Review Article

Pollination Strategies for Advancing Protected Cultivation of Vegetable Crops

ABSTRACT

Protected cultivation is a transformative agrotechnology offering enhanced yield, quality, and resource efficiency. Pollination, a critical determinant of crop productivity, faces unique challenges in controlled environments, necessitating innovative strategies. This review highlights various pollination techniques, including manual, mechanical, and biotic methods, and their application in vegetable crop cultivation. While manual methods like hand pollination ensure precision, they are labor-intensive. Mechanical solutions, such as handheld vibrators, air blowers, and electrostatic devices, provide scalable alternatives but often lack the efficiency of natural pollinators. Biotic agents, including bumblebees, honeybees, stingless bees, and solitary species like carpenter bees and Australian blue-banded bees, emerge as sustainable and effective solutions. Their adaptability to greenhouse conditions and selective pollen transfer capabilities significantly enhance fruit set, quality, and yield. Emerging technologies, such as robotic pollinators and pulsating air systems, further complement traditional methods. This review underscores the importance of integrating diverse pollination strategies to optimize productivity in protected cultivation systems.

KEYWORDS: *Protected cultivation, Manual pollination, Bee pollination, Solitary bees, Robotics*

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INTRODUCTION

Protected cultivation is an advanced agrotechnology that optimizes plant growth by regulating environmental conditions, enabling extended production periods, earlier harvests, and higher-quality yields (Gruda and Tanny, 2015). It is ideal for high-value or off-season crops, conserving water, reducing pesticide use, and protecting against pests, diseases, and abiotic stresses (Ummyiah *et al*., 2017; Nordey *et al*., 2017). Farmers adopt various covered structures based on crop type, climate, and desired outcomes. Over 120 countries worldwide are actively involved in greenhouse farming, driven by the need to enhance food security and adapt to climate change. The global area under greenhouse cultivation has grown to approximately 720,000 hectares, with 450,000 hectares devoted to vegetable production and over 110,000 hectares using soilless and hydroponic systems (Sciencedaily, 2024). In India, protected cultivation spans around 50,000 hectares for horticultural crops, with 2,000 hectares specifically for greenhouse vegetables (Sindhu and Chatterjee, 2020).

In an open field, wind and insect activity can generate the vibrations necessary to release pollen grains (Gaglianone *et al*., 2018). However, in greenhouse environments, the involvement of pollinators or specific actions is essential to achieve adequate fruit set and quality (Morandin *et al*. (2001); Palma *et al*. (2008)).Insufficient pollination can result in limited pollen availability, which negatively impacts progeny vigour by diminishing the selection process among gametes both before and during fertilization (Bertin, 1990). Therefore, the use of pollination agents is essential for achieving high-quality fruit and seed production.

Tomato, a key crop grown in protected environments, is primarily self-fertile (Rick, 1950; Free, 1970), but supplementary pollination can improve fruit quality and yield (Stoner, 1971; McGregor, 1976; Picken, 1984). Outdoor tomatoes rely on wind and biotic factors for pollination (Free, 1970; Groenewegen *et al*., 1994), while greenhouses require deliberate methods to facilitate pollen transfer (Neiswander, 1954). Tomatoes' poricidal anthers need rapid vibrations for pollen release, a process known as buzz pollination (Buchmann, 1983, 1986, 1992). While mechanical vibration is an option, it is labor-intensive and costly (Cribb *et al*., 1990; Ilbi *et al*., 1994). Insect pollinators, like bumblebees, are more efficient due to their ability to generate strong vibrations and their larger size, which allows for better pollen collection (Free, 1993). Bumblebees outperform honeybees in greenhouse settings, increasing fruit set and size (Banda and Paxton, 1991). Other bees, like stingless bees and *Amegilla holmesi*, also enhance pollination (de Ruijter *et al*., 1991; Bartelli *et al*., 2014; Bell *et al.,* 2006). Cucumber, widely cultivated in greenhouses, benefits from insect pollination for better fruit set and yield (Nicodemo, 2013). For cucumbers, which have separate male and female flowers, bees are essential for transferring pollen (Free, 1993). The introduction of stingless bees and carpenter bees has shown to improve cucumber and melon yields in greenhouses (Sadeh *et al*., 2007).

One approach to address pollination deficit under protected cultivation is manual pollination, using paint brush, electric vibrators or air blowers, which involves human effort to meet pollination needs. However, this method is labor-intensive, time-consuming, lacks selective vigor, and is relatively expensive. Robotic pollinators are also used for supplementing pollination inside commercial protected structures. Alternatively, a more effective solution is utilizing insect pollinators including honey bees, bumble bees, stingless bees and other solitary bees like carpenter bees and Australian blue banded bees, which can selectively enhance vigour, making the process efficient, less labour-intensive, and cost-effective. Integrated Crop Pollination can also be adopted under which various strategies supporting crop pollination can be developed and coordinated (Issacs *et al*., 2017) This review outlines the various pollination techniques, both mechanical and biotic, that can be employed successfully for enhancing the crop quality and yield under protected cultivation.

