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REVIEW

Entomopathogenic fungi in crops protection with an emphasis on bioactive metabolites and biological activities

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Abstract

Plant pathogens with their abundance are harmful and cause huge damage to different agricultural crops and economy of a country as well as lead towards the shortage of food for humans. For their management, the utilization of entomopathogenic fungi is an eco-friendly technique, sustainable to the environment, safe for humans and has promising effect over chemical-based pesticides. This process requires a biochemical mechanism, including the production of enzymes, toxins, and other metabolites that facilitate host infection and invasion. Essential enzymes such as chitinase, proteinase, and lipase play a direct role in breaking down the host cuticle, the primary barrier to EPF (Entomopathogenic Fungi) infection. Additionally, secondary metabolites such as destruxins in *Metarhizium*, beauvericin in *Beauveria*, hirsutellides in *Hirsutella*, isarolides in *Isaria*, cordyols in *Cordyceps*, and vertihemipterins in *Verticillium*, among others, act both directly and indirectly to disable the defense mechanisms of insect hosts, thereby accelerating the EPF infection process. The chemical composition of these secondary metabolites varies, ranging from simple non-peptide pigments such as oosporine to highly complex piperazine derivatives such as vertihemiptellides. The biocontrol efficacy of EPF is extensively studied, with numerous fungal strains commercially available on a large scale for managing arthropod pests. This review emphasizes the role of proteins and enzymes against crop pathogens, detailing their mode of action, and describing the metabolites from entomopathogenic fungi and their biological activities. In doing so, these findings contribute to establishing a symbiotic equilibrium between agricultural productivity and environmental conservation.

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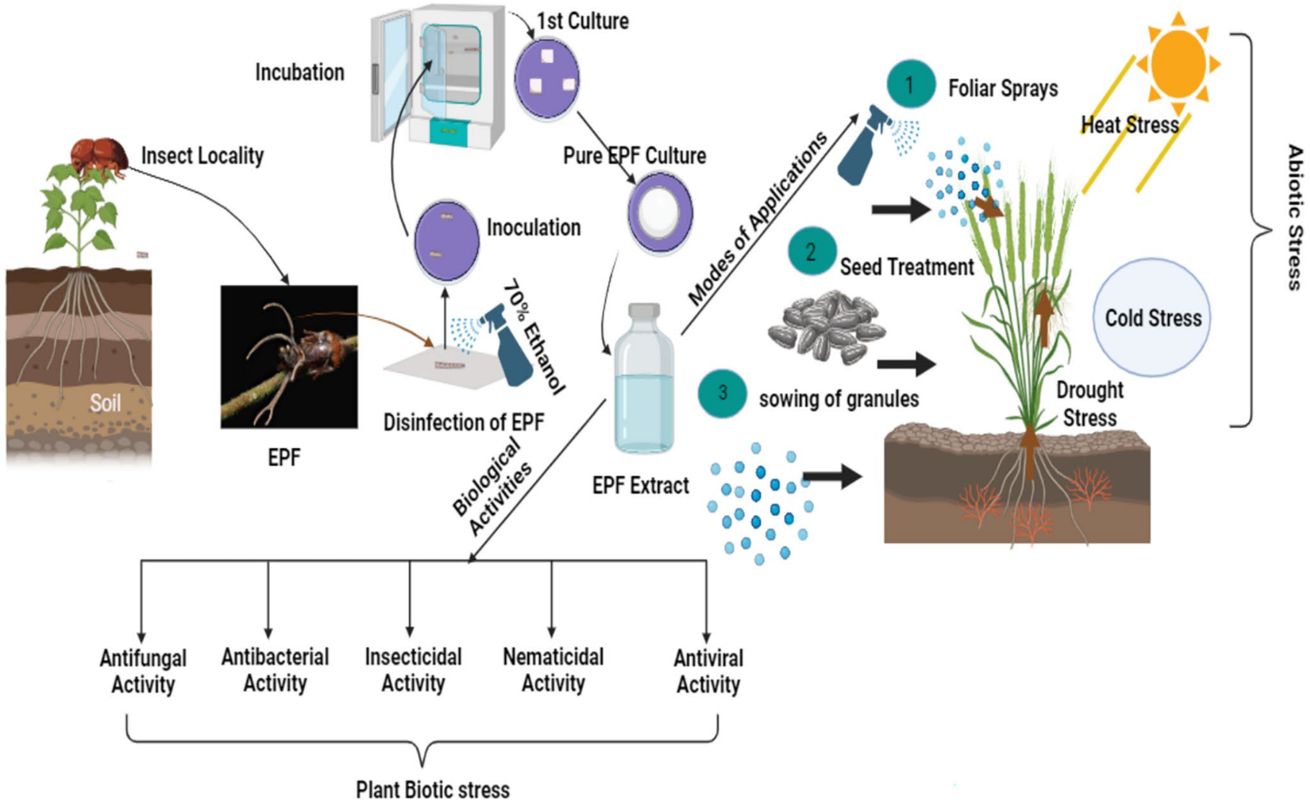
Graphical abstract



