (2021). The use of different stingless bee species to pollinate cherry tomatoes under protected cultivation. *Sociobiology*, 68: e5227-e5227. <https://doi.org/10.13102/sociobiology.v68i1.5227>
- Del Sarto, M., Peruquetti, R. & Campos, L. (2005). Evaluation of the neotropical stingless bee *Melipona quadrifasciata* (Hymenoptera: Apidae) as pollinator of greenhouse tomatoes. *Journal of Economic Entomology*, 98: 260-266.
- DeTar, W. R., Haugh, C. & Hamilton, J. (1968). Acoustically forced vibration of greenhouse tomato blossoms to induce pollination. *Transactions of the ASAE*, 11: 731-735.
- Dogterom, M., Matteoni, J. & Plowright, R. (1998). Pollination of greenhouse tomatoes by the North American *Bombus vosnesenskii* (Hymenoptera: Apidae). *Journal of Economic Entomology*, 91: 71-75. <https://doi.org/10.1093/jee/91.1.71>
- Dos Santos, S., Roselino, A., Hrnecir, M. & Bego, L. (2009). Pollination of tomatoes by the stingless bee *Melipona quadrifasciata* and the honey bee *Apis mellifera* (Hymenoptera, Apidae). *Genetics and Molecular Research*, 8: 751-757. <https://doi.org/10.4238/vol8-2kerr015>
- FAOSTAT. (2023). [https://www.fao.org/statistics/highlights-archive/highlights-detail/agricultural-production-statistics-\(2000-2022\)/](https://www.fao.org/statistics/highlights-archive/highlights-detail/agricultural-production-statistics-(2000-2022)/)
- Fletcher, S.W. & Gregg, O.I. (1907). Pollination of forced tomatoes. *Special Bulletin of the Michigan Agricultural Experiment Station*, 39: 294-301.
- Free, J.B. (1970). *Insect pollination of crops*. New York: Academic Press, 544 p.
- Freitas, L. (2013). Concepts of pollinator performance: is a simple approach necessary to achieve a standardized terminology? *Brazilian Journal of Botany*, 36: 3-8. <https://doi.org/10.1007/s40415-013-0005-6>
- Gaglianone, M., Campos, M., Franceschinelli, E., Deprá, M., Silva, P., Montagnana, P., Hautequestt, A., Morais, M. & Campos, L. (2015). Plano de manejo para os polinizadores do tomateiro. *Funbio*, Rio de Janeiro, 23.
- Hanna, H. Y. (1999). Assisting Natural Wind Pollination of Field Tomatoes with an Air Blower Enhances Yield. *HortScience*, 34: 846-847. <https://doi.org/10.21273/hortsci.34.5.846>
- Hanna, H. Y. (2004). Air blowers are less effective pollinators of greenhouse tomatoes than electric vibrators but cost less to operate. *HortTechnology*, 14: 104-107. <https://doi.org/10.21273/HORTTECH.14.1.0104>
- Hatami, M., Monfared, A., Haghani, M. & Fahlani, R. (2013). Effect of *Bombus terrestris* L. (Hymenoptera, Apidae) pollinating on flowering and fruiting trends of greenhouse tomato (*Lycopersicon esculentum*). *Linzer biologische Beiträge*, 45: 1907-1919.
- Hikawa, M. & Miyayama, R. (2009). Effects of pollination by *Melipona quadrifasciata* (Hymenoptera: Apidae) on tomatoes in protected culture. *Applied Entomology and Zoology*, 44: 301-307. <https://doi.org/10.1303/aez.2009.301>
- Hiraguri, T., Shimizu, H., Kimura, T., Matsuda, T., Maruta, K., Takemura, Y., ... & Takanashi, T. (2023). Autonomous drone-based pollination system using AI classifier to replace bees for greenhouse tomato cultivation. *IEEE Access*, 11: 99352-99364. <https://doi.org/10.1109/ACCESS.2023.3312151>
- Hogendoorn, K., Gross, C. L., Sedgley, M. & Keller, M. A. (2006). Increased tomato yield through pollination by native Australian *Amegilla chlorocyanea* (Hymenoptera: Anthophoridae). *Journal of Economic Entomology*, 99: 828-833. <https://doi.org/10.1603/0022-0493-99.3.828>
- Hogendoorn, K., Steen, Z. & Schwarz, M. P. (2000). Native Australian carpenter bees as a potential alternative to introducing bumble bees for tomato pollination in greenhouses. *Journal of Apicultural Research*, 39: 67-74. <https://doi.org/10.1080/00218839.2000.11101023>
- Ilbi, H. & Boztok, K. (1993). The effects of different truss-vibration durations on pollination and fruit set of greenhouse grown tomatoes. *Acta Horticulturae*, 366: 73-78. <https://doi.org/10.17660/ActaHortic.1994.366.6>

- Kevan, P. G. & Phillips, T. P. (2001). The Economic Impacts of Pollinator Declines: An Approach to Assessing the Consequences. *Conservation Ecology and Society*, 5: Article 8. <http://www.jstor.org/stable/26271801>
- Kevan, P., Straver, W., Offer, M. & Laverty, T. (1991). Pollination of greenhouse tomatoes by bumble bees in Ontario. *Proceedings of the Entomological Society of Ontario*, 122: 15-19.
