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Review Article

Application of entomopathogenic fungi for managing fruit flies (Diptera: Tephritidae and Lonchaeidae): strategies to optimize bioinputs and enhance the production of healthy guava

Aplicação de fungos entomopatogênicos no controle de moscas-das-frutas (Diptera: Tephritidae e Lonchaeidae): estratégias para otimizar insumos biológicos e aumentar a produção de goiaba saudável

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Abstract

The guava tree, *Psidium guajava* (Myrtales: Myrtaceae), is a tropical fruit species native to South and Central America and is widely cultivated in Brazil due to favorable soil and climate conditions for commercial production. Brazil is the third-largest guava-producing country in the world. Consequently, the fruit's nutritional value, agricultural production, industrial processing, and exports have expanded. However, this fruit tree is susceptible to pest infestations throughout its phenological cycle, resulting in qualitative and quantitative losses that may render the fruit unsuitable for fresh consumption. Fruit flies (Diptera: Tephritidae and Lonchaeidae) are the main pests affecting guava. Growing restrictions on chemical pesticide use, due to their toxicity to human health and the development of insecticide resistance in pest species, have intensified the search for sustainable alternatives for pest control. Microbial control using entomopathogenic fungi against these pest species is essential for the economic sustainability of guava production. Entomopathogenic fungi are effective because they infect hosts at multiple developmental stages, penetrate the cuticle, and persist in the environment, leading to greater control efficacy. They pose minimal risk to non-target beneficial organisms, including bees, earthworms, collembolans, parasitoids, and predators. This review examines how *Beauveria bassiana* and *Metarhizium anisopliae* can enhance fruit fly management, improve plant, and fruit health, increase yield, and provide effective biological control solutions. It also promotes sustainability by encouraging agricultural practices that conserve environmental integrity and biodiversity.

Keywords: *Beauveria bassiana*, biological control, *Metarhizium anisopliae*, sustainability, tropical fruit tree.

Resumo

A goiabeira, *Psidium guajava* (Myrtales: Myrtaceae), é uma espécie frutífera tropical nativa da América do Sul e Central, amplamente cultivada no Brasil devido às condições favoráveis de solo e clima para a produção comercial. O Brasil é o terceiro maior produtor mundial de goiaba. Consequentemente, o valor nutricional, a produção agrícola, o processamento industrial e as exportações da fruta têm se expandido. No entanto, essa frutífera é suscetível a infestações de pragas ao longo de seu ciclo fenológico, resultando em perdas qualitativas e quantitativas que podem tornar a fruta imprópria para consumo in natura. As moscas-das-frutas (Diptera: Tephritidae e Lonchaeidae) são as principais pragas que afetam a goiaba. As crescentes restrições ao uso de pesticidas químicos, devido à sua toxicidade para a saúde humana e ao desenvolvimento de resistência a inseticidas em espécies-praga, têm intensificado a busca por alternativas sustentáveis para o controle de pragas. O controle microbiano utilizando fungos entomopatogênicos contra essas espécies-praga é essencial para a sustentabilidade econômica da produção de goiaba. Os fungos entomopatogênicos são eficazes porque infectam os hospedeiros em múltiplos estágios de desenvolvimento, penetram na cutícula e persistem no ambiente, resultando em maior eficácia de controle. Eles representam um risco mínimo para organismos benéficos não-alvo, incluindo abelhas, minhocas, colêmbolos, parasitoides e predadores. Esta revisão examina como *Beauveria bassiana* e *Metarhizium anisopliae* podem aprimorar o manejo da mosca-das-frutas, melhorar a saúde das plantas e dos frutos, aumentar a produtividade e fornecer soluções eficazes de controle biológico. Também promove a sustentabilidade, incentivando práticas agrícolas que conservam a integridade ambiental e a biodiversidade.

Palavras-chave: *Beauveria bassiana*, controle biológico, *Metarhizium anisopliae*, sustentabilidade, árvore frutífera tropical.

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1. Introduction

The guava tree, *Psidium guajava* Linnaeus, 1753 (Myrtales: Myrtaceae), is a tropical fruit species native to South and Central America and is widely cultivated in Brazil (Montes et al., 2016) due to favorable soil and climate conditions for commercial production. In addition to the fruit's nutritional value and contribution to agricultural production, industrial processing, and exports, *P. guajava* provides ecological benefits by serving as habitat and food for associated organisms (Rozane et al., 2003). Furthermore, *P. guajava* contributes to carbon sequestration by absorbing atmospheric carbon dioxide (CO_2) through photosynthesis.

In 2023 Brazil exported 1.24 million Mg of fruits, valued at US$ 1.16 billion (Brasil, 2023). Brazil is the third-largest guava-producing country in the world. However, this fruit tree is susceptible to pest infestations throughout its phenological cycle, resulting in qualitative and quantitative losses that may render the fruit unsuitable for fresh consumption (Dolinski et al., 2006).