Keywords Mycopesticides · Phytopathogens · Food crops · Eco-friendly solutions · Nature-based solution · Commercial products

Introduction

Plant diseases are thought to be responsible for 14.1% of crop losses worldwide and cause $220 billion loss every year. Abiotic elements such as the environment and biotic agents such as oomycetes, fungi, viruses, bacteria, nematodes, and viroid can all contribute to crop loss (Shahrajabian et al. 2023). The crop production is affected by fungi (10–23%), bacteria (20–40%), and herbivores insects (18%) (Spescha et al. 2023).

Crop protection by using chemical-based management is considered a non-friendly and non-sustainable way to the environment (Ahsan et al. 2020). Fungi-based macromolecules represent an eco-friendly approach in biological control. (Sani et al. 2020). The application of EPF enhanced the yields and biodiversity in the ecosystem and utilized less amount of chemicals within the environment as compared to conventional pesticides (Fig. 1). The genera *Beauveria* and *Metarhizium* and their mode of action is like endophytes (Branine et al. 2019; Akram et al. 2023; Zhang et al. 2023a, b).

The objective of this review is to describe EPF for sustainable mode of crop protection. Application of EPF for sustainable crop protection increased the environmental and ecological beneficial aspects. EPF are insect-parasitizing fungi and have an excellent mechanism compared to other fungi that decompose organic matters, and reproduced through sexual, sexual, or combined spore production ways. The primary host for EPF attack is insect and possesses saprophytic features that enable the EPF to occur in soil and can be isolated from these sources (Bihal et al. 2023; from these sources and enhances their potential for utilization as effective biological agents (Islam et al. 2021). EPF produce spores that enter the insect's cuticle, where they start germination and then cause infection (Wang et al. 2019a, b). In Brazil, in approximately 10 million hectares agricultural land area, the application of 60% registered beneficial fungi-based pesticides have been used (Mascarin et al. 2019). EPF have a network of different species that have variations in morphology, phylogeny, and ecological niches exhibit a diverse array of fungal species with variations in morphology, phylogeny and ecological niches (Pattnaik and

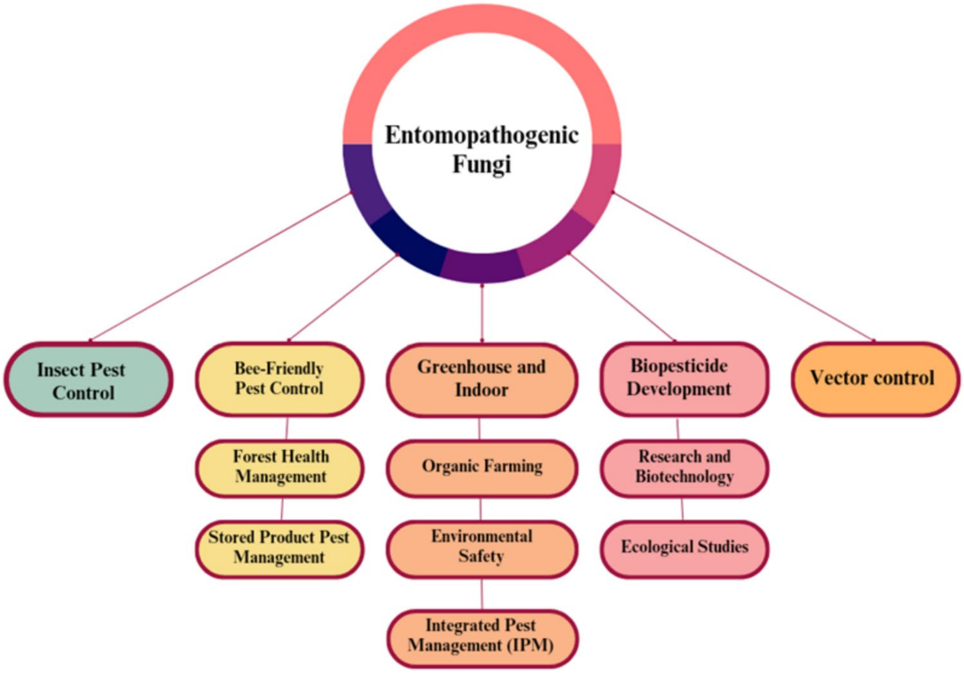


Fig. 1 Demonstrates the uses of entomopathogenic fungus. Applications for EPF in pest management include protection of stored grains, forestry, and agriculture. Different crops are affected by various pests such aphids, caterpillars, wood-boring insects, and disease vectors