POLLINATION TECHNIQUES FOR PROTECTED CULTIVATION

1.HAND POLLINATION

In polyhouse environments, where natural pollination agents like wind or insects are absent, manual pollination using a paintbrush is a simple method, especially for self-pollinated crops like tomatoes, peppers, and eggplants. This technique involves gently brushing the anthers of a flower to collect pollen and transferring it to the stigma of the same or another flower, typically performed in the morning when pollen viability is highest. Using a soft-bristled brush ensures minimal damage to delicate flower structures, and the process is repeated 2–3 times a week to maximize fruit set. While paintbrush pollination offers precision, accessibility, and cost-effectiveness, it is labor-intensive and impractical for large-scale polyhouse operations due to its time-consuming nature. It is best suited for small-scale or experimental setups where targeted pollination is required, such as hybrid seed production (Wurz *et al*., 2021).Though effective, the technique is less efficient and scalable compared to mechanized methods like air jets or vibrating devices, which are better suited for commercial polyhouses (Broussard *et al*., 2023).

Table 1- List of different pollination methods

Pollination method	Crop	References
Hand pollination	*Solanum lycopersicum*	Wurz *et al*.(2021)
Handheld devices	*Solanum lycopersicum* *Capsicum annum*	Peet and Welles (2005)

	Solanum melongena	
Electrostatic pollination	*Solanum lycopersicum* *Momordica charantia*	Lukose *et al*. (2022)
Pulsating air pollinator	*Solanum lycopersicum*	Nahir *et al*.(1984) Mahadik *et al*. (2021)
Bumble bee (*Bombus spp.*)	*Solanum lycopersicum* *Solanum melongena* *Capsicum annum* *Cucurbita pepo* *Capsicum annum*	Yankit *et al*. (2018) Abak *et al*. (2000) Serrano *et al*. (2006) Nault *et al*.(2011) Thakur *et al*. (2020)
Honey bee(*Apis spp*.)	*Cucurbita pepo*, *Cucurbitamoschata* *Cucurbita maxima* *Cucumis melo* *Cucumis sativus* *Solanum lycopersicum*	Walters and Taylor (2006) Huang *et al*. (2017) Kumar *et al*. (2015) Sabara *et al*. (2004)
Stingless bee *Tetragonulairidipennis* *Heterotrigonaspp*. *Nannotrigonaperilampoides* *Tetragonulapagdeni*	 *Cucumis sativus* *Cucumis melo* *Solanum lycopersicum* *Solanum lycopersicum*	 Kishan *et al*. (2017) Atmowidi *et al*. (2022) Cauich *et al*.(2004) Wongsa *et al*.(2023)
American blue banded bee *Amegillaholmesi* *Amegillachlorocyanea*	 *Solanum lycopersicum* *Solanum lycopersicum*	 Bell *et al*. (2006) Hogendoorn *et al*. (2006)

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Carpenter bee		
Xylocopapubescens	*Solanum lycopersicum*	Hogendoorn *et al*.(2000)
	Cucumis melo	Sadeh *et al*. (2007)

Hand pollination

2. HANDHELD DEVICES

Handheld equipment like blowers, sprayers, and vibratory wands offer a faster and more convenient method for applying pollen compared to basic tools like paintbrushes. Traditionally, greenhouse tomatoes have been pollinated manually using electric vibrating tools, often referred to as “electric bees” (Cottrell-Dormer, 1945; Short and Bauerle, 1974; Cribb, 1990; Straver and Plowright, 1991; Cribb *et al*., 1993). While effective, this method is labor-intensive and costly with labour costs amounting to approximately US$12,000 per hectare annually (Stoner, 1971; Short and Bauerle, 1974; Ravestijn and van der Sande, 1991; Straver and Plowright, 1991). Research has shown that tomatoes pollinated with these wands are significantly heavier and produce more seeds compared to those left unpollinated (Hogendoorn*et al*., 2006). Additionally, Banda and Paxton (1991) reported a 120% increase in seed count in wand-pollinated tomatoes compared to those that were not pollinated. It has been reported that among three methods of pollination, *viz*., pollination by stick, pollination by using vibrator and pollination by using air blower in cherry tomato grown under protected structures, air-blowing recorded more fruit set, berry weight, berry width, berry length, number of seeds, 100-seed weight, seed yield per berry and seed germination (Vidyadhar*et al*., 2015) . Traditional methods using vibrators or blowers are limited to inducing pollen release through vibration without effectively guiding particle movement. Study by Liu *et al*., 2024, introduced a combined method of vibration-induced pollen release and airflow-guided pollen movement, supported by a numerical simulation model. The model, based on a gas–solid two-phase flow approach, accounts for the shape and surface properties of tomato pollen. A response surface analysis examined the effects of airflow angle, start time, and velocity on pollination effectiveness, with results identifying optimal parameters: airflow angle of 12.67°, start time of 519.45 ms, and velocity of 0.72 m/s. The optimized method achieved an average stigma pollen coverage rate of 9.59%, which was 85.85 % and 100.63 % relatively higher than vibration pollination and airflow pollination.