Fruit flies (Diptera: Tephritidae and Lonchaeidae) are the primary pests of guava varieties in South and Central America. Fruit flies of the genera *Anastrepha* Schiner, 1868 (Diptera: Tephritidae), *Neosilba* McAlpine, 1962 (Diptera: Lonchaeidae), and the species *Ceratitis capitata* (Wiedemann, 1824) (Diptera: Tephritidae) attack ripe or ripening fruits (Uchoa, 2012). Fruit fly larvae feed on the fruit pulp, reducing fruit yield and rendering the fruit unsuitable for fresh consumption and commercially unviable for both table guava and industrial processing (Azevedo et al., 2016).

The life cycle of Tephritidae and Lonchaeidae species occurs across three environments: vegetation, fruit, and soil. Adults typically remain on the host plant or on alternative hosts near the crop. After mating, females oviposit inside the fruits, and upon hatching, larvae develop within the fruit, feeding on the pulp. Upon reaching the final instar, larvae exit the fruit and burrow into the soil for pupation, and after two to three weeks, adults emerge to initiate a new cycle (Nicácio and Uchoa, 2011).

Fresh guava fruit exports are subjected to quarantine restrictions imposed by importing countries when pest insects are detected in production regions, resulting in economic losses (Costa, 2011). This issue is particularly critical for fruit fly species, as they represent a major barrier to the international trade of fruits and vegetables (Gould and Raga, 2002).

The control of pest insects in guava cultivation is essential for maintaining production, with chemical control being the most widely used method, often applied excessively or incorrectly. An alternative for reducing the use of agrochemicals without compromising economically viable production is Integrated Pest Management (IPM) (Madalon et al., 2017), in which biological control constitutes a central strategy. Several factors promote the adoption of biological control, including pest resistance management, consumer demand for residue-free products, safety for pollinators and natural enemies, operational safety, and flexibility for agricultural producers, and increasing restrictions on chemical pesticides (Arthurs and Dara, 2019; Parra, 2023).

Entomopathogenic fungi are key biological control agents, exhibiting advantages such as high genetic diversity (Lacey et al., 2015), infection across multiple host developmental stages (Polanczyk et al., 2010), cuticular penetration by propagules with high dispersal capacity (Alves et al., 2008; Arakere et al., 2022), and environmental persistence, enhancing biological control efficacy (Ding et al., 2023). These agents initiate infection in susceptible hosts through direct cuticular penetration (Ortiz-Urquiza and Keyhani, 2013). In guava cultivation, these infections occur in fruit fly species and the guava weevil (Oliveira et al., 2023). Entomopathogenic fungi pose minimal risk to non-target beneficial organisms, including bees, earthworms, and collembolans (Portilla et al., 2017), as well as to natural enemies such as parasitoids and predators (Potrich et al., 2009; Rossoni et al., 2014; Dias et al., 2019, 2020).

More than 90 genera of entomopathogenic fungi act as biological control agents for pest arthropods, with *Beauveria bassiana* and *Metarhizium anisopliae* being extensively studied for the control of insects in the orders Blattaria, Orthoptera (Kershaw et al., 1999), Hemiptera, Coleoptera, Diptera, and Lepidoptera, which damage economically important crops (Loureiro et al., 2024). These fungi show considerable potential for application in pest management of fruit crops. This review addresses aspects of commercial guava cultivation, as well as the infestation and management of fruit flies and the guava weevil using entomopathogenic fungi, and provides perspectives for future research.

2. Myrtaceae Family

The Myrtaceae family, a diverse group of angiosperms, comprises trees and shrubs characterized by prominent oil glands and edible fruits (Mitra et al., 2012). Genera including *Acca*, *Eugenia*, *Psidium*, and *Syzygium* are among the most relevant for fruit production (Mitra et al., 2012). Numerous Myrtaceae species hold economic and cultural value, including *Pimenta racemosa* (bay rum tree), *Syzygium aromaticum* (clove), *Psidium guajava* (guava), and *Pimenta dioica* (allspice). Species of the Myrtaceae family are also used for ornamental purposes, as spices, and in traditional medicine. The family is recognized for producing essential oils and is classified among the principal groups of aromatic plants (Fehlberg et al., 2023). *P. guajava* is particularly notable for its fruits and for substantial nutritional and medicinal potential.

2.1. Psidium guajava L. 1753: Guava tree

The guava tree (*Psidium guajava* L.) is a tropical fruit species of the family Myrtaceae, widely cultivated in tropical and subtropical regions (Kumar et al., 2023). It is native to tropical South and Central America, and its fruit is characterized by a sweet flavor, mild aroma, and high concentrations of bioactive compounds, making it valuable for research on functional foods and nutrition (Díaz-de-Cerio et al., 2017; Lima et al., 2019). Consequently, this nutritious and versatile fruit is consumed fresh or processed into a variety of products (Lima et al., 2019, Kumar et al., 2022).

