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REVIEW ARTICLE

Endophytic entomopathogens: An ecofriendly way for pest management

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Abstract

Global food security poses a significant challenge in meeting the needs of a rapidly growing population. Currently, producers rely on chemical pesticides to overcome pest-related problems in crop husbandry. However, the extensive use of synthetic molecules results in environmental pollution, resistance development, residual toxicity, pest recurrence and negative impacts on human and animal health. The expanding worldwide population has generated a substantial need for agricultural goods in terms of both quality and quantity, leading to a notable rise in the application of agricultural chemicals, including chemical pesticides, to combat insect pests. As a result, the use of entomopathogens for biological control has emerged as a prominent choice among these options. Currently, farmers are using microbial biopesticide solutions to counteract the negative effects of specific insects on crops. Microbes present a sustainable and adaptable solution that can effectively combat harmful pests without causing significant economic damage while simultaneously improving the health and productivity of plants. In 2020, biopesticides held a 6 % share in the global pesticide industry, with projections indicating a twofold increase to approximately 15 % by 2031. The purpose of this review was to highlight the widely accessible endophytic entomopathogens and explore their potential as a substitute for chemical pesticides. The primary goal of using endophytic entomopathogens is to maintain an optimal level of production, improve environmental well-being, reduce pesticide use and conserve natural resources. Moreover, research is now being conducted to investigate further potential characteristics, particularly concentrating on effective and rapidly spreading endophytic entomopathogens. This paper presents an overview of the mechanisms of action and the resistance they provide against herbivore insects, along with their respective benefits and limitations.

Keywords

actinomycetes; bacteria; endophytic entomopathogens; fungi; mechanisms; resistance

Introduction

The burgeoning global agricultural product markets have necessitated the development of agricultural practices aimed at mitigating environmental impacts and ensuring the production of safe foods for human consumption. The noticeable decrease in yield due to insects, plant diseases and weeds is a significant drawback of the increased agricultural output (1-3). These variables contribute to significant reductions in plant production, resulting in agricultural losses of up to 26 % and a total worth of $ 470 billion (4). Moreover, the statistics indicate that crop losses have remained rather stable despite the significant rise in pesticide usage (5). The widespread use of chemical insecticides in the later part of the 1940s neglected the potential of microbial agents as pest management agents and established an inadequate paradigm centered around chemical insecticides (6). Agriculturists rely extensively on chemical pesticides and inorganic fertilizers to effectively address these issues and achieve maximum output in farmed plants. Agriculturists have challenges due to their overreliance on synthetic pesticides and fertilizers to enhance plant development (7). The excessive dependence on these compounds gives rise to many adverse consequences for users, non-target creatures and the environment. The control of insect pests involves the use of a combination of chemical and non-chemical strategies to reduce the potential harm to both human health and the environment (8). Following the advent of chemical insecticides, genetically modified plants designed to be resistant to insects, fungi and herbicides assumed a significant role (9). Nevertheless, the replacement of pesticides with genetically engineered plants does not signify a fundamental shift in strategy. It signifies a basic replacement in which the delivery methods differ while the fundamental approach remains the same (10).

A paradigm shifts away from chemical dependence and towards a holistic, systemic approach would be necessary (10, 11). In contemporary times, there has been significant interest in biological control as an alternative to chemical pesticides (12). The primary goal of these methods is to gain a deeper understanding of the myriad ecological components that make up an ecosystem, including the biological agents that are responsible for ecosystem control. Gaining an understanding of these relationships could improve the effective use of entomopathogens for pest biocontrol techniques worldwide, even in areas where other approaches might not be financially feasible. Tanzini coined the term "entomopathogens" in 2001 to describe microorganisms that control the population of insect pests at levels that do not cause crop damage. A definition was provided that encompasses microbial communities capable of attacking insect pests by incorporating them into their life cycle and utilizing them as hosts (13). They classified these microorganisms as either facultative or obligate parasites, with strong abilities to survive and combat insect pests. Currently, the most common microbial biocontrol agents are fungi, bacteria, viruses and nematodes (14).

Fungi, among the several entomopathogens, have a critical function because of their extensive range of species and ability to effectively control a wide range of insects. The mutualistic association between entomopathogenic fungi and insects developed simultaneously, showcasing reciprocal assistance. The idea of using fungal insect diseases to manage insect pests came from extensive research into silkworm disease. Agostino Bassi first identified *Beauveria bassiana* (Balsamo) Vuillemin (Clavicipitaceae; Hypocreales), the cause of white muscardine disease, in silkworms (15). This study of silkworm infections not only highlighted the fungus's ability to infect diverse insects, but also popularized the idea of using fungal diseases to combat insect infestations (16).