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Electric vibrator

Air blower

3. ARTIFICIAL POLLINIZERS

Two artificial pollinizers specifically designed for pollinating tropical vegetables under protected cultivation, utilizing air and water as mediums for pollen collection were developed by Ramya (2018). The first model employs air-based pollen collection using a vacuum pump that creates suction through a pollen collection tip and chamber. A brush at the tip dislodges pollen grains from flowers, which are then drawn through hollow tubes into a collection chamber. Inside the chamber, a screen mesh separates the pollen grains from the air, and the filtered air is released into the atmosphere via the vacuum pump. The second model adopts a water-based approach, where a pneumatic hand sprayer is used to spray water onto male flowers positioned inside a watertight container. The water spray washes pollen grains into the container, creating a water-pollen mixture that can be directly used for artificial pollination. These innovative pollinizer models offer efficient and effective methods for enhancing the productivity of tropical vegetable cultivation in controlled environments.

4. ELECTROSTATIC POLLINATION

Electrostatics focuses on electric forces involving electrons and ions, as well as the associated electric fields and potentials. An object becomes electrostatically charged by either gaining electrons, resulting in a "negative" charge, or losing them, leading to a "positive" charge. Like charges repel, while opposite charges attract. The electrostatic force (F) between two charged objects is governed by Coulomb's law. Electrostatic interactions are significant in various biological processes, including plant pollination in natural and agricultural settings (Honig and Nicholls, 1995).Under normal fair-weather conditions, plants typically carry a slight negative surface charge, surrounded by weak electric fields (Maw, 1962). The electric field distribution around a plant varies based on its shape, with the strongest fields typically occurring near sharp points, such as plant tips and flowers (Dai and Law, 1995). Foraging bees usually carry a positively charged surface (Schwartz, 1991). Experimental analyses revealed that the average electrical charge on a bee following active flight was approximately 23.1 pC. The detachment forces observed for pollen across selected horticultural species ranged between 4×10^{-10} and 39×10^{-10} N. Mathematical models indicated that the charge accumulated by honeybees could, in some cases, enable pollen detachment without direct contact (Gan Mor *et al*., 1995). As bees fly through the air, they encounter electrical currents, which cause their bodies to become electrostatically charged due to "frictional electricity" (Warnke, 1977). Warnke (1977) and Thorp (1979) proposed that when an insect carrying an electrical charge approaches a flower, the opposite charge flows into the plant's stem and flowers, creating an electric field between the insect and the flower. As the distance between them decreases, the strength of this electric field increases. The resulting attraction between the insect and the flower causes pollen grains to detach from the anther and attach to the insect's body. These same forces also facilitate the transfer of pollen from the insect’s body to different parts of the flower, including the

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stigma. The electrostatic force can act as a temporary adhesive, particularly when pollen grains are deposited on a dry stigma, allowing them to stay on the receptive surface long enough for successful germination (Woittiez and Willemse, 1979).

The use of electrostatic charge in artificial pollination holds great promise and has yielded encouraging results in preliminary studies conducted by numerous researchers in the field. This method, which involves the non-contact detachment and deposition of charged pollen, minimizes physical damage to the pollen. As a result, it has the potential to enhance both the fruit set and its quality. Electrostatic pollinator consists of an electrode and high voltage amplification unit. High voltage applied to charging electrode creates electrostatic field around the electrode which induces an equal and opposite charge on flower. Opposite charges create a temporary force of attraction and initiates the detachment of pollen towards the high voltage electrode. The fruit set efficiency was 70% in tomato and 100% in bitter gourd with electrostatic pollination whereas it was 30% after hand pollination (Lukose *et al*., 2022). Electrostatic dusting has demonstrated three times greater pollen deposition on flowers compared to traditional pollen blowing. By applying an electrostatic charge to pollen, fruit set can increase by an average of 85% to 175%, depending on the amount of pollen used. This method can also double the percentage of fully developed seeds without compromising their viability. Additionally, electrostatic pollen deposition can achieve the same or even higher yields while using nearly 50% less pollen compared to manual methods (Dipak, 2020).