2.2. Composition and potential as a functional food

Guava is rich in dietary fiber, polyphenols, and antioxidants, including ascorbic acid, β-carotene, lycopene,

and flavonoids (Jiménez-Escrig et al., 2001; Musa et al., 2011; Correa et al., 2012). Its high phenolic content qualifies it as a "superfruit" (Lima et al., 2019). The leaves contain bioactive compounds with therapeutic potential, such as quercetin and catechin (Díaz-de-Cerio et al., 2017). Guava seeds are edible and rich in proteins, fatty acids, minerals, and phenolic compounds with diverse bioactivities. Seed extracts exhibit antioxidant, anti-inflammatory, neuroprotective, antidiabetic, and anticancer activities, showing potential to enhance functional food applications (Kumar et al., 2022).

2.3. Economic importance of guava

Guava is an important economic resource that contributes to income generation for producers across different production scales. The global guava market, valued at US$ 968.2 million in 2024, is projected to grow at an annual rate of 4.7% through 2031 (Cognitive Market Research, 2025). In South America, guava sales reached US$ 48.41 million in 2023, underscoring the fruit's regional economic relevance (Cognitive Market Research, 2025). Brazil ranks among the leading global producers of guava, together with Thailand, China, and India (Molla et al., 2022). In Brazil, guava cultivation benefits from integrated pest and disease management practices, including fruit bagging, which enhance fruit quality and reduce dependence on chemical pesticides.

The economic significance of guava extends beyond fresh consumption to include a wide range of processed products, such as sweets, jellies, juices, and pulps. Fresh guava is widely consumed and marketed through local markets, fairs, and large supermarket chains. The processing industry enhances the fruit value, expanding its market through diverse processed products that cater to varied consumer preferences and drive industrial growth. Guava is a promising raw material for emerging sectors, including the animal feed, pharmaceutical, and cosmetic industries (Kumar et al., 2022). This diversification underscores the fruit's versatility and potential for continued economic expansion. In summary, guava contributes to the economy by generating income for producers, supporting the processing industry, and promoting regional and national development.

2.4. Medicinal properties and industrial applications

Guava exhibits therapeutic properties and is used in the management of various health conditions, as it is rich in vitamins—particularly vitamin C, which occurs in higher concentrations than in orange—and contains minerals and phytochemicals with hepatoprotective, anticancer, anti-inflammatory, antibacterial, and antioxidant activities. In the food industry, guava is used in the production of juices, jellies, and other processed products (Worku et al., 2024). Beyond its established applications in the food industry, guava shows potential for use in the animal feed, pharmaceutical, and cosmetic industries due to its rich chemical composition (Kumar et al., 2022)

2.5. Future perspectives

The potential of guava can be further enhanced through future research focused on isolating bioactive compounds to develop functional ingredients and therapeutic agents (Díaz-de-Cerio et al., 2017; Kumar et al., 2022; Worku et al., 2024). Clinical studies are essential to determine safe dosages and confirm the efficacy of guava-derived compounds (Worku et al., 2024). Continued investigation of the nutritional and pharmacological properties of guava may expand its applications, establishing it as a valuable resource for health promotion and product innovation. Additionally, addressing phytosanitary challenges in guava cultivation remains essential, as the effective management key pests, such as fruit fly species and the guava weevil, is crucial to maintaining fruit yield and quality. Therefore, advancing research on efficient and sustainable pest control methods is essential for the future of guava cultivation.

3. Fruit Flies

Fruit flies, particularly from the families Tephritidae and Lonchaeidae, pose a significant challenge to guava cultivation. Female oviposition within guava fruits leads to larval development, during which the larvae feed on the pulp, compromising fruit quality for both fresh consumption and industrial processing (Martins et al., 2024). In addition, fruit fly infestation often results in premature fruit drop or causes fruits to rot or develop off-flavors at maturity, thereby reducing harvest yield.

South America hosts a high diversity of fruit fly species, with approximately 5,000 Tephritidae species and 800 Lonchaeidae species, which have been extensively studied regarding their species diversity, host plants, population dynamics, and natural enemies (Uchoa et al., 2003; Dias et al., 2018). In guava orchards, species such as *Anastrepha striata*, *A. sororcula*, *A. obliqua*, and *A. fraterculus* (Tephritidae), along with *Neosilba* species (Lonchaeidae), are frequently observed, posing serious constraints to economically sustainable production (Marsaro Júnior et al., 2013; Uchoa, 2012).