Entomopathogenic bacteria are frequently used in pest management due to their high efficacy in delivering rapid results compared to other entomopathogens. The bacteria present in the Bacillaceae family viz., *Bacillus papillae*, *B. sphericus* and *B. thuringinesis* are widely used against insect pests (17). The bacterium produces parasporal bodies which contain insecticidal toxins (18). The product based on *B. thuringinesis* is used in rotation with chemical insecticides to manage resistance development in insects. The development of resistance to *B. thuringiensis* insecticidal crystal proteins in many lepidopteran and dipteran insects is a major concern for researchers and farmers. Actinomycetes are microorganisms that form symbiotic relationships with plants by inhabiting their tissues as endophytes. Actinomycetes help in disease and pest suppression by producing antimicrobial compounds that inhibit plant pathogens (19). Additionally, they contribute to plant health by promoting root growth, improving nutrient availability and enhancing the plant's defense mechanisms.

The use of entomopathogenic microorganisms in pest management is not only efficient against the intended pest but also beneficial for humans and non-target animals. Fungal biocontrol agents are particularly important because of their diverse pathogenic strains, intrinsic proteins, external toxins, versatile mass production techniques and adaptable field formulations (20). They have a wide range of functions as biological control agents, effectively dealing with sap-sucking pests including mosquitoes and aphids as well as pests with chewing mouthparts (21, 22). Fungal entomopathogens restrict insect populations without significantly altering the biotic balance of crop ecosystems (23). Though the overreliance and improper use of entomopathogens may lead to resistant development, the intricate mechanism of action of microbial biocontrol agents makes it challenging for pests to acquire resistance to them (24).

Concerns about pest specificity, their susceptibility to dry conditions and ultraviolet (UV) light are some of the other things that make them hard to widely use and effective (25). Due to these constraints, the pursuit of alternative methods of utilizing entomopathogens continues to gain momentum. An alternative approach is to use entomopathogens as endophytes (26). Endophytic entomo-pathogens have a lot of potential for pest control. However, there is a limited understanding of the many forms of endophytic entomopathogens, their modes of action, field applications and future prospects (27). This paper seeks to provide a comprehensive overview of endophytic entomopathogens and their utility in sustainable pest management.

Endophytes

Epiphytes, which reside on the outer surfaces of aerial plant components and endophytes, which reside inside the tissues, comprise the phyllosphere community (28). Since ancient times, the definition of an endophyte has remained fundamentally consistent: a microbe that dwells in living plant tissues without displaying any obvious indicators of its existence or causing harm to the host (29). An endophyte is a microbe that resides within a plant and engages in a mutually beneficial interaction with its host (30). Researchers have detected endophytes in almost every plant part, including roots, stems, leaves, flowers, fruits and seeds (Table 1). The majority of these endophytes are fungi, particularly Ascomycete fungi associated with the fungus Imperfecti. In addition to fungi, bacteria such as filamentous actinomycetes can promote plant growth and provide tolerance to biotic and abiotic stressors. The phyllosphere is home to four major bacterial phyla: Proteobacteria, Firmicutes, Bacteroides and Actinobacteria (54). All plant species, especially those in maritime environments, likely serve as hosts or potential hosts for one or more endophytes (55). Additionally, some lower plant forms, such as mosses and liverworts, are known to sustain endophytes.

Endophytic entomopathogens- a hidden Allie

Endophytic entomopathogens, including fungi and bacteria, play a crucial role in biological pest control by residing within plant tissues and enhancing plant resistance to pests and pathogens. These microorganisms not only contribute to plant health but also serve as potential biocontrol agents against insect pests. Endophytes can internally colonize plant tissues, acting as biological control agents by inducing resistance to phytopathogens and mitigating abiotic stresses. They produce bioactive compounds that form a protective shield around plants, reducing damage from pests and diseases (56) (Table 2).

Endophytic entomopathogenic fungi

Endophytic entomopathogenic fungi (EEPF) are a unique group of fungi that can live inside plant tissues (as endophytes) and act as pathogens to insects (as entomopathogens). These fungi form mutualistic relationships with their host plants, protecting herbivorous insects and other pests (63). They achieve this by infecting and killing insect pests, which reduces the need for chemical pesticides (64). Common examples of endophytic entomopathogenic fungi include species from genera such as

