Invisible Allies: The Role of Endophytic Entomopathogenic Microbes in Insect Pest Control

Review article

ABSTRACT

Endophytic entomopathogenic microbes, including both bacteria and fungi, hold significant promise as biocontrol agents in sustainable pest management. While the biocontrol potential of entomopathogenic fungi is well-established, their role as mutualistic endophytes within plant tissues offers a relatively new avenue for enhancing pest suppression. The ability of these microbes to colonize plant tissues allows them to serve as internal defense agents against insect pests, while simultaneously promoting plant health and resilience to environmental stressors. Here, we explore the growing body of knowledge surrounding the use of endophytic entomopathogenic bacteria and fungi in pest management. These microbes contribute to pest control through direct effects on insect populations, such as mortality and feeding inhibition, as well as indirect plant-mediated mechanisms that enhance plant defenses. Additionally, endophytic entomopathogens provide a range of benefits to their plant hosts, including growth promotion, nutrient acquisition, and protection against pathogens. Despite the clear advantages of using endophytic entomopathogens, there remain key challenges to their widespread implementation. Environmental factors can influence their persistence and efficacy in the field, and their relatively slow mode of action compared to chemical pesticides presents a hurdle for rapid adoption in commercial agriculture. Non-target effects and the development of effective formulations to ensure consistent colonization are also areas that require further investigation. Addressing these challenges through continued research into the complex interactions between endophytes, insects, plants, and their environments will be essential for advancing the integration of endophytic entomopathogenic microbes into sustainable pest management systems.

Keywords: Endophytic microbes, Insect pathogens, *Bacillus, Beauveria, Metarhizium,* Integrated pest management

1. INTRODUCTION

The world population is expected to reach 10 billion people by 2050, which necessitates a more than 50% increase in current global food production to meet the growing demands and reduce the risk of hunger [1]. An estimated 593 million hectares of additional vegetated land approximately twice the size of India will be needed to expand agricultural land to meet this demand at current productivity levels [2]. However, this expansion poses significant environmental risks, particularly through deforestation and its associated negative effects on climate change. To address these challenges and ensure a sustainable future, it is imperative to prioritize strategies that enhance the efficacy and effectiveness of crop production. Crop losses due to various biotic and abiotic stresses, including insect pests, are another critical factor that considerably reduces overall yield, hindering our ability to meet the growing demand. Insect pests alone contribute a significant portion of the total food crop loss, ranging from 18% to 26%, and accounting for approximately USD 470 billion in economic loss annually [3]. While insecticides have been a cornerstone of pest control, their widespread and indiscriminate use has led to serious environmental and health consequences. Insecticide resistance, pest resurgence, harmful effects on non-target organisms, and residual insecticide effects further exacerbate these problems. In recent years, there has been increased awareness about pesticides toxicity and changing dietary preference of the people towards plant-based diets necessitates a paradigm shift in agricultural practices. This shift should emphasize sustainable and environmentally friendly alternatives to control insect pest damage and curb yield losses.

Biological control by employing entomopathogenic microbes are amongst the better alternatives to the conventional synthetic insecticides. These microbes persist close to insect habitat cause epizootic and subsequently control the insect pressure in the field without any off-target effects on environment and human health. More than 700 fungal species from around 90 genera have been identified as potent pathogens affecting insects [4]. Most of the entomopathogenic fungi are from the order Hypocreals of the class Sordoriomycetes. In case of bacteria more than 100 species belonging to various families including, Pseudomonadaceae, Enterobacteriaceae, Lactobacilliaceae, Micrococcaceae, and Bacillaceae recognized as entomopathogens [5]. However, their active persistent in the field are limited due to exposure to various environmental factors like UV (photodegradation), moisture (washing off inoculants during raining) and their slow mode of action against the target pests, lack of improved formulations and short life span of these inoculants are few bottlenecks that hinders the wider adoption of biological control using entomopathogenic microbes [6]. Interestingly, many entomopathogens have been observed to colonize plant tissues as endophytes, functioning as "invisible bodyguards" against insect herbivores. This endophytic behavior enhances the protective capabilities of these microbes, allowing them to exert their influence directly within the plant system [7]. By integrating this endophytic approach with existing biological control methods, the challenges posed by environmental factors and formulation limitations could potentially be mitigated, thereby enhancing the overall efficacy of entomopathogenic microbes in pest management strategies. In this review, detailed information about entomopathogenic endophytic microbes, their effects on insect pest when colonized on the plants, their role in providing additional benefits and challenges associated with implementations will be explored.