3.1. Life cycle and biology of fruit flies

The life cycle of Tephritidae and Lonchaeidae fruit flies comprises three distinct environments: vegetation, fruit, and soil. Adults typically remain on the host plant or on nearby vegetation, where they obtain shelter and food resources. After mating, females oviposit inside the fruits, inserting eggs into the pulp with their sclerotized ovipositor. After hatching, larvae feed on the fruit pulp or seeds, depending on the species, and pass through three larval instars that are essential for growth and development. When larvae reach the final instar, they exit the fruit and burrow into the soil to pupate, with adults emerging after two to three weeks depending on environmental conditions. In temperate regions, pupae may enter diapause, an adaptive mechanism that enables survival during unfavorable environmental conditions until the following season (Nicácio and Uchoa, 2011).

Fruit fly larvae (Tephritidae and Lonchaeidae) utilize fruit pulp or other plant tissues as substrates for their development (Uchoa, 2012). The South American fruit fly, *Anastrepha fraterculus* (Wiedemann, 1830), requires 11 to 17 days between oviposition and larval emergence, and its pupal stage lasts from 13 to 16 days. The total duration from oviposition to adult emergence ranges from 27 to 31 days, depending on the species and edaphoclimatic

conditions, particularly temperature, air humidity, and soil moisture. After adult emergence, the pre-oviposition period—defined as the time between adult emergence and the first oviposition—ranges from 8 to 15 days. The oviposition period may extend from 6 to 71 days (Bisognin et al., 2013). Laboratory studies indicate that adults of *Anastrepha fraterculus* and *A. sororcula* can survive for up to approximately 180 days. This extended adult longevity may represent an adaptive mechanism that enables these insects to synchronize oviposition with optimal host fruit development under field conditions, thereby promoting species persistence (Uchoa, 2012). Diapause, a development pause that allow insects to withstand unfavorable conditions, has been reported in *A. obliqua* pupae, confirming adaptive mechanisms in tropical regions (Bressan-Nascimento, 2001).

3.2. Insecticide resistance

Recent studies indicate that selection pressure from insecticides has driven the development of resistance in fruit flies, posing an increasing challenge to their control. Resistance can result from mutations in target populations exposed to insecticides, which enhance detoxification capacity and reducing the efficacy of chemical pesticides. Alterations in cuticular chemical composition or behavioral adaptations may also contribute to resistance of fruit flies to synthetic pesticides (Vontas et al., 2011).

Managing pest Tephritidae and Lonchaeidae fruit flies is challenging because eggs are oviposited within fruits, where larvae feed and remain protected from contact with chemical pesticides. After completing the third instar, larvae exit the fruit to pupate in the soil, thereby avoiding direct exposure to insecticide applications (Heve et al., 2017).

3.3. Economic impact

Tephritidae and Lonchaeidae fruit flies infest a broad range of fruit and vegetable crops, causing global economic losses estimated at billions of dollars annually (Aluja et al., 2024). Infestations also restrict international trade by limiting market access and imposing substantial economic burdens on producers and exporters (Papadopoulos et al., 2024). In guava cultivation, infestations by *Anastrepha* species substantially reduce fruit yield and quality, impacting local trade, industrial processing, and exports (Marsaro Júnior et al., 2013).

Fruit fly infestations cause premature fruit drop and commercial rejection due to oviposition punctures and larval feeding damage (Malavasi et al., 2000; Costa, 2011). This damage not only decreases production but also triggers phytosanitary restrictions imposed by importing countries (Grové et al., 2019). Oviposition punctures made by female fruit flies compromise fruit appearance and facilitate infection by opportunistic pathogens, including fungi and bacteria, leading to necrosis and rot (Souza-Filho et al., 2009; Borges, 2022; Martins et al., 2024). Infested fruits are often discarded before reaching consumers, intensifying commercial losses for both domestic markets and exports (Louzeiro et al., 2021).

Tephritidae and Lonchaeidae fruit flies also limit the commercialization of fresh fruits, as visible damage reduces consumer acceptance. Higher infestation rates occur in preferred host fruits, such as starfruit (Oxalidaceae) and guava (Myrtaceae). The presence of immature stages within fruits increases the risk of their dissemination to new regions through fruit transport, thereby expanding the species' geographical range and aggravating economic and phytosanitary challenges (Louzeiro et al., 2021).

3.4. Future research on fruit flies

Currently research priorities should include evaluating the effects of climate change on fruit fly biology, as higher temperatures may accelerate development and expand their geographical distribution. Given the economic significance of fruit flies and challenges in their control, investment in research to develop integrated pest management strategies, particularly those incorporating biological control, is essential. Advances in understanding insecticide resistance mechanisms and in developing sustainable management methods, such as biological control, are crucial for mitigating the adverse impacts of fruit flies on global agriculture.