Table 1. Variety of endophytic entomopathogens in various crops

S. No	Endophytes	Crop	Insect targeted	Reference
1	*Beauveria*, *Isaria* & *Lecanicillium*	Bean plant	*Tetranychus urticae*	(31)
2	*B. bassiana* strain EABb 04/01	Opium poppy	*Timaspis papaveris*	(32)
3	*B. bassiana* & *Metarhizium acridum*	Potato	*Aphis gossypii*	(33)
4	*B. bassiana* & *L. muscarium*	Vegetable	Sucking pest	(34)
5	*M. anisopliae & B. bassiana*	Cassava	*Cyrtomenus bergi*	(35)
6	*B. bassiana*	Tobacco	*Myzus persicae*	(36)
7	*B. bassiana* & *Aspergillus parasiticus*	Wheat	*Chortoicetes terminifera*	(37)
8	*B. bassiana*	Banana	*Cosmopolites sordidus*	(38)
9	*B. bassiana* & *L. lecanii*	Cotton	*Aphis gossypii*	(37)
10	*B. bassiana*	Coffee	*Hypothenemus hampei*	(39)
11	*Penicillium spp.*	Coffee	*Hypothenemus hampei*	(40)
12	*B. bassiana* & *Penicillium oxalicum*	Bacao	*Theobroma cacao*	(41)
13	*B. bassiana*, *L. dimorphum* & *L. psalliotae*	Date palm	*Phoenicoccus marlattii*	(42)
14	*B. bassiana, M. anisopliae* & *M. robertsii*	Soybean	*Aphis glycines*	(43)
15	*M. anisopliae*	Rapeseed	*Plutella xylostella*	(44)
16	*Beauveria* (ICIPE279), *Hypocrea*, *Gibberella*, *Fusarium* & *Trichoderma*	*Broad bean* and *Common bean*	*Liriomyza huidobrensis*	(45)
17	*B. varroae* & *B. bassiana*	Sugar beet	*Spodoptera littoralis*	(46)
18	*B. bassiana* & *Bionectria ochroleuca*	Artichoke	*Capitophorus elaeagni*	(47)
19	*Neotyphodium spp.*	*Barley*	*Mayetiola destructor, Rhopalosiphum padi, Metopolophium dirhodum*	(48)
20	*Acremonium*	*Tomato*	*Helicoverpa armigera*	(49)
21	*B. bassiana*	Pine seed	*Dendroctonus frontalis*	(50)
22	*Bacillus amyloliquefaciens*	Ornamental host	*Spodoptera fruigiperda*	(51)
23	*Methylobacterium* spp. & *Curtobacterium laccumfaciens*	Citrus	*Bothrogonia addita*	(52)
24	*Serratia marcescens*	Rice	*Nilaparvata lugens*	(53)

Table 2. Secondary metabolites produced by endophytic entomopathogens

S. No	Secondary metabolite	Endophytes	Author
1	Peramine	*Neotyphodium coenophialum*, *N. lolli*	(57)
2	Nodulisporic acid	*Nodulisporium spp.*	(58)
3	Naphthalene	*Muscodor vitigenus*	(59)
4	Heptelidic acid chlorohydrin & hydroheptelidic acid	*Phyllosticta spp.*	(60)
5	Phomin, phomodione, sesquiterpenoid, cytochalasin B, deoxaphomin, usnic acid, trichodermin, beta-sitosterol, cercosporamide, sirodesmin, phomasetin	*Phoma spp.*	(61)
6	Bisabolane sesquiterpenes, polyketides, & ergosterols	*Schizophyllum commune*	(62)

Beauveria, *Metarhizium* and *Lecanicillium*. Besides insect control, these fungi also contribute to plant growth, stress tolerance and overall plant health, making them valuable in sustainable agriculture and integrated pest management strategies. Their dual function as plant protectors and insect pathogens provides an eco-friendly alternative to chemical control methods, helping reduce environmental impact while supporting crop productivity (65).

General characteristics of endophytic entomopathogenic fungi

Fungi are naturally occurring pathogens that have a worldwide distribution and have the potential to induce illnesses in arthropod populations and several other creatures (66). Insect populations frequently exhibit epizootics, demonstrating the significant ability of these microorganisms to regulate insect pests. One of the types of fungus that may cause death or severe disability in insects is endophytic entomopathogenic fungi (EEPF) (67). Entomopathogenic fungi fall under the categories Oomycetes, Chytridiomycota, Microsporidia, Entomophtoromycota, Basidiomycota and Ascomycota (68).

Entomopathogenic fungi were the first organisms used in biological pest management. These entomopathogens are favored for their environmentally friendly nature and ability to survive in living organisms, making them ideal for killing insects at different phases of their life cycle (68). The pathogenicity of entomopathogens, such as *Metarhizium anisopliae* and *Beauveria bassiana*, has been extensively studied and documented about several insect orders. *B. bassiana* and *M. anisopliae* are two of the first entomopathogenic fungi that are effective at controlling insect pests through microbiological means. Agricultural pest control has extensively studied many species, including *B. bassiana, B. brongniartii, M. anisopliae, Lecanicillium lecanii, Hirsutella thompsonii, Nomuraea rileyi* and *Isaria fumosorosea* (69).

Fungi can infect several orders of insects, with a higher prevalence seen in Hemiptera, Diptera, Coleoptera, Lepidoptera, Orthoptera and Hymenoptera. Researchers have identified about 700 to 1000 fungal species as potential disease -causing agents in arthropods (66). The orders Hypocreales and Entomophthorales are mostly used for the microbial management of insects and mites. Only fungi belonging to the Hypocreales family, such as *B. bassiana*, *Metarhizium* spp., *I. fumosorosea* and *Lecanicillium* spp., are commercially produced for microbial management. These fungi are used to combat several pests in various crops (69).

Various endophytic entomopathogenic fungi and their morphology

Beauveria spp.