2. ENTOMOPATHOGENS AS ENDOPHYTES

Microbial endophytes are associated with nearly all plant species in the world ranging from annuals to perennials in all their parts from root to shoot [8]. Anton de Bary first introduced the term "endophytes" in 1866 to describe all organisms residing within plant tissues [9]. Later, Carroll refined this definition by specifying that endophytes are organisms that cause asymptomatic infections, excluding pathogenic and mutualistic fungi such as mycorrhizae [10]. Subsequently, Petrini defined endophytes as organisms that live either part of their life cycle or their entire life cycle inside plants without causing any harm [11]. In 1996, Chanway [12] expanded the definition to include bacteria that can also colonize plant tissues, categorizing them as endophytes. Microbes naturally exist as endophytes, which may enter the host from the surrounding environment of the host plant or be acquired from the mother plant as seed endophytes. Additionally, through artificial inoculation methods such as seed treatment, soil drenching, and foliar application, microbes can also establish themselves as endophytes within plants.

Rodriguez et al., [13] classified fungal endophytes into four classes i.e., clavicipitaceous endophytes (class 1) and non clavicipitaceous endophytes into three functional groups (class 2, class 3 and class 4) based on host colonization and transmission, in planta biodiversity and fitness benefits conferred to hosts. Endophytic insect pathogenic microbes from the genera Epichloe/Neotyphoidium and Acremonium fall under class 1 endophytes, as they predominantly colonize grasses and sedges. Class 2 includes other Hypocreales entomopathogens that extensively colonize the roots, stems, and leaves of non-grass plants. The first report of class 1 endophytes providing insect resistance appeared in the early 1980s, where *A. lolii* colonized perennial ryegrass, conferring resistance against *Listronotus bonariensis* (Kuschel) [14] and *Crampus* Spp [15]. Similarly, earlier evidence of endophytic colonization by class 2 entomopathogenic endophytes emerged from an experiment investigating the interactions among maize, *Beauveria bassiana* and the pest *Ostrinia nubilalis* [16], where the application of *B. bassiana* provided season-long protection to maize, resulting in a significant reduction in tunneling damage caused by the insect [17]. The idea that endophytic bacteria mediated insect pest control stems from Fahey et al [18] discussion about incorporation of cry gene into beneficial endophytic bacterial genome helps to reduce the insect infestation by expression of cry toxins while colonizing the plants as plants incorporated protectants. Accordingly, endophytic colonization of genetically engineered *Clavibacter xyli* subsp. *cynodontis* with *cryIA(c)* gene of *Bacillus thuringiensis* showed significant insecticidal activity against *O. nubilalis* in maize [19].

All beneficial endophytic microbes possess characteristics similar to their pathogenic counterparts, which may be perceived by the host plant as a threat, triggering an initial defense response to hinder colonization. The balance between beneficial endophyte colonization and plant defense is maintained by various attributes of the colonizing microbes [20]. For instance, endophytes have strong antioxidant mechanisms that allow them to survive in the highly oxidative environment within the host plant [21]. Additionally, they have the ability to mask key microbe- or pathogen-associated molecular patterns (MAMPs/PAMPs). For example, some endophytic bacteria can mask flagellin, a crucial PAMP recognized by plants to detect pathogenic bacteria and activate defense responses. These bacteria enhance flagellin motor rotation, enabling faster movement within the plant to promote colonization [22].

Moreover, mutualistic endophytes possess distinct anabolic pathways and gene clusters, which help the plant differentiate them from pathogens and support efficient colonization [23]. As long as the balance between microbial virulence and the host's defense response was maintained, symptomless colonization could proceed [24].

Due to the intricate relationship between endophytes and their host plants, this symbiosis may positively enhance the host plant's vigor, helping it cope with various biotic and abiotic stressors, including insect attacks [25]. Many entomopathogenic endophytes have been shown to act against plant-feeding insects through mechanisms beyond simply causing direct mortality [26]. Additionally, secondary metabolites produced by various entomopathogenic endophytes could serve as potential sources of novel compounds with insecticidal properties [27]. In addition to controlling insect infestations, the colonization of entomopathogenic endophytes also promotes plant growth and development by producing various plant growth hormones, solubilizing otherwise unavailable plant nutrients, and helping the plant fend off infestations from pathogenic microbes [28, 29, 30]. A comprehensive understanding of the benefits of utilizing endophytic entomopathogens in pest suppression can enhance the management of insect pest pressure in the field.

3. ENDOPHYTIC ENTOMOPATHOGENIC MICROBES MEDIATED INSECT CONTROL

Endophytic colonization by entomopathogenic microbes (fungi and bacteria) plays a pivotal role in suppressing insect herbivores through direct and indirect mechanisms. These microbes not only act as biocontrol agents in their free-living state but also establish themselves either through natural or artificial inoculation inside plant tissues, creating an internal defense system that actively impacts the behavior, development, and survival of plant-feeding insects (Table 1).