4. Entomopathogenic Fungi

Entomopathogenic fungi are ubiquitous soil-dwelling microorganisms that parasitize insects, functioning as natural biological control agents for numerous insect species and often inducing epizootics that suppress pest populations. These fungi exhibit several characteristics, including enzyme production (Qasim et al., 2020), contact-based infection across all insect developmental stages (Lacey et al., 2015), and high potential for pest insect control (Mondal et al., 2016; Rojas et al., 2023).

In biological control programs, entomopathogenic fungi represent an environmentally sustainable alternative that minimizes ecosystem impacts (Ortiz-Urquiza et al., 2015; Wang and Wang, 2017). They are considered safe for beneficial organisms that provide ecosystem services, including bees, earthworms (Annelida), and collembolans (Arthropoda: Ellipura), as well as for natural enemies such as mites (Arthropoda: Acarina), parasitoids, and predators (Brownbridge and Glare, 2007; Loureiro and Moino Junior, 2008; Rossoni et al., 2014; Dias et al., 2019; Peng et al., 2021).

In integrated pest management (IPM), preserving natural enemies enhances their contribution to pest population regulation (Lacey et al., 2015), while maintaining biodiversity is increasingly recognized as essential for long-term agricultural and forest productivity. The conservation of biodiversity also enhances the efficacy of entomopathogenic fungi in IPM programs (Lacey et al., 2015; Dias et al., 2020; Loureiro et al., 2024). In addition to controlling pest insects, species of *Metarhizium* and *Beauveria*, commonly found in soil, establish complex interactions with plants as endophytes or biofertilizers (Behie et al., 2012; Lacey et al., 2015; Jaber and Enkerli, 2017; Litwin et al., 2020; Velozo et al., 2025), contributing to plant protection by suppressing microbial pathogens and enhancing plant defense responses (Moonjely et al., 2016; Loureiro et al., 2026a).

Key advantages of using fungi for pest insect control compared with conventional chemical pesticides include: minimal environmental impact and safety for biodiversity; absence of significant toxic residues, since mycotoxin levels are insufficient to harm vertebrates (Rojas et al., 2023); high selectivity and host specificity; reduced likelihood of selecting resistant insect populations due to contact-based infection and genetic diversity; ability to infect all insect developmental stages through contact; persistence and dispersal under adverse environmental conditions; compatibility with other biological control agents and synthetic insecticides, often producing synergistic effects; and decreased dependence on chemical insecticides (Fontes and Valadares-Inglis, 2020), many of which are imported.

Entomopathogenic fungi exhibit high potential for managing pest species; however, their application is subject to certain limitations. They require a period free from fungicide applications and favorable environmental conditions, including high humidity, moderate temperatures, and protection from solar radiation, to ensure successful germination and infection. Furthermore, their persistence and infection efficiency may decrease under unfavorable environmental conditions. Their action is comparatively slow, typically requiring 2 to 3 weeks to cause insect mortality, which may restrict their use in crops where pest survival leads to significant economic losses (Islam et al., 2021; Licona-Juárez et al., 2023).

4.1. Mechanism of action of entomopathogenic fungi

Entomopathogenic fungi infect insects through direct contact, with the infection process involving adhesion of fungal structures to the host exoskeleton, followed by germination, penetration, and internal colonization (Fontes and Valadares-Inglis, 2020). Infection begins with the attachment of unicellular fungal propagules, such as conidia or blastospores, to the insect cuticle (Ortiz-Urquiza and Keyhani, 2013).

4.2. Adhesion and attachment of entomopathogenic fungi

Conidia adhere to the insect exoskeleton through passive dispersal mediated by air and water currents (Islam et al., 2021). The adhesion of infectious propagules is a dynamic process driven by electrostatic and hydrophobic interactions. Entomopathogenic fungi commonly used in pest population suppression, such as *Beauveria bassiana* and *Metarhizium anisopliae*, are hydrophobic and form a surface rodlet layer composed of hydrophobin proteins. In addition to hydrophobins, adhesins are key proteins that facilitate fungal attachment to the insect cuticle. The adhesion capacity of conidia may be influenced by the type and length of hydrocarbon chains present on the insect cuticle (Fontes and Valadares-Inglis, 2020).

4.3. Germination of entomopathogenic fungi

After adhering to the host exoskeleton, conidia germinate, with subsequent growth is influenced by abiotic factors such as pH, temperature, oxygen availability, and nutrient levels. Conidial germination is also affected by host-derived cuticular toxins. Germination, fungal growth on the exoskeleton, and subsequent penetration depend on favorable environmental conditions, host specificity, high propagule vigor, and other biotic and abiotic factors (Faria et al., 2015; Fontes and Valadares-Inglis, 2020; Islam et al., 2021).