- McGregor, S.E. (1976). Insect pollination of cultivated crop plants. Washington, D.C.: Agricultural Research Service, U.S. Department of Agriculture. (Agriculture Handbook No. 496).
- Morandin, L., Laverty, T. & Kevan, P. (2001a). Bumble bee (Hymenoptera: Apidae) activity and pollination levels in commercial tomato greenhouses. *Journal of Economic Entomology*, 94: 462-467. <https://doi.org/10.1603/0022-0493-94.2.462>
- Morandin, L., Laverty, T. & Kevan, P. (2001b). Effect of bumble bee (Hymenoptera: Apidae) pollination intensity on the quality of greenhouse tomatoes. *Journal of Economic Entomology*, 94: 172-179. <https://doi.org/10.1603/0022-0493-94.1.172>
- Nahir, D., Gan-Mor, S., Rylski, I. & Frankel, H. (1984). Pollination of tomato flowers by a pulsating air jet. *Transactions of the ASAE*, 27: 894-896. <https://doi.org/10.13031/2013.32891>
- Naika, S., Lidth de Jeude, J. V., Goffau, M. D., Hilmi, M. & Dam, B. V. (2005). La culture de la tomate: production, transformation et commercialisation. *Agrodok* (17).
- Nazer, I., Kasrawi, M. & Al-Attal, Y. (2003). Influence of Pollination Technique on Greenhouse Tomato Production. *Journal of Agricultural and Marine Sciences*, 8: 21-26. <https://doi.org/10.24200/jams.vol8iss1pp21-26>
- Neiswander, R. B. (1956). Pollination of greenhouse tomatoes by honey bees. *Journal of Economic Entomology*, 49: 436-437. <https://doi.org/10.1093/jec/49.4.436>
- Niño, E. L. & Cameron Jasper, W. (2015). Improving the future of honey bee breeding programs by employing recent scientific advances. *Current Opinions in Insect Science*, 10: 163-169. <https://doi.org/10.1016/j.cois.2015.05.005>
- Nogueira-Neto, P. (1997). Vida e criação de abelhas indígenas sem ferrão. São Paulo: Editora Nogueirapis, 446 p.
- Palma, G., Quezada-Euán, J., Reyes-Oregel, V., Meléndez, V. & Moo-Valle, H. (2008). Production of greenhouse tomatoes (*Lycopersicon esculentum*) using *Nannotrigona perilampoides*, *Bombus impatiens* and mechanical vibration (Hym.: Apoidea). *Journal of Applied Entomology*, 132: 79-85. <https://doi.org/10.1111/j.1439-0418.2007.01246.x>
- Petit, J. (2013). Identification et validation fonctionnelle de gènes candidats contrôlant la composition de la cuticule chez le fruit de tomate. Thèse de doctorat, Université Bordeaux 1, École doctorale des Sciences de la Vie et de la Santé, spécialité Biologie Végétale.
- Picken, A. (1984). A review of pollination and fruit set in the tomato (*Lycopersicon esculentum* Mill.). *Journal of Horticultural Science*, 59: 1-13. <https://doi.org/10.1080/00221589.1984.11515163>
- Pressman, E., Shaked, R., Rosenfeld, K., & Hefetz, A. (1999). A comparative study of the efficiency of bumble bees and an electric bee in pollinating unheated greenhouse tomatoes. *The Journal of Horticultural Science and Biotechnology*, 74: 101-104. <https://doi.org/10.1080/14620316.1999.11511080>
- Ranc, N. (2010). Analyse du polymorphisme moléculaire de gènes de composantes de la qualité des fruits dans les ressources génétiques sauvages et cultivées de tomate; recherche d'associations gènes/QTL. Thèse de doctorat, École Nationale Supérieure Agronomique de Montpellier – SUPAGRO, 275 p.
- Ratnayake, M. N., Amarathunga, D. C., Zaman, A., Dyer, A. G. & Dorin, A. (2023). Spatial monitoring and insect behavioural analysis using computer vision for precision pollination. *International Journal of Computer Vision*, 131: 591-606. <https://doi.org/10.1007/s11263-022-01715-4>
- Ritchie, H., Rosado, P. & Roser, M. (2023). Agricultural production. <https://ourworldindata.org/agricultural-production> (accessed date: 21 August 2025).