3.1 Direct effect on insect pest

When entomopathogens colonize inside plants, they can directly contact feeding insects as the insects begin consuming endophyte-colonized plant tissues, such as leaves. Once ingested, these pathogens cause direct mortality, similar to the effects of topical application. For instance, endophytic colonization of *Bacillus thuringiensis* in brinjal through seed treatment caused approximately 27% direct mortality in *Leucinodes orbonalis* [31]. Similarly, endophytic colonization of *B. bassiana* in tissue-cultured banana resulted in about 60% mortality in *Cosmopolites sordidus* [32].

However, in most studies, direct mortality due to endophytic colonization by entomopathogens has been minimal. Instead, the predominant effects observed include significant reductions in insect fitness, feeding deterrence, decreased insect pressure, and reduced plant damage. The decrease in insect weight gain was more pronounced in endophyte-colonized plants. For instance, *Spodoptera frugiperda* feeding on *B. thuringiensis*-colonized maize plants showed less weight gain compared to larvae feeding on control plants [33]. Similarly, *B. bassiana*-colonized wheat plants reduced the weight gain of *Chortoicetes terminifera* [34]. This reduced weight gain may be due to the hindered absorption of essential plant nutrients by the insect pests. To obtain sufficient nutrition for their life cycle progression, the instars remain longer on the plants, attempting to absorb enough nutrients without experiencing mortality.

Endophytes often trigger plants to produce or enhance the production of various secondary metabolites. Additionally, the secondary metabolites produced by the endophytes themselves have been shown to exhibit antifeedant effects on insect pests. According to Wei et al. [35], *Bemisia tabaci* avoids *B. bassiana*-inoculated tomato seedlings, likely due to the production of bioactive compounds such as chitin and glucans in the plants. Similarly, various endophytic *Bacillus* species, including *B. thuringiensis* and *B. subtilis*, colonized potato plants and reduced the incidence of *Leptinotarsa decemlineata*, which was attributed to their antifeedant activity [36]. Changes in plant cues caused by endophytes often deter insects from ovipositing on endophyte-colonized plants. For example, *B. thuringiensis*-colonized cotton plants had fewer *B. tabaci* eggs compared to control plants treated with sterile water [37].

Endophytic colonization by entomopathogenic microbes also triggers indirect defenses in plants that influence insect herbivory. One significant indirect effect is the enhancement of antioxidant enzyme activity in colonized plants. These enzymes, such as superoxide dismutase (SOD), catalase (CAT), and peroxidase (POD), play crucial roles in reducing oxidative stress caused by insect feeding. When herbivorous insects feed on endophyte-colonized plants, the elevated levels of these antioxidant enzymes hinder their ability to extract essential nutrients from the plants, leading to reduced growth and development. This impaired nutrient acquisition can force insects to remain on the plants for extended periods, further exposing them to both direct and indirect defenses. *B. amyloliquefaciens* colonised maize plant showed enhanced production of antioxidants which impair *S. frugiperda* fitness [38].

In most cases, plants colonized by entomopathogens experienced less damage than their non-colonized counterparts. Endophytic colonization of *B. bassiana* reduced *Helicoverpa armigera* infestation in tomato plants and *Hypothenemus hampei* infestation in coffee plants [39, 40].

3.2 Indirect effect on insect pest

The modified nutritional profile of host plants due to entomopathogenic endophytes impacts the feeding herbivores by extending the duration of each instar, which in turn improves the qualitative and quantitative foraging efficiency of various predators and parasitoids. Along with plants colonized by endophytes proven to emits the enhanced stress volatiles which tend to attract more natural enemies to the vicinity of endophyte treated insect feeding plants [41]. For instance, cotton plants colonized by the fungus *B. bassiana* were found to release increased levels of decanal and caryophyllene, which are typically produced by cotton when attacked by the *Heliothis virescens* [42]. These volatiles have been shown to enhance the recruitment of *Microplitis croceipes*, a larval parasitoid of the tobacco budworm [42]. Similarly, endophytic colonization by *Trichoderma atroviride* led to the release of the fungal metabolite 6-pentyl-2H-pyran-2-one, which further increased the parasitism rate of the fall armyworm by its natural enemy *Campoletis sonorensis* [43]. Additionally, root colonization by *Trichoderma longibrachiatum* in tomato plants heightened the attractiveness of the aphid predator *Macrolophus pygmaeus* and the parasitoid *Aphidius ervi* by altering the volatile profile [44]. These findings suggest that endophytic fungi can enhance plant defenses against pests by altering the composition of plant volatiles.