B. bassiana (Balsamo) Vuillemin is the asexual form of the *Cordyceps bassiana* fungus; the sexual form is known as teleomorph (70). *Beauveria* is an entomopathogenic endophyte that targets several insect orders, including Lepidoptera and Coleoptera (71). *Beauveria* colonies are normally white to pale yellow on the dorsal side, with red coloring on the underside. *Beauveria* conidia are hyaline, smooth, short and flask-shaped, with an apical denticulate rachis that gives them a distinctive zig-zag look (72). Both *B. brongniartii* (Saccardo) Petch and *B. amorpha* have endophytic features (73).

Metarhizium spp.

M. anisopliae (Metchnikoff) Sorokin (Clavicipita-ceae; Hypocreales) is a well-known soil-inhabiting fungus that can be found in a variety of environments, spanning the Arctic and tropical regions (74). This fungi colony appears white and flat during the vegetative phase, but as it matures, it turns dark green with a yellow tint on the reverse. *M. anisopliae* conidia are commonly oblong or elliptical in shape with varied lengths (75). *M. brunneum* and *M. robertsii* have been shown to have an endophytic entomopathogenic characteristic (76).

Paecilomyces lilacinum

Bainier first defined the genus *Paecilomyces* in 1907 and it is closely related to *Pencilium* (77). Based on morphological characteristics, the colonies can range in color from brown to yellow-brown, but certain mesophilic species may appear white or brightly colored. Conidiophores are divergent and found in branches; cylindrical phialides have a long, unique neck and produce hyaline conidia in basipetal chains (78).

Neotyphodium spp.

These fungi exhibit a variety of morphological traits. They generate stromata of various lengths on host plants, with certain species, such as *Neotyphodium pampeanum* (Clavicipitaceae; Hypocreales), producing stromata ranging from 47.5 to 186 mm (79). *Neotyphodium spp.* also has a lot of genetic diversity, as shown by the different shapes, growth rates and conidial ontogeny seen in different groups (80). The recently discovered *N. gansuense* has distinct morphological and cultural characteristics that indicate species-specific features. Overall, *Neotyphodium* fungus exhibits a variety of physical traits determined by genetic diversity and host specificity.

The resistance provided by EEPF

Endophytic fungi, such as those in grasses, produce mycotoxins that deter herbivores. For instance, studies have shown that the endophytes in perennial ryegrass and tall fescue significantly reduce the survival and growth of fall armyworm larvae (81). They trigger systemic plant defenses, enhancing resistance upon herbivore attack. The endophyte *N. coenophialum* in tall fescue provides both constitutive and wound-inducible resistance through alkaloid production (82). EEPFs are capable of inhibiting the development of disease-causing organisms in the host plants (83). They are capable of reducing the insect's fitness in the crop environment. *B. bassiana* reduced survival rates and weight, primarily through feeding deterrence rather than direct infection (84).

Mechanism of EEPF

Endophytic entomopathogenic fungi naturally reside in plants, protecting against diseases and insects that would otherwise attack plant tissues. Establishing endophytic EPFs is challenging because both the plant and the fungi produce unique compounds during colonization. Plants release various secondary metabolites, such as alkaloids, flavonoids, phenolics and others, to defend against pathogens (85), which can inhibit the colonization of endophytic fungi (86) (Fig. 1). However, endophytic fungi have adapted by producing detoxifying and degrading enzymes, including β-1,3-glucanases, chitinases, amylases, laccases and cellulases (87). Additionally, fungal

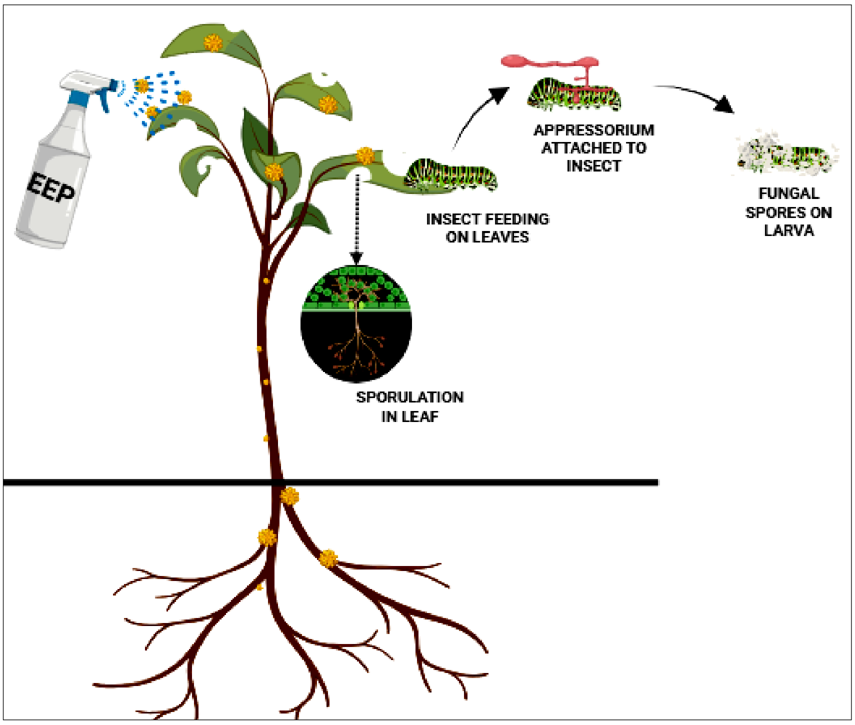

Fig. 1. The effect of EEPF on insects through direct feeding (Direct defense mechanism).

metabolites play a significant role in fungus-insect interactions, influencing pathogenicity and other communication processes (88).