Busi 2019), showcasing substantial phylogenetic diversity that is significant with respect to biocontrol agent for over 200 years (Bamisile et al. 2021; Wu et al. 2022). For the management of insect pests, EPF is utilized in classical, augmentation, and conservation biological control. Classical control introduces EPF to new environments lacking natural enemies; augmentation involves mass application for immediate pest reduction, while conservation adjusts farming practices to enhance EPF activity and diversity (Karthi et al. 2024). Today, the market offers a plethora of biopesticides, predominantly derived from hypocrealean ascomycetes like *Beauveria*, *Metarhizium*, *Akanthomyces*, and *Cordyceps* fungi. These biopesticides effectively target various arthropod pests spanning locusts, grasshoppers, soil-dwelling insects, piercing-sucking insects, mites, stored-grain pests, forestry pests, and invasive, medical, and veterinary pests (Quesada-Moraga et al. 2020).

It is estimated that around 750 EPF species are reported, and these species belong to the phyla *Chytridiomycota*, *Blastocladiomycota, Zoopagomycota, Basidiomycota*, and *Ascomycota*. The phylum *Ascomycota* harbours a significant number of economically relevant species (Landinez-Torres et al. 2019). The key genera that have been extensively studied in biological control and sustainable agriculture are *Metarhizium* (Family: *Clavicipitaceae*) and *Beauveria* (Family: *Cordycipitaceae*). Entomopathogenic fungi (EPF) belong to the phylum *Ascomycota* and are classified within the order *Hypocreales*.

There is similarity among all EPF fungi with respect to mode of action. Insect pest management begins when vulnerable host affected by many infective propagules, and favorable conditions make fungus to grow (Sani et al. 2020). Insect cuticle is the direct entry point of EPF, consists of various physical and enzymatic mode of actions. Infection starts when fungal conidia fully enter into host cuticle, start germination directly or by formation of aspersorium (Boni et al. 2021). This process involves physical and enzymatic mechanisms. The EPF mechanism of action begins when fungal conidia settle onto the insect's cuticle, and then these germinate and gain entry into the cuticle directly or by forming a structure known as an appressorium (Batool et al. 2020). The fungal hyphae produce within the insects hypodermis and then proliferating within the blood cells and finally death occurs (Fig. 2). These fungi can cause the death of the insect, but they also cause pathologies that regulate their population without directly causing death (Liu et al. 2022). Toxins from fungi such as *B. bassiana*, such as nonribosomal peptides and polyketides, help regulate environmental stress, aiding fungal invasion and acting as virulence factors (Park et al. 2023). These substances can potentially induce insect mortality even before the fungal spores spread and form within the parasitized tissue (Altinok et al. 2019). In many cases, the demise of insects caused by fungal propagules primarily results from toxic effects rather than direct mycosis (Pedrini 2018).

Role of enzymes and proteins in pest management as a complement to EPF

The larvicidal activity has been evaluated using *Beauveria bassiana* (TV and OZ1 strains) and *Metarhizium anisopliae* (CS1 strain) based proteins against *Plodia interpunctella*