4.4. Penetration of entomopathogenic fungi

After germination, fungal penetration occurs primarily through less sclerotized regions of the insect cuticle, such as intersegmental membranes, to access internal tissues for nutrient acquisition supporting vegetative and reproductive growth (Fontes and Valadares-Inglis, 2020). Penetration involves the application of mechanical pressure by specialized structures (appressoria), which develop from germ tubes and produce hyphae that extend laterally within the endocuticle layers. The penetration process is complex due to the heterogeneous composition of insect cuticles, which varies among species, developmental stages, and diets (Ortiz-Urquiza and Keyhani, 2013).

In addition to specialized penetrating structures, entomopathogenic fungi produce and secrete extracellular catabolic enzymes that contribute to the infection process. The insect cuticle is penetrated directly by the extracellular enzymatic activity of lipases, esterases, proteases, and chitinases, which facilitate entry into the hemocoel or through mouthparts (Sánchez-Pérez et al., 2014). These enzymes collectively enable successful penetration of the insect cuticle.

4.5. Colonization of entomopathogenic fungi in hosts

After entering the insect body, entomopathogenic fungi transition from hyphal to yeast-like forms (hyphal bodies or blastospores), which disseminate through the hemolymph. Following extensive proliferation, the fungi revert to the hyphal form, invading muscle tissues, fat bodies, Malpighian tubules, and other organs. Upon nutrient depletion and the host death, hyphae penetrate outward through the cuticle, emerging on the surface and, under favorable environmental conditions, initiating reproduction through conidial formation. External hyphal growth continues, consuming the host and culminating in mycelial expansion and sporulation on the insect cadaver. Insect mortality results from multiple factors, including nutrient depletion, tissue invasion, and the production of toxic metabolites (Lacey et al., 2015; Islam et al., 2021). Entomopathogenic fungi synthesize toxic metabolites, including nonribosomal peptides (NRPs), polyketides, lysine derivatives, terpenoids, and sterols; notable NRPs include destruxins, efrapeptins, beauvericin, bassianolides, and cyclosporins (Fontes and Valadares-Inglis, 2020).

4.6. Reproduction of entomopathogenic fungi

Following host death, hyphae emerge through spiracles and intersegmental membranes, sporulating externally on the insect exoskeleton under conditions of high humidity (above 70%) and moderate temperature (25-28 °C), forming hyphae and mycelia through conidiogenesis. The abundant conidia produced externally facilitate efficient dispersal (Faria et al., 2015).

4.7. Main fungal species for insect control

Among entomopathogenic fungi used for insect control, *B. bassiana* and *M. anisopliae* are the most widely used

species for biological control programs (Zhou et al., 2021; Loureiro et al., 2026b). These fungi have cosmopolitan distributions and are commonly isolated from insects and soil using selective media or insect baiting methods (Khun et al., 2021). *B. bassiana* is pathogenic to a wide range of insect species, exhibiting low host specificity. Infected insects develop dense white mycelium covering on the exoskeleton due to extensive mycelial growth and conidial production (Rohrlich et al., 2018), leading to host mortality.

Metarhizium anisopliae is an important entomopathogen (Brunner-Mendoza et al., 2018) characterized by densely interwoven conidiophores with conical apices arranged in a compact hymenium of conidiogenic cells (Mongkolsamrit et al., 2020). Its aseptate conidia are light green to yellowish green in color (Leadmon et al., 2020).

Entomopathogenic fungi exhibit a broad spectrum of activity, infecting diverse arthropod species (Khan et al., 2012; Ríos-Moreno et al., 2016), primarily insects and mites. Numerous studies demonstrate the efficacy of *B. bassiana* and *M. anisopliae* in suppressing populations of various insect orders, particularly pest species in Diptera (Amobonye et al., 2020), Lepidoptera (Ullah et al., 2019), Hemiptera, and Coleoptera (Bhadani et al., 2021). Insects of the families Curculionidae (Coleoptera) and Tephritidae (Diptera), major pests in global agriculture, are primary targets for entomopathogenic fungi, with several key studies focusing on their control.

5. Control of Tephritidae and Lonchaeidae Species with Entomopathogenic Fungi

Several studies have evaluated the efficacy of entomopathogenic fungi to control Tephritidae and Lonchaeidae species, including *Anastrepha fraterculus* (Wiedemann, 1830), *Anastrepha ludens* (Loew, 1873), *Anastrepha obliqua* (Macquart, 1835), *Bactrocera carambolae* (Drew & Hancock, 1994), *Bactrocera cucurbitae* (Coquillett, 1899), *Bactrocera dorsalis* (Hendel, 1912), *Bactrocera oleae* (Rossi, 1790), *Bactrocera zonata* (Saunders, 1842), *Bactrocera tryoni* (Froggatt, 1897), *Ceratitis capitata* (Wiedemann, 1824), *Ceratitis cosyra* (Walker, 1849), *Ceratitis fasciventris* (Bezzi, 1920), *Rhagoletis cerasi* (Linnaeus, 1758), *Rhagoletis indifferens* (Curran, 1932), *Rhagoletis mendax* (Curran, 1932), *Rhagoletis suavis* (Loew, 1862), and *Zeugodacus cucurbitae* (Coquillett, 1899) (Table 1).