4. OTHER PLANT BENEFITS OF ENDOPHYTIC ENTOMOPATHOGENS

Endophytic entomopathogens not only protect plants from insect pests but also play a role in defending against plant disease-causing pathogens by exhibiting antimicrobial properties and inducing plant resistance to disease. Additionally, these entomopathogens assist plants in nutrient acquisition from the soil and contribute to the synthesis of various plant growth hormones within the plant, promoting growth and enhancing resilience against both biotic and abiotic stresses.

4.1 Plant growth promoting attributes of endophytic entomopathogens

Endophytic entomopathogens are known to synthesize phytohormones such as auxins, gibberellins, and cytokinins, which are key regulators of plant growth. For instance, certain strains of *B. bassiana* [45] *Trichoderma* species [46] *B. thuringiensis* [47] and *Serratia marcescens* [48] have been reported to produce indole-3-acetic acid (IAA), a vital auxin that stimulates root elongation, cell division, and differentiation, leading to improved root and shoot development. By boosting root architecture, these endophytes enable the plant to explore a larger volume of soil, thereby enhancing water and nutrient uptake.

Endophytic entomopathogens also contribute to plant nutrition by solubilizing essential minerals that are otherwise unavailable to the plant. For instance, several species of endophytic *Bacillus* and *Trichoderma* have been documented to solubilize phosphates, making this crucial nutrient more readily available for plant uptake [49, 50]. Additionally, they can assist in the assimilation of nitrogen and other essential elements, facilitating better plant nutrition. In maize and tomato, endophytic *B. bassiana* has been found to increase the bioavailability of nutrients, particularly under nutrient-limited conditions, further promoting plant growth [51, 52].

Endophytic entomopathogenic fungi can stimulate plant growth by increasing the expression of genes responsible for nutrient transport. A notable example is *Metarhizium robertsii*, which can transfer nitrogen from insect larvae to its host plants [53]. Research has revealed that several endophytic fungi, including *M. robertsii, B bassiana, M. brunneum, and M. guizhouense*, can promote the growth of soybeans, wheat, green beans, and switchgrass by providing insect-derived nitrogen [54, 55].

4.1 Plant disease suppression by endophytic entomopathogens

Endophytic microbes, particularly species of *B. bassiana*, *Trichoderma*, and *Bacillus*, have been shown to produce antimicrobial compounds such as antibiotics, volatile organic compounds (VOCs), and lytic enzymes that inhibit the growth of pathogenic fungi, bacteria, and oomycetes [56, 57]. For example, *T. harzianum* secretes cell wall-degrading enzymes such as chitinases, β-glucanases, and proteases, which lyse the cell walls of fungal pathogens, reducing their ability to infect host plants. Similarly, *B. subtilis* produces antifungal lipopeptides, such as iturins and surfactins, that can disrupt the membrane integrity of pathogenic fungi [58].

Moreover, endophytic colonization by entomopathogens triggers an induced systemic resistance (ISR) response in plants, similar to systemic acquired resistance (SAR) triggered by pathogen infection. ISR involves the priming of plant defense pathways, such as the jasmonic acid (JA) and ethylene (ET) signaling pathways, leading to the production of defense-related compounds like pathogenesis-related proteins (PRs), phytoalexins, and reactive oxygen species (ROS). These defense mechanisms help plants fend off a wide range of pathogens . For instance, *B. bassiana* has been found to activate ISR in tomato and coffee plants, leading to enhanced resistance against *Fusarium oxysporum* and *Phytophthora capsici*, respectively [59, 60].

Endophytic entomopathogens also compete with plant pathogens for nutrients and space within plant tissues, effectively reducing the pathogen's ability to colonize the host. By occupying ecological niches within plant tissues, these beneficial microbes create a competitive environment that limits pathogen invasion. This phenomenon, known as niche exclusion, has been observed with endophytic *Bacillus* and *Trichoderma* species, which outcompete harmful pathogens like *Rhizoctonia solani* and *Pythium ultimum* [61].

5. CHALLENGES AND FUTURE PROSPECTS

Although the potential benefits of using endophytic entomopathogens in agriculture are considerable, several challenges still limit their widespread application. One significant challenge is the variable efficacy of these microbes in different environmental conditions. Factors such as temperature, humidity, UV radiation, and soil pH can influence the colonization efficiency and persistence of entomopathogenic microbes within plant tissues. Additionally, the slow mode of action of some microbial agents, compared to synthetic insecticides, poses a hurdle for their rapid adoption in commercial agriculture. Another challenge lies in the development of effective formulations that ensure consistent colonization and pest control. Current formulations often suffer from short shelf life and are vulnerable to environmental degradation. Developing more stable and user-friendly products will be essential for promoting the widespread use of these microbes. Lastly, more research is needed to fully understand the complex interactions between endophytes, plants, and pests. Future studies should focus on optimizing inoculation methods, identifying key genetic traits that enhance endophytic colonization, and developing microbial strains that are well-suited to diverse agroecological zones.