These fungal metabolites also help mitigate both biotic and abiotic stresses. They provide systemic resistance to insects by reducing reproduction rates, slowing feeding behaviour and lowering larval survival (89). The fungi can enter the plant through wounds, epidermal cells, or natural openings like stomata, then proliferate and spread within the plant tissues, establishing themselves as endophytes. Depending on the fungal species, they may grow either intracellularly or intercellularly. When infecting insects, fungal pathogens attach asexual spores to the insect's surface, penetrate the live tissue and proliferate within the body (Fig. 2). Endophytic fungi produce secondary metabolites like mycotoxins (e.g., beauvericin, destruxins, gliotoxin), enzymes (e.g., proteases, chitinases, lipases, cellulases) and volatile organic compounds that are detrimental to insects (90).

These chemical compounds serve as cues, attracting insects to the infection site. Secondary metabolites are crucial for interactions with both the host plant and insect pests, with some compounds attracting natural enemies as an indirect defense mechanism (Fig. 3). Endophytic entomopathogenic fungi can infect insects by hyphae penetration or spore absorption when they eat a plant containing them (26). Conidial surface proteins recognize insect-specific chemicals and initiate the breakdown of the insect's cuticle (91). Once inside the insect, the fungi proliferate and bypass the immune system, reaching the haemolymph and forming blastospores (92). Blastospores absorb nutrients from the haemocoel and produce insecticidal compounds, toxins, or enzymes that disrupt the insect's physiological functions, leading to death within days (93).

After the insect's death, the fungi may produce antimicrobial substances to reduce microbial competition, allowing for further fungal growth and reproduction. Once established, the fungi rapidly destroy the insect, resulting in its death. Afterward, the fungi continue to grow and sporulate within the insect cadaver, which serves as a spore reservoir that can infect other insects that come into contact with it. Furthermore, some endophytic entomopathogenic fungi can spread from dead insect cadavers to healthy plants, completing the fungal life cycle and ensuring their persistence in the ecosystem.

Endophytic entomopathogenic bacteria

Endophytic entomopathogenic bacteria are a type of endophytic bacteria that can colonize plant interior tissues and transmit pathogens to insects (94). These bacteria can form symbiotic associations with their host plants and act as biological control agents against insect pests (94). Endophytic bacterial strains also help the plants to grow by making phytohormones like indole-3-acetic acid (IAA), cytokinins and gibberellins, or by controlling the number of hormones inside the plant (95).

Various EEPB and their morphology

Bacillus spp.

These are the bacteria that have a rod-shaped morphology. The colour of these colonies varies according to environmental conditions (96). *B. sphaericus* Meyer & Neide (Bacillaceae; Bacillales) is a gram-positive bacterium that produces cylindrical endospores. These bacteria have parasporal inclusion bodies called crystals, or δ-endoto-xins. Cry genes encode cry proteins ranging in molecular weight from 30 to 140 kDa (97). Additionally, *B. sphaericus* produces several enzymes and poisons that enable it to grow in a variety of conditions (98). The gram-positive bacterium *Bacillus cereus* Frankland & Frankland (Bacilla-ceae; Bacillales), is dangerous due to the production of its enterotoxins (99). *B. cereus* strains have been genetically split into different groups based on the presence of virulence protein-coding genes. This changes how well they can cause enterotoxicity (100).

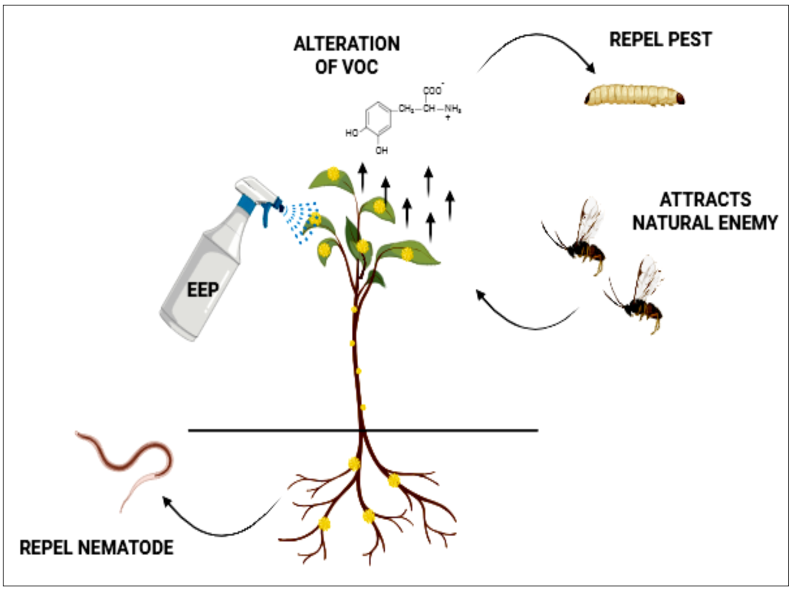

Fig. 2. Illustration of the sequential stages of infection by endophytic entomopathogenic fungi.