Beauveria bassiana and *Metarhizium anisopliae* demonstrate high efficacy against fruit fly species, with studies reporting significant mortality across various developmental stages, supporting their potential as biological control agents.

The efficacy of entomopathogenic fungi against Tephritidae and Lonchaeidae fruit fly species is influenced by factors such as conidial concentration, application method, and environmental conditions. Concentrations ranging from 10^7 to 10^9 conidia mL^{-1} are typically required to achieve control levels exceeding 60% mortality (Destéfano et al., 2005; Toledo et al., 2007, 2017; Daniel and Wyss, 2009; Queiroz de Oliveira et al., 2010; Osorio-Fajardo and Canal, 2011; Sánchez-Roblero et al., 2012; Fernández-Bravo et al., 2017; Chergui et al., 2020; Lezama-Gutiérrez et al., 2000; Onsongo et al., 2019; Yee, 2020; Iqbal et al., 2021; Wang et al., 2021).

Mortality rates of Tephritidae species such as *Ceratitis capitata* and *Bactrocera oleae* vary significantly depending on the fungal isolate and application rate, with lethal concentration values causing 50% population mortality (LC_{50}) differing by species and geographical origin (Dimbi et al., 2003; Quesada-Moraga et al., 2006; Mahmoud, 2009; Ortiz-Urquiza et al., 2010; Queiroz de Oliveira et al., 2010; Flores et al., 2013; Imoulan and Elmeziane, 2014; San Andrés et al., 2014; Bissoli et al., 2014; Navarro-Llopis et al., 2015; Rabea et al., 2014; Toledo et al., 2017; Chergui et al., 2020; Soliman et al., 2020).

In addition to causing direct mortality, entomopathogenic fungi reduce fecundity and impair development in Tephritidae and Lonchaeidae species. Infection by *B. bassiana* and *M. anisopliae* significantly decreases eggs production, hatching rates, and larval development in various studies (Destéfano et al., 2005; Daniel and Wyss, 2009; Queiroz de Oliveira et al., 2010; Imoulan and Elmeziane, 2014; Bissoli et al., 2014; Sookar et al., 2014; Chaneiko et al., 2019; Brito et al., 2019; Lezama-Gutiérrez et al., 2000; Renkema et al., 2020; Soliman et al., 2020; Usman et al., 2021). These fungi also reduce fecundity and fertility in *C. capitata* (Quesada-Moraga et al., 2006). These findings indicate that entomopathogenic fungi not only control adult Tephritidae and Lonchaeidae populations but also suppress reproductive capacity, increasing their potential for long-term population management.

The efficacy of entomopathogenic fungi varies considerably among Tephritidae species and the fungal isolates tested. For example, *B. bassiana* achieved 100% adult mortality and up to 94.5% pupal mortality in *C. capitata*, whereas *M. anisopliae* caused 95% adult mortality and 45% pupal mortality (Quesada-Moraga et al., 2006).

This variability highlights the need to select specific fungal strains for biological control based on target Tephritidae and Lonchaeidae species and local environmental conditions. Although laboratory studies demonstrated 100% mortality in several Tephritidae species, field trials showed reduced efficacy, primarily due to environmental factors such as temperature and humidity affecting conidial viability. Nevertheless, entomopathogenic fungi remain viable for biological control, particularly when integrated with strategies such baited traps with food attractants to target adults during the reproductive phase.

In field conditions, the efficacy of entomopathogenic fungi is strongly influenced by climate factors, including relative humidity and temperature. In hot and dry regions, fungal efficacy is reduced due to low conidial viability, emphasizing the need to adapt formulations and application methods to local climate conditions and develop technologies to enhance spore resilience under adverse conditions. Adjusting the timing of entomopathogenic fungal applications can enhance this effectiveness of this biological control method.

Entomopathogenic fungi exhibit significant potential for suppressing Tephritidae and Lonchaeidae populations in integrated pest management programs due to their efficacy across different developmental stages and ability

Table 1. Studies demonstrating the pathogenicity of *Beauveria bassiana* (Balsamo-Crivelli, 1835) Vuillemin, 1912 (Hypocreales: Cordycipitaceae) and *Metarhizium anisopliae* (Metschnikoff, 1879) Sorokin, 1883 (Hypocreales: Clavicipitaceae) against Tephritidae and Lonchaeidae (Insecta: Diptera) worldwide.