5. PULSATING AIR POLLINATOR

In self pollinated crops like tomato, grown under protected conditions, pollen can be released through the application of mechanical force or by using an air blast. The vibration force or acceleration must be strong enough to release pollen from the sacs and ensure its deposition on the stigma. Vibration energy can be delivered through methods such as mechanical shaking (Short and Banerte, 1973), air blasts (Short and Banerte, 1972, 1973), or sound waves (De Tar *et al*., 1968). Mechanical devices are advantageous because they can apply strong forces directly to the flower; however, they require individual cluster application, making manual systems labor-intensive and time-consuming. While sound waves are theoretically viable as energy carriers, achieving sufficient vibration for pollen release requires noise levels of 150 decibels (De Tar *et al*., 1968), which is impractically loud. In this context, air jets emerge as a promising alternative for effectively facilitating pollination. The dynamic response of tomato flowers to a pulsating air jet was analyzed (Nahir *et al*., 1984). Within the frequency range of 5 to 60 Hz, the flowers exhibited a single natural (resonant) frequency near 22 Hz. Maximum effectiveness of the air jet occurred when the open time-to-cycle rate ratio was 0.5. Increasing air velocity up to 60 m/s enhanced flower acceleration and pollen deposition. Effective pollination, defined as producing more than 60 seeds per fruit, required a minimum of three air pulses. On average, fruit weight increased by 2.4 with the mechanical bee and by 2.2 with the pulsating air jet compared to untreated controls. Mahadik *et al*. (2021) developed a pollinator based on the principle of a pulsating air jet to enhance pollination. The device incorporated three 3D-printed pulsation units, allowing for adjustable air pulsation frequencies and angular movements to cover an entire flower bed. It was designed to be portable, enabling easy operation in greenhouse alleys. The pollinator's performance was compared to hand pollination and pollination using a blower in tomato crops and key variables such as airflow rates, pulsation frequencies, and exposure times were analyzed for their effects on pollination efficiency and yield. Experiments conducted in greenhouse-grown tomato plants showed that the highest pollination efficiency (83.66%) was achieved at an airflow rate of 1.99 m^3/min, a pulsation frequency of 23.50 Hz, and an exposure time of 19.40 seconds. Optimal yield was observed under similar airflow conditions, with a pulsation frequency of 22.25 Hz and an exposure time of 15.78 seconds for 5-meter flower sections. The developed pollinator resulted in significantly higher yields compared to the blower (36.6% increase) and control plots (95.7% increase).

6. ROBOTIC BEES

Robot bees, also known as mechanical or artificial bees, are designed to replicate the pollination role of natural bees, often by mimicking their behaviors and actions. These machines are primarily used in agricultural settings to assist with pollination when natural bee populations are insufficient. One of the

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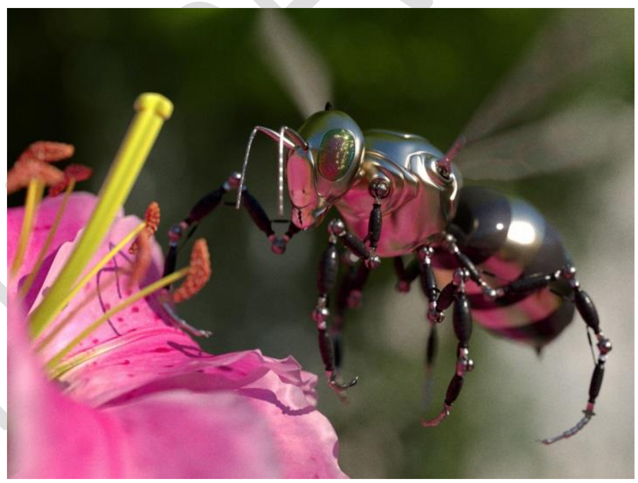
notable developments in this field comes from Arugga, a startup based in Israel, which commercialized a robotic pollinator called Polly. Polly mimics the buzzing of a bumblebee, producing strong vibrations that help dislodge pollen from flowers, enabling them to be fertilized and subsequently produce fruit. This technology aims to address challenges such as the decline in natural bee populations and the difficulty of pollinating certain crops.

In addition to Polly, there are other robotic pollinators like the Fairy Robot Fly. These are designed as seed-like structures equipped with a soft actuator made from light-responsive liquid crystalline elastomers. When exposed to visible light, the actuator induces movements that cause the bristles on the robot to open or close, assisting in pollination. These devices are intended to enhance the pollination process by mimicking the action of natural pollinators.

However, while these robotic bees show promise, they are still not as efficient as natural bees in terms of pollination. Studies have highlighted that the performance of robot bees in pollination tasks is currently limited compared to the natural capabilities of bees, especially when considering the variety and complexity of flower interactions. Furthermore, their use is not yet economically viable on a large scale, as the cost of development, maintenance, and operation of these robotic systems remains high (Potts *et al*., 2018).