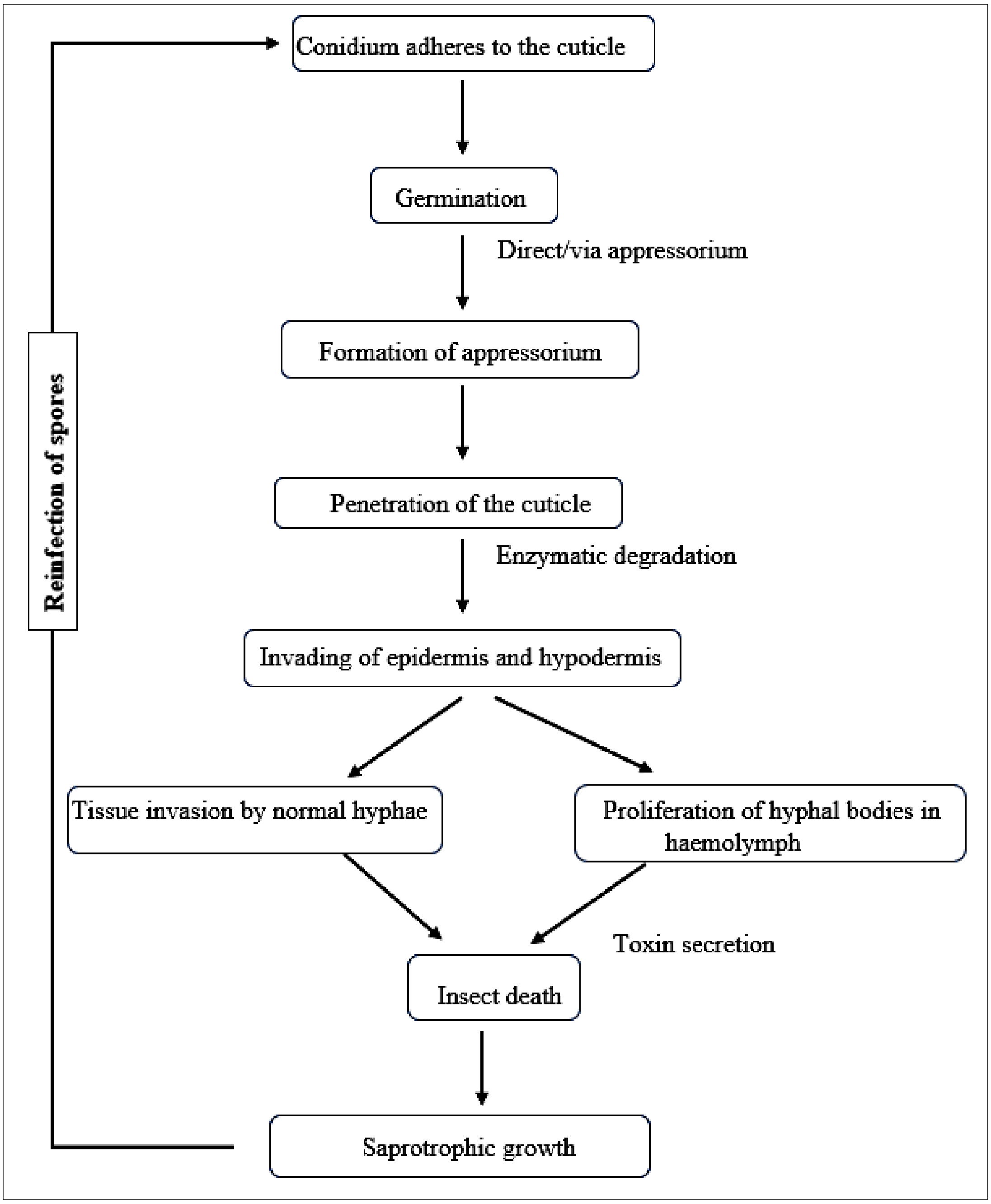

Fig. 3. The effect of EEPF alters the volatiles from plants attracts natural enemies and repels pest and nematodes (Indirect defense mechanism).

Methylobacterium spp.

Methylobacterium spp. was described as a new genus of facultative methylotrophic bacteria (101). These are gram-negative, aerobic rod-shaped bacteria that belong to the Methylobacteriaceae family (102). When produced on solid media, *Methylobacterium* colonies are typically tiny, smooth, round and mucoid. The colour of these colonies varies from pale pink to crimson, depending on the strain and environmental conditions (103).