Species	Entomopathogenic fungi	Local	Authors
Bactrocera dorsalis	*B. bassiana*; *M. anisopliae*	Laboratory	Wang et al. (2021)
Bactrocera cucurbitae	*B. bassiana*; *M. anisopliae*	Field	Hamzah et al. (2021)
Bactrocera oleae	*B. bassiana*; *M. anisopliae*	Laboratory	Mahmoud (2009)
B. zonata; B. cucurbitae	*M. anisopliae*	Laboratory	Sookar et al. (2014)
B. zonata; B. cucurbitae	*B. bassiana*; *M. anisopliae*	Laboratory	Sookar et al. (2008)
B. cucurbitae	*B. bassiana*; *M. anisopliae*	Laboratory	Iqbal et al. (2021)
B. zonata; B. dorsalis	*B. bassiana*; *M. anisopliae*	Field; Laboratory	Usman et al. (2021)
Bactrocera carambolae	*M. anisopliae*; *B. bassiana*	Laboratory	Brito et al. (2019)
Bactrocera tryoni	*M. anisopliae*	Laboratory	Carswell et al. (1998)
Ceratitis capitata	*B. bassiana*	Laboratory	Chergui et al. (2020)
Ceratitis capitata	*B. bassiana*; *M. anisopliae*	Laboratory	Quesada-Moraga et al. (2006)
Ceratitis capitata	*B. bassiana*; *M. anisopliae*	Laboratory	Queiroz de Oliveira et al. (2010)
Ceratitis capitata	*B. bassiana*	Laboratory	Rabea et al. (2014)
C. capitata; C. cosyra; C. fasciventris	*M. anisopliae*	Laboratory	Dimbi et al. (2003)
Ceratitis capitata	*B. bassiana*; *M. anisopliae*	Laboratory	Soliman et al. (2020)
Ceratitis capitata	*B. bassiana*; *M. anisopliae*	Laboratory	Bissoli et al. (2014)
Ceratitis capitata	*B. bassiana*	Laboratory	Imoulan and Elmeziane (2014)
Ceratitis capitata	*B. bassiana*	Field	Flores et al. (2013)
Ceratitis capitata	*M. anisopliae*	Field	Navarro-Llopis et al. (2015)
Ceratitis capitata	*M. anisopliae*	Laboratory	San Andrés et al. (2014)
Ceratitis capitata	*M. anisopliae*	Laboratory	Ortiz-Urquiza et al. (2010)
Ceratitis capitata	*B. bassiana*	Laboratory	Toledo et al. (2017)
Anastrepha obliqua	*B. bassiana*; *M. anisopliae*	Laboratory	Díaz-Ordaz et al. (2010)
Anastrepha obliqua	*B. bassiana*; *M. anisopliae*	Laboratory	Osorio-Fajardo and Canal (2011)
Anastrepha obliqua	*B. bassiana*	Field; Laboratory	Martínez-Barrera et al. (2020)
Anastrepha ludens	*M. anisopliae*	Laboratory	Presa-Parra et al. (2021)
Anastrepha ludens	*B. bassiana*	Laboratory	De la Rosa et al. (2002)
Anastrepha ludens	*B. bassiana*	Laboratory	Sánchez-Roblero et al. (2012)
Anastrepha ludens	*M. anisopliae*	Laboratory	Lezama-Gutiérrez et al. (2000)
Anastrepha ludens	*B. bassiana*	Field; Laboratory	Toledo et al. (2007)
Anastrepha ludens	*B. bassiana*	Laboratory	Wilson et al. (2017)
Anastrepha fraterculus	*B. bassiana*; *M. anisopliae*	Laboratory	Chaneiko et al. (2019)
Anastrepha fraterculus	*M. anisopliae*	Laboratory	Destéfano et al. (2005)
Zeugodacus cucurbitae	*M. anisopliae*	Laboratory	Onsongo et al. (2019)
Rhagoletis cerasi	*B. bassiana*	Laboratory	Daniel and Wyss (2010)
Rhagoletis cerasi	*B. bassiana*; *M. anisopliae*	Field	Daniel and Wyss (2009)
Rhagoletis indifferens	*B. bassiana*	Laboratory	Yee (2020)
Rhagoletis indifferens	*B. bassiana*	Laboratory	Cossentine et al. (2010)
Rhagoleti mendax	*M. anisopliae*	Laboratory	Renkema et al. (2020)
Rhagoleti suavis	*B. bassiana*	Laboratory	Nisar et al. (2019)

to reduce fecundity and larval survival. However, variability of efficacy among species and environmental influence necessitate targeted research to optimize their application across diverse regions and agricultural systems. Integrations with other control methods, particularly biological control, a central component of IPM, enhances the efficacy and sustainability in managing key pests in agroecosystems, supporting biodiversity conservation and the health of producers and consumers of food, condiments, and fibers.

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Data Availability Statement

Data supporting the findings of this study are available from the corresponding author upon reasonable request.

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