Robotic pollinator



Robotic bee

7. INSECT POLLINATORS

7.1. BUMBLE BEE

Bumblebees (family: Apidae, order: Hymenoptera) offer a cost-effective and efficient alternative to manual pollination in greenhouse agriculture. Bumblebees (*Bombus* spp.) encompass approximately 250 species worldwide (Williams *et al*., 2008), with India hosting 48 species along the Himalayan region at altitudes ranging from 2,000 to 15,000 feet (Williams, 1991). They possess distinct adaptations, such as robust, hairy bodies, long proboscis for deep flowers, and the ability to generate heat through muscle contractions, enabling them to forage efficiently in cooler climates (Heinrich, 1979; Abrol, 2011). Bumblebees are organized into colonies comprising queens, workers, and males, with annual life cycles influenced by environmental conditions. Their foraging behavior includes visiting 8–12 flowers per minute and detecting floral cues like electric fields and temperature, enhancing pollination efficiency (Clarke *et al*., 2013; Harrap *et al*., 2017).

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Buzz pollination, a unique ability of bumblebees and some solitary bees, involves rapid contraction of flight muscles to dislodge pollen. This mechanism is critical for crops like tomatoes, eggplants, and peppers, which require vibration for effective pollination (Plowright and Laverty, 1984; Cane and Payne, 1990, 1993). Bumblebees' initial vibrations and floral characteristics jointly influence pollen release and deposition (Arroyo *et al*., 2019). Additionally, their ability to detect previously visited flowers through electric fields aids in efficient foraging (Clarke *et al*., 2013). Bumblebees outperform honeybees in greenhouse environments due to their superior thermoregulation, faster foraging rates, and lower swarming tendencies. Unlike honeybees, which require 7–10 visits for effective pollination, bumblebees can achieve it in a single visit. Their ability to forage in UV-blocking structures and cooler conditions further enhances their utility in protected agriculture (Ahn *et al*., 1988; Dyer and Chittka, 2004; Morandin *et al*., 2001). Bumblebee species like *Bombus terrestris, B. impatiens,* and *B. occidentalis* are widely employed for pollination worldwide (Kwon and Saeed, 2003; Velthuis and van Doorn, 2006; Klein et al., 2007). In India, efforts to domesticate native species like *Bombus haemorrhoidalis* began in 1997–98 under laboratory conditions (Thakur, 2002). The first successful rearing of *B. haemorrhoidalis* in captivity was achieved in 2004 by Dayal and Rana, who reared overwintered queens in controlled environments.

Studies reveal distinct foraging activity patterns influenced by crop type, time of day, and environmental conditions. Abak *et al.* (2000) observed that bumblebee activity in unheated plastic houses cultivating eggplants peaked between 10:00 and 11:00 a.m., declined by midday, and resumed in the late afternoon. Similar findings were reported for cucumbers (Kashyap, 2007), bell peppers (Thakur *et al*., 2008), and tomatoes (Yankit *et al*., 2018). These studies indicate that aligning pollinator introduction with peak activity periods can optimize pollination efficiency and crop yield.Bumblebee pollination significantly enhances crop yield and quality. Studies by Banda and Paxton (1991) emphasized that bumblebees are more effective than honeybees for greenhouse tomatoes. Laboratory-reared colonies led to yield increases of 23% in eggplants and 17% in tomatoes, with significant improvements in fruit size, seed count, and quality attributes (Abak *et al*., 1995, 2000). Similar benefits were observed in peppers (Serrano *et al*., 2006), pumpkins (Nault *et al*., 2011), and other crops. Yankit *et al*. (2018) reported increases in the number of fruits per cluster and yield, alongside improvements in fruit dimensions and reduced deformities in tomato. Thakur *et al.* (2021) documented enhancements in bell peppers, including a 24.6% increase in fruit weight and an 89.4% rise in yield per plant. Bumblebee pollination offers a robust solution for enhancing greenhouse crop productivity, outperforming traditional pollination methods in efficiency and yield improvements. The integration of bumblebee pollination into protected cultivation systems holds immense potential for achieving high-quality, sustainable yields.

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Bombus haemorrhoidalis

Bombus terrestris

Bombus impatiens ***Bombus occidentalis***

7.2. HONEY BEE

Honey bee pollination has become an integral practice in protected cultivation, particularly in greenhouse settings, where beehives are placed inside to minimize the labor costs of artificial pollination (Liu *et al*., 2011). Among the various pollinators, *Apis mellifera* is widely recognized for its efficiency, especially in melon fields across the globe (Tschoeke *et al*., 2015). Honey bees are favored for their versatility, as they can be managed across different numbers, locations, and times. Their ability to exhibit floral constancy and fidelity makes them reliable pollinators, as they collect pollen for nourishment while also producing honey.