Resistance provided by EEPB

The induced systemic resistance, increase in the endophytic symbionts in the host plants and bioactive compound production are some of the major mechanisms of EEPB. They trigger systemic resistance in host plants, leading to the activation of defense-related enzymes such as chitinase and peroxidase, which help combat external infestation (104). The presence of entomopathogenic fungi like *B. bassiana* alters the endophytic bacterial community, increasing beneficial bacteria such as *Burkholderia* and *Pseudomonas*, which contribute to disease resistance (105). Endophytes produce siderophores and lytic enzymes that inhibit pathogen growth, enhancing plant resilience without relying on synthetic chemicals (104).

Mechanism of EEPB

The production of exopolysaccharides (EPS) that do not harm plants facilitates the attachment of bacterial cells to the plant surface, which is the first stage of bacterial endophyte colonization (106). *Gluconacetobacter diazotrophicus* Pal5 (Acetobacteraceae; Rhodospirillales), an endophytic bacterium, produces EPS, which helps it stick to and colonize rice root surfaces. It also lowers the number of free radicals in the plant (107). Apart from exopolysaccharides, bacterial structures such as flagella, fimbriae and cell surface polysaccharides are unlikely to be involved in the attachment process (108). The bacteria around the roots are attracted to the root exudates and enter through the lateral roots or other holes made by wounds or mechanical stress (109). Once inside the plant, EEPB multiplies in intercellular gaps, vascular tissues, or specialized plant organs, forming a peaceful cohabitation with the plant. Many EEPB strains produce insecticidal toxins that are essential for their pathogenicity, including proteins, peptides, or secondary metabolites with insecticidal characteristics (110). It is well known that cry proteins from *Bacillus thuringiensis* Berliner (Bt) (Bacillaceae; Bacillales) can kill a wide range of insect pests (111). When insects consume plant parts that contain EEPB, they consume bacterial toxins that mess up important body functions like digestion, ion balance and cell membrane integrity. This makes the insects paralyzed, unable to feed and eventually kills them (112). Following the insect's death, EEPB can proliferate within the cadaver, using its tissues as a nutrition source for growth and reproduction and may spread to other vulnerable insects nearby. This horizontal transmission mechanism promotes the spread of entomopathogenic bacteria throughout the insect population (113). Furthermore, some EEB strains can indirectly protect host plants by making them resistant to herbivorous insects and activating plant defense systems. This means that insects do less damage to plants and the plants become healthier (114) (Fig. 4).

Endophytic entomopathogenic actinomycetes

Endophytic entomopathogenic actinomycetes are a special type of bacteria from the order Actinomycetales. They live inside plant cells (as endophytes) and can kill insects (as entomopathogens) (115). These bacteria establish symbiotic relationships with plants, offering protection against a wide range of insect pests and contributing to plant health. Actinomycetes, particularly from the *Streptomyces* genus, are well known for their ability to produce bioactive compounds such as antibiotics, enzymes and insecticidal toxins (116). These compounds can help defend plants from both biotic stressors, such as herbivorous insects and abiotic stressors like drought and soil salinity.

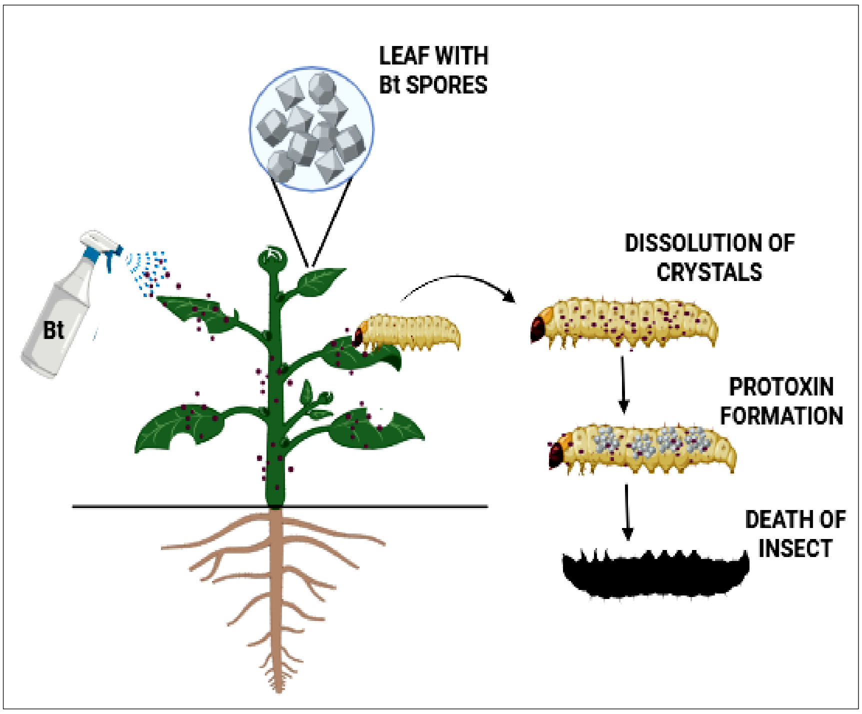

Fig. 4. Mechanism of endophytic entomopathogenic bacteria.