- Salvarrey, S., Santos, E., Arbulo, N., Giménez, G. & Invernizzi, C. (2020). Characteristics of the tomato fruit (*Solanum lycopersicum*) using native bumble bees (*Bombus atratus*) as pollinators in greenhouse. *Agrociencia Uruguaiy*, 24: e1101. <https://doi.org/10.31285/agro.24.101>
- Santos, A., Bartelli, B. & Nogueira-Ferreira, F. (2014). Potential pollinators of tomato, *Lycopersicon esculentum* (Solanaceae), in open crops and the effect of a solitary bee in fruit set and quality. *Journal of Economic Entomology*, 107: 987-994. <https://doi.org/10.1603/EC13378>
- Schneck, H.W. (1928). Pollination of greenhouse tomatoes. Ithaca, N.Y.: Cornell University Agricultural Experiment Station, Special Bulletin, 470.
- Short, T.H. & Bauerle, W.L. (1973). Pollinating greenhouse tomatoes with a vibrating trellis system. *Research Summary, Ohio Agricultural Research and Development Center*, 66: 13-15.
- Short, T.H. & Bauerle, W.L. (1974). Pollinating greenhouse tomatoes with synchronized air cylinders. *Research Bulletin, Ohio Agricultural Research and Development Center*, 73: 9-13.
- Silva-Neto, C.D.M.E., Ribeiro, A.C.C., Gomes, F.L., Melo, A.P.C.D., Oliveira, G.M.D., Faquinello, P., Franceschinelli, E.V. & Nascimento, A.D.R. (2018). The stingless bee mandaçaia (*Melipona quadrifasciata* Lepeletier) increases the quality of greenhouse tomatoes. *Journal of Apicultural Research*, 58: 9-15. <https://doi.org/10.1080/00218839.2018.1494913>

- Smith, A. F. (2001). *The tomato in America: early history, culture, and cookery*. University of Illinois Press.
- Stoner, A. K. (1971). *Commercial production of greenhouse tomatoes*. US Agricultural Research Service.
- Strange, J. P. (2015). *Bombus huntii*, *Bombus impatiens*, and *Bombus vosnesenskii* (Hymenoptera: Apidae) pollinate greenhouse-grown tomatoes in western North America. *Journal of Economic Entomology*, 108: 873-879. <https://doi.org/10.1093/jee/tov078>
- Sung, I.-H. & Chiang, C.-H. (2014). Study of honey bee and bumble bee pollination for screen-house tomatoes in Taiwan. *Formosan Entomology*, 34: 21-31.
- Torres-Ruiz, A. & Jones, R. W. (2012). Comparison of the Efficiency of the Bumble Bees *Bombus impatiens* and *Bombus ephippiatus* (Hymenoptera: Apidae) as Pollinators of Tomato in Greenhouses. *Journal of Economic Entomology*, 105: 1871-1877. <https://doi.org/10.1603/ec12171>
- Tridge. (2020). Tridge: your global sourcing hub. <https://www.tridge.com/products/tomato>
- Van Ravestijn, W. & Van der Sande, J. (1990). Use of bumble bees for the pollination of glasshouse tomatoes. *Acta Horticulturae* 288: 204-212. <https://doi.org/10.17660/ActaHortic.1991.288.30>
- Velthuis, H. H. W. & Doorn, A. V. (2006). A century of advances in bumble beedomestication and the economic and environmental aspects of its commercialization for pollination. *Apidologie*, 37: 421-451. <https://doi.org/10.1051/apido:2006019>
- Vergara, C. H. & Fonseca-Buendía, P. (2012). Pollination of greenhouse tomatoes by the Mexican bumble bee *Bombus ephippiatus* (Hymenoptera: Apidae). *Journal of Pollination Ecology*, 7: 27-30. [https://doi.org/10.26786/1920-7603\(2012\)1](https://doi.org/10.26786/1920-7603(2012)1)
- Verkerk, K. (1957). The pollination of tomatoes. *Netherlands Journal of Agricultural Science*, 5: 37-54. <https://doi.org/10.18174/njas.v5i1.17747>.
- Westerkamp, C. & Gottsberger, G. (2000). Diversity pays in crop pollination. *Crop Science*, 40: 1209-1222. <https://doi.org/10.2135/cropsci2000.4051209x>
- Wongsa, K., Duangphakdee, O. & Rattanawanee, A. (2023). Pollination efficacy of stingless bees, *Tetragonula pagdeni* Schwarz (Apidae: Meliponini), on greenhouse tomatoes (*Solanum lycopersicum* Linnaeus). *PeerJ*, 11: e15367. <https://doi.org/10.7717/peerj.15367>