Honey bees belong to the family Apidae and the subfamily Apinae, and they live in colonies that include species like *Apis mellifera* and *Apis florea*. However, large colonies with extensive flight ranges, such as *Apis mellifera*, may not be well-suited for protected environments due to space limitations and the risk of collisions with greenhouse walls. In contrast, *Apis florea*, with its shorter flight range, is more adaptable to smaller, more confined spaces. *Apis mellifera* can still be utilized in larger enclosures if managed carefully by limiting colony size (no more than two bee frames) and supplementing them with sugar feed (Kumar *et al*., 2018). For effective pollination, a minimum of five honeybee visits per flower is essential, with each bee typically visiting around 100 flowers per foraging trip (Rorry, 2000).Several studies have shown that the method of fruit setting, whether through natural or artificial pollination, has significant impacts on fruit development and quality (Hayata *et al*., 2000, 2001; Klatt *et al*., 2014). Research by Walters and Taylor (2006) demonstrated that fruit weight in *Cucurbita pepo*, *C. moschata*, and *C. maxima* increased by 26%, 70%, and 78%, respectively, when honey bee pollination was employed, compared to natural pollination. Additionally, studies by Huang *et al.* (2017) have shown that honey bee pollination not only improves fruit quality but also outperforms artificial pollination. Specifically, honey bee-pollinated melons had 28% more amino acids, along with improved taste and single fruit weight, compared to those pollinated artificially.

Honey bees are recognized as the dominant pollinators in cucurbits, accounting for 77.2% of the pollination activity (Grewal and Sidhu, 1978). In greenhouse environments, *Apis mellifera* has been identified as the primary pollinator for melon crops in countries like Israel (Dag *et al*., 1992), and it has also been found to contribute significantly to cucumber pollination, with up to 82.6% of the visitors to cucumber flowers being honey bees (Nogueira and Calmora, 1993). Combining bee pollination with hand pollination has been shown to increase fruit set, size, and quality in cucumbers (Kumar *et al*., 2015). Additionally, honey bee pollination under poly-house conditions has been linked to a 494.12% increase in fruit set and a 24.46% higher yield compared to open field conditions (Rai *et al*., 2008).

In the case of greenhouse tomatoes, the use of honey bees for pollination has produced mixed results. While Neiswander (1956) found that honey bees, in conjunction with a vibrating wand, resulted in larger fruit compared to no pollination, other studies have highlighted the challenges in utilizing honey bees in these settings. Banda and Paxton (1991) noted that honey bees were "erratic" and less effective, possibly

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due to external competing vegetation and insufficient acclimatization time. Similarly, Cribb *et al*. (1993) observed improvements in tomato yield with honey bee treatments, though the colonies experienced negative effects, potentially caused by limited foraging area and pollen deprivation. Sabara *et al.* (2004) found that, although honey bees do not perform buzz pollination like bumblebees, the fruit produced in their presence was comparable to that of bumblebee-pollinated tomatoes. Nonetheless, negative colony effects, such as reduced brood production, were also noted.

Apis mellifera

Apis cerana indica

7.3. STINGLESS BEE

Stingless bees, a diverse group of eusocial bees, play a crucial role as pollinators in tropical and subtropical regions. Comprising approximately 500 species (Quezada-Euán, 2018), they significantly contribute to ecosystem functioning and agricultural productivity by pollinating a wide range of native and cultivated plant species (Heard, 1999; Momose *et al.,* 1998).

One of the notable advantages of stingless bees over other pollinators, such as honeybees and bumblebees, is their lack of a functional sting. This trait makes them ideal for pollination in confined spaces like greenhouses and polyhouses, where frequent human interaction occurs, and the presence of aggressive pollinators could pose a risk (Roubik, 1995). Their non-swarming behavior further enhances their suitability for managed pollination, as mature queens cannot fly, and new colonies are established only when nests become full (Slaa *et al*., 2000).Stingless bees exhibit higher resilience and adaptability to enclosed environments compared to other pollinators. They are less susceptible to pests and diseases commonly affecting honeybees, simplifying their management (Slaa *et al*., 2000). Their smaller foraging range, compared to honeybees, makes them especially effective for small-scale agriculture and homestead gardening (Wille, 1964). Despite this limitation, they excel in environments like greenhouses with UV-proof roofing, where other bees may face challenges (Kakutani *et al*., 1993).