Endophytic actinomycetes can enter plants through natural openings such as stomata or via wounds and once inside, they colonize the plant's tissues without causing any harm. They produce enzymes like cellulases, chitinases and proteases, which aid in breaking down insect exoskeletons and cell walls, thus facilitating the infection and eventual death of the insect host (117). Additionally, actinomycetes produce secondary metabolites, including insecticidal toxins, that can limit insect reproduction, feeding and survival.

In addition to killing insects, endophytic actinomycetes help plants grow by making hormones that help plants grow, such as indole-3-acetic acid (IAA) and by dissolving nutrients so that plants can use them more easily. This dual role of enhancing plant health and controlling insect pests makes endophytic entomopathogenic actinomycetes a promising tool in sustainable agriculture and integrated pest management (118).

The resistance provided by EEPA

Herbivore Identity

The effectiveness of endophyte-mediated resistance varies with different herbivore species. In trials with various insects, preferences shifted based on the presence of endophytes, indicating that resistance is context-dependent (119).

Plant Fitness

Endophytes not only enhance resistance but also influence plant competitive abilities and community dynamics under herbivory pressure (120).

Artificial inoculation of endophytes

Despite the natural occurrence of these endophytes in plants, their introduction as an artificial inoculation triggers a plant's priming defense through the activation of induced systemic resistance (ISR) (121). Various processes, such as soil drenching with suspensions, spraying on leaves, injecting the inoculum into stems, dipping the seeds in the suspension and the seedling dip method, achieve artificial inoculations (122). These will colonize the plant throughout their lives or for some life stages based on nutrient availability (123).

Limitations of endophytic entomopathogens

Endophytes, like other entomopathogens, have some limitations. Environmental factors, such as atmospheric humidity and rainfall, are impacted by their biology and ecology. Geographic and climatic parameters stated in numerous studies influence the localization and biodiversity of endophytes (124). In addition, UV light has a critical role in the efficacy and survival of fungal spores in crop environments. Despite its benefits, several studies have shown that fungal endophytes harm parasitoids, carnivores, pollinators and wildlife (125). To minimize undesirable effects such as lower growth, fertility and the survival of natural enemies, it is important to choose specified strains and application methodologies (126).

The method used for artificial inoculation can also affect the results. Traditional cultural techniques fail to reveal the entire range of endophyte variety and taxonomy (127). It has been demonstrated that several endophytic symbioses do not give insect pest resistance, as only a few species interactions serve as mutualistic defenses (128). This could be because some plants accumulate non-structural carbohydrates in response to water stress. Plants growing in metal-contaminated soils accumulate higher amounts of heavy metals, which can provide a metal-stressed environment for endophytes (129). The complex interactions between endophytes, host plants, herbivores and natural enemies occur in ecosystems. It is important to study this relationship between target insect pests and their natural enemies (130). The regulatory procedures for using endophytic entomopathogens as biocontrol agents can be challenging and time-consuming. Adhering to regulatory criteria for safety, environmental impact and efficacy evaluation may pose challenges to their commercialization and widespread application.

Future outlook

Climate change is expected to alter the distribution and abundance of insect pests, creating a challenging situation for endophytes and forcing researchers to focus their efforts on drought-resistant endophytes. The creation of genetically engineered crops with intrinsic endophytic resistance may lead to the cultivation of insect pest-resistant crops.

The efficacy of endophytes depends on their type, capability to spread and health. Before using some endophytes in the field, it is important to thoroughly investigate their potential to become pathogens to plants, humans and animals. The study of microbial diversity in different environments has the potential to uncover previously unknown endophytic entomopathogens with unique characteristics and capacities. The study of these microbes may reveal new techniques for pest control and plant protection. We must prioritize the development of affordable products that demonstrate effectiveness in all environments. However, more study and development are required to fully realize the potential of these microbes and properly incorporate them into agricultural methods.

Conclusion

Endophytic entomopathogens are critical for long-term pest management in agriculture and beyond. Their ability to live within plant tissues while killing insect pests makes them a viable alternative to traditional chemical pesticides, decreasing environmental damage and supporting ecological balance. As the success of endophyte depends on its efficacy in spreading, the identification of potential strains is inevitable for its success. Also, developing novel applications for endophytic entomopathogens in agriculture, such as formulation methods and delivery systems, is critical. As we attempt to apply more sustainable and environmentally friendly pest management tactics, endophytic entomopathogens provide an alternate solution that protects crops.

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Authors' contributions

PSS and UM conceived the study. UM drafted the manuscript. PSS and MM corrected the manuscript. SJ, RR, TS and KI supervised and provided the inputs. NY, RY, MN and SS collected the literature pertaining to the review and drew figures. All authors have read and approved the final manuscript.

Compliance with ethical standards

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