6. CONCLUSION

The integration of endophytic entomopathogens into sustainable pest management systems holds great promise. Advances in biotechnology and microbial formulation could lead to more efficient, eco-friendly pest control strategies that simultaneously promote plant growth and productivity. As agricultural practices continue to evolve, the role of these beneficial microbes is likely to expand, offering a greener, more sustainable approach to food production.

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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Table 1. Effects of endophytic entomopathogenic microbes against herbivore

Endophytic microbe	Target insect	Host plant	Effect on the insect	Reference
Endophytic bacteria				
Bacillus subtilis 26D	Colorado potato beetles, *Leptinotarsa decemlineata*	Potato	Disturbing the endosymbionts of insects thus cause mortality	[62]
Bacillus velezensis YC7010	green peach aphid (GPA), *Myzus persicae*	Arabidopsis	Hyper sensitive response such as H_2O_2 burst, callose deposition and cell death	[63]
	Brown planthopper, *Nilaparvata lugens*	Rice	Physical barrier reinforcement via jasmonic and salicylic acid pathway	[64]
Bacillus pumilus strain INR-7	Western corn rootworm, *Diabrotica virgifera virgifera*	Maize	Deterrent activity along with reduced weight gain on insect	[65]
Bacillus thuringiensis	Asian citrus psyllid *Diaphorina citri*	Citrus	Direct nymphal morality up to 90 percent	[66]
Serratia marcescens S-JS1	Brown planthopper, *Nilaparvata lugens*	Rice	induction of defense-related secondary metabolites reduces the survivability of nymphs	[67]
B. subtilis 26D and 11VM	Greenbug aphid *Schizaphis graminum*	Wheat	Increases endurance of plants against aphid infestation by plants redox mechanism	[68]
Endophytic fungi				
Beauveria bassiana and *Metarhizium brunneum*	Green peach aphid *Myzus persicae*	Sweet pepper	Fungal inoculated plants affect the population characteristics of aphids	[69]
Trichoderma asperellum M2RT4, *Beauveria bassiana*	*Tuta absoluta*	Tomato	Reduction in egg laying, pupal development, adult	[70]

ICIPE 706 and *Hypocrea lixii* F3ST1			emergence and mining damages in host plants	
Epichloe gansuensis	Aphid *Rhopalosiphum padi*	Grasses	Endophytes induces plant tolerant to herbivory via jasmonic acid signalling	[71]
Beauveria bassiana UHSB-END-1	*Spodoptera litura*	Tomato	Increased the mortality of insect	[72]
Beauveria bassiana and *Metarhizium anisopliae*	Fall armyworm, *Spodoptera frugiperda*	Corn	Endophytes affects pupal emergence, oviposition and hatching of the eggs	[73]
Beauveria bassiana and *Metarhizium anisopliae*	Fall armyworm, *Spodoptera frugiperda*	Maize	Slower development of instars and reduced egg laying; affects overall population parameters of insect	[74]
B. bassiana ARSEF 3097 and *Trichoderma harzianum* T22	Green stink bug *Nezara viridula* L.	Sweet pepper	Improved the plan growth and reduced the overall damage caused by insect	[75]
Beauveria bassiana ARSEF 3097, *Metarhizium brunneum* ARSEF 1095 and *Trichoderma harzianum* T22	Predator, *Nesidiocoris tenuis*	Tomato	Cultivar dependent lesser feeding damage was observed in the fungal inoculated plants	[76]
Akanthomyces muscarius ARSEF 5128	Tobacco peach aphid *Myzus persicae var. nicotianae*	Sweet pepper	Fungus inoculated insect fed plants emit increased amount of indole, (E)-nerolidol, (3E,7E)-4,8,12-trimethyltrideca-1,3,7,11-tetraene which tend to attract more parasitoids	[77]
Beauveria bassiana	Diamond back moth, *Plutella xylostella* Green peach aphid *Myzus persicae*	Cabbage	Endophytic fungus cause mortality up to 96 percent in both the insects	[78]
Aspergillus nomiae	*Spodoptera litura*	Soybean	Increased protection against both disease and affects the	[79]

			performance of feeding insect	