The benefits of using stingless bees as pollinators are manifold. Their perennial colonies can be maintained over extended periods, providing a steady supply of pollinators, unlike bumblebees, which have shorter life cycles (Jones and Rosa, 1928). Transportable stingless bee colonies further enhance their utility in large-scale agricultural operations (Heard, 1999). Additionally, their small size and behavior make them highly effective at pollinating flowers with narrow openings, which are inaccessible to larger bee species (Roubik, 1995). For instance, stingless bees have been shown to efficiently pollinate cucumber flowers, leading to improved fruit size and quality (Santos *et al*., 2008).The foraging activity of stingless bees varies depending on species and environmental factors. Studies have demonstrated that foraging times can differ greatly across species. For example, *Tetragonula iridipennis*, a species often used in greenhouse pollination, starts its foraging activity early in the morning (Kishan *et al.,* 2017) and continues until late afternoon, with floral handling time being shorter for pollen collection than for nectar

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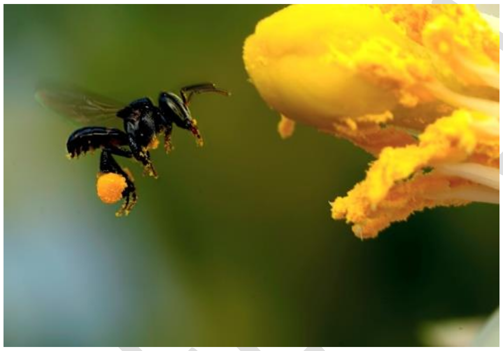
collection. Other species, such as *Nannotrigona testaceicornis*, show peak foraging activity between 10:00 and 12:00 h (Nicodemo *et al*., 2013), while *Trigona minangkabau* forages consistently throughout the day (Inoue *et al*., 1985). Environmental factors like temperature and light intensity positively influence their foraging activity, while humidity tends to have a negative effect (Sajap *et al*., 2015; Soares *et al*., 2019).

The ability of stingless bees to pollinate crops in greenhouses has been a subject of numerous studies. For instance, Kishan *et al*. (2017) found that *Tetragonula iridipennis* significantly improved cucumber yield in greenhouses by enhancing fruit length, girth, weight, and overall productivity. Similarly, Mitta *et al*. (2017) demonstrated the efficiency of this species in cucumber pollination in Malaysia. Other studies, such as those by Atmowidi et al. (2022), have shown that *Heterotrigona* species can also improve the quantity and quality of melon crops in greenhouses. *Nannotrigona perilampoides* has been identified as a particularly effective pollinator for greenhouse tomatoes, where it improves fruit set, seed production, and overall productivity compared to mechanical pollination methods (Cauich *et al*., 2004). Likewise, *Tetragonula pagdeni* has been found to be highly effective for tomato pollination, improving fruit set and weight (Wongsa *et al*., 2023). This demonstrates the potential of stingless bees as an effective pollination alternative, particularly when honeybees are not available or suitable.



Tetragonula iridipennis

8. SOLITARY BEES

8.1. AUSTRALIAN BLUE-BANDED BEE

The genus *Amegilla*, commonly known as blue-banded bees, includes several species characterized by blue bands across their abdomens. These solitary bees are native to regions such as Australia, Southeast Asia, and parts of the Pacific, where they play a critical role in pollinating both native plants and specific agricultural crops. Typically medium-sized, with lengths ranging from 8 to 14 mm, these bees are easily recognizable by their striking blue or white bands, which vary depending on the species and environmental conditions. Unlike honeybees, which have fine hairs to carry pollen, *Amegilla* bees possess specialized leg hairs and a stockier build, making them more efficient at pollen collection. *Amegilla* bees are solitary creatures that typically nest in soil, mud, or soft clay. Each female bee digs a burrow and creates individual cells, which she fills with nectar and pollen for her larvae. These bees are efficient foragers, with swift and direct flight paths that minimize travel time between flowers. Their foraging range tends to be relatively short, often within a few hundred meters, conserving energy and allowing them to stay close to their nesting sites.

One of the most distinctive features of *Amegilla* species is their ability to perform "buzz pollination" or sonication. Species such as *Amegilla cingulata* and *Amegilla holmesi* are known for employing this technique, which is essential for pollination in certain crops like tomatoes and eggplants.The pollination behavior of the Australian blue-banded bee *Amegilla pulchra*, which may be synonymous with *A. holmesi*, led to the development of the original electric tomato pollinator (Cottrell-Dormer, 1945). *A. holmesi* was found to be particularly adaptable in greenhouse environments, where they readily accepted nectar from

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artificial sources, nested in artificial blocks, and were able to mate and reproduce. Bell *et al.* (2006) confirmed the effectiveness of *A. holmesi* in greenhouse tomato pollination, showing that their pollination significantly improved fruit set, weight, diameter, roundness, and seed number compared to plants that received no pollination. This performance was comparable to mechanical pollination, positioning *A. holmesi* as a viable alternative for enhancing crop yields.

Furthermore, research by Hogendoorn *et al*. (2006) highlighted *Amegilla chlorocyanea* as a suitable substitute for bumblebees in greenhouse tomato pollination. Their study demonstrated that buzzing activity from *A. chlorocyanea* boosted fruit weight by up to 21% compared to industrial pollination methods. They estimated that approximately 282 actively nesting female bees per hectare were necessary for effective pollination, underscoring the potential of *Amegilla* species to contribute significantly to agricultural pollination, especially in controlled environments.

8.2. CARPENTER BEE

The genus *Xylocopa*, encompassing approximately 469 species (Michener, 1974), is distributed across tropical and subtropical regions, with occasional occurrences in temperate zones (Hurd and Moure, 1963). These carpenter bees are large and robust, measuring 12–25 mm in length depending on the species. Their shiny, black, hairless abdomens distinguish them from bumblebees, which are fuzzier, and *Amegilla species*, known for their vibrant blue bands. Carpenter bees exhibit black, metallic blue, or green hues, and their stocky bodies are well-adapted for their wood-nesting habits.

Carpenter bees are solitary insects, with females excavating nests by boring into untreated, soft wood. These tunnels are divided into brood cells, each provisioned with nectar and pollen for the developing larvae. Unlike ground-nesting bees such as *Amegilla*, carpenter bees prefer wood structures for nesting, which sometimes leads to minor structural damage. Their foraging range is generally localized, extending a few hundred meters from their nests to conserve energy and protect the nesting site.A defining characteristic of carpenter bees is their ability to perform buzz pollination (sonication), a technique where they vibrate their bodies to release pollen from flowers with tightly-held anthers. This unique behavior makes them efficient pollinators for crops such as tomatoes, peppers, and other plants with poricidal anthers. They are also known for their remarkable tolerance to high temperatures, remaining active in conditions exceeding 40°C (Gerling *et al*., 1981), and their ability to forage in low-light conditions, which is advantageous for night-blooming crops.

Among carpenter bees, *Xylocopa pubescens*, native to Israel and originating from Ethiopia, is a well-studied species. Females create branched nests in dead wood (Ben Mordechai *et al*., 1978), hibernating from late October to mid-March and becoming active from March to October. During this period, they construct brood cells, lay eggs, and provision them with nectar and pollen. The development from egg to adult takes 27–35 days. *X. pubescens* is multivoltine, producing 4–5 generations annually, with females remaining reproductively active for up to 120 days (Gerling *et al*., 1981).Carpenter bees play a vital ecological and agricultural role as pollinators. Their ability to forage on a wide range of plants and their buzz pollination technique enable them to pollinate crops that are challenging for other bees. For example, *X. pubescens* has been shown to effectively pollinate greenhouse-grown honeydew melons, achieving similar fruit mass and seed numbers to honeybees while significantly increasing fruit set (Sadeh*et al*., 2007). The subgenus *Lestis*, endemic to Australia and Papua New Guinea, includes *Xylocopa aeratus* (L.) and *X. bombylans* (L.). Their natural occurrence in major tomato-growing regions, coupled with their buzz pollination capability, makes them effective for greenhouse pollination. Studies have shown that *Xylocopa (*Lestis*)* species can increase tomato yield in greenhouses, producing heavier fruits with more seeds (Hogendoorn *et al*., 2000).

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Amegilla zonata

Xylocopa pubescens

9. CONCLUSION

Pollination is a pivotal factor in optimizing crop yields and quality in protected cultivation systems. While manual and mechanical methods have been employed to address pollination deficits, they often entail significant labor, costs, and scalability challenges. In contrast, biotic pollination techniques, particularly those involving insect pollinators such as bumblebees, honeybees, stingless bees, and solitary bees like carpenter bees and Australian blue-banded bees, have proven to be highly effective and sustainable alternatives. The adaptability of these pollinators to controlled environments, combined with their capacity for efficient and selective pollen transfer, significantly enhances fruit set, quality, and yield across a wide range of crops. Among these, bumblebees stand out for their superior buzz pollination capabilities and performance under diverse environmental conditions. Additionally, innovative technologies such as electrostatic pollination, robotic pollinators, and pulsating air pollinators offer promising avenues for supplementing natural pollination methods.

Future strategies should focus on integrating biotic and mechanical pollination approaches, optimizing greenhouse designs to support pollinator activity, and advancing research into emerging technologies. By leveraging the strengths of both traditional and modern techniques, protected cultivation systems can achieve higher productivity and sustainability, meeting the growing demand for high-quality produce in a changing global climate.

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Disclaimer (Artificial intelligence)

Author(s) hereby declare that NO generative AI technologies such as Large Language Models (ChatGPT, COPILOT, etc.) and text-to-image generators have been used during the writing or editing of this manuscript.

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