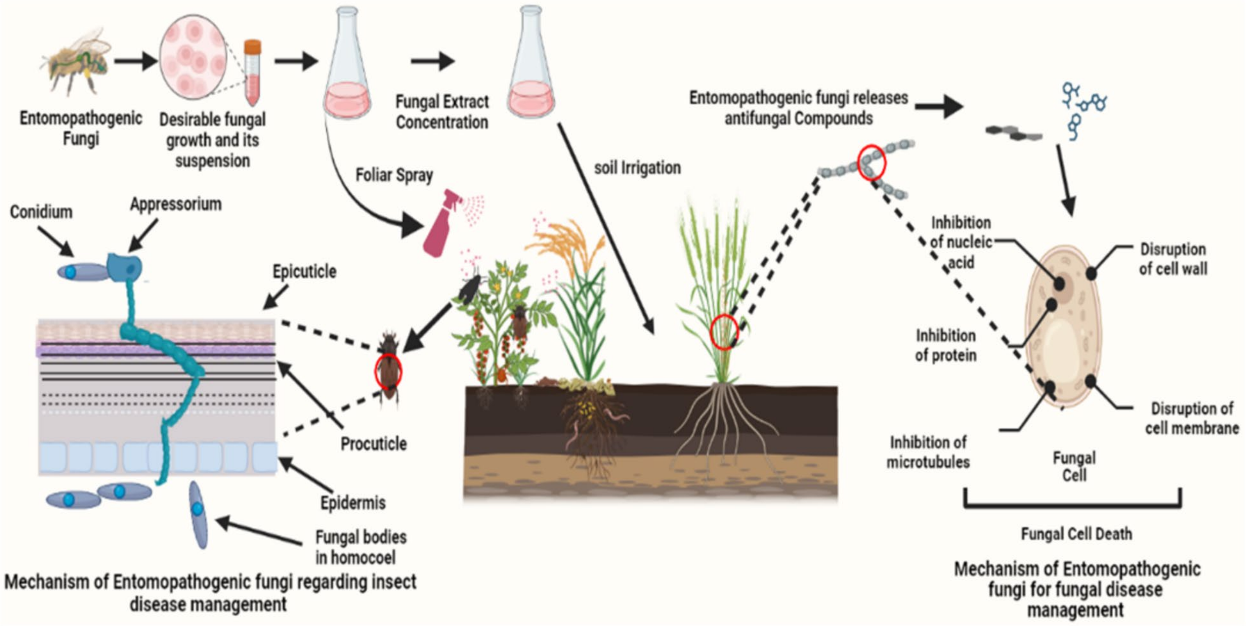


Fig. 2 The mode of action of entomopathogenic fungi. In the first step EPF is isolated from its respective host (insect) then, after growth has occurred, fungal extract with desirable concentrations are applied either as foliar spray or soil irrigation and sometimes is inoculated into the stem to cope with the target phytopathogens

larvae. The TV strain, exhibiting the highest mortality rate (41.7%), displayed increased specific activity in exochitinase, protease, and lipase enzymes. These findings imply a positive association between protease and lipase activities and fungal virulence, underscoring their potential significance in controlling *P. interpunctella* larvae (Golzan et al. 2023).

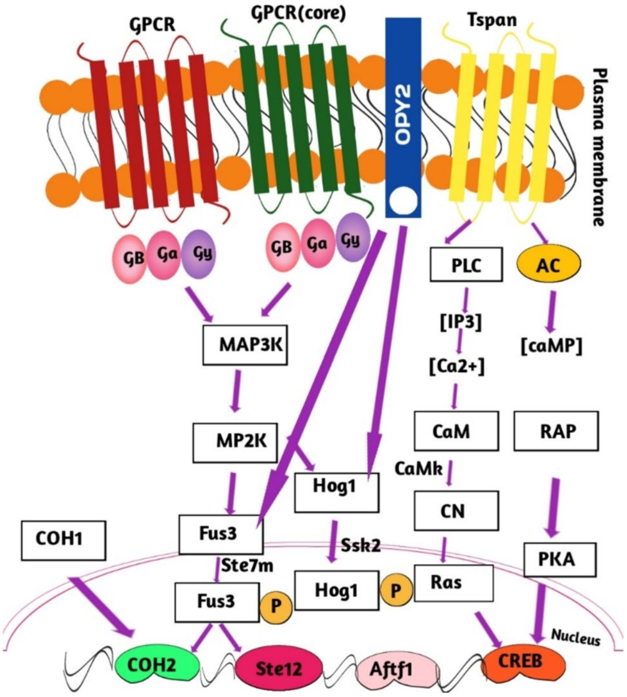


Fig. 3 Genetic pathways of fungal sensing and infection of insects

Several studies have examined the insecticidal potential of extracellular proteins from entomopathogenic fungi (Fig. 3). Farooq and Freed (2018) investigated larvicidal activity using crude proteins from *M. anisopliae, B. bassiana,* and *I. fumosorosea* against *Musca domestica* adults. The crude proteins derived from entomopathogenic fungi induced notable mortality (52.0–91.0%) in *Musca domestica*. Concentrations of 8 and 10 mg/mL resulted in 100.0% mortality within 2.77 to 3.77 days, with *B. bassiana* (Bb-01) at 10 mg/mL causing 100.0% mortality within 96 h. Ayudya et al. (2019) studied *B. bassiana* strain to investigate larvicidal activity against *Spodoptera litura* larvae and the culture filtrates of *Beauveria bassiana* at pH 6 demonstrated high toxicity (92% mortality) against *Spodoptera litura larvae*. Quesada-Moraga et al. (2006) found that proteic macromolecules in *B. bassiana* supernatant significantly contributed to larvae mortality. Ortiz-Urquiza et al. (2009) conducted a study affirming the biocontrol potential of proteins from entomopathogenic fungi. They assessed soluble proteins from the supernatant of *M. anisopliae* (EAMa 01/58-Su) using liquid chromatography on *Ceratitis capitata* (Wiedemann) flies, noting chronic insecticidal effects with long-term oral application) (Rosa et al. 2018). The same proteins, when presented to *Drosophila melanogaster* (Meigen) adults, resulted in a 70%

mortality rate after continuous exposure for 3 days (Zhou et al. 2016).

The protein extracted from *Lecanicillium lecanii* exhibited a dose-dependent reduction in the survival and fecundity of *Myzus persicae* on tomato plants. The application of protein extract upregulates the genes linked with salicylic acid, and genes associated with jasmonic acid were upregulate moderately. It suggests that EPF-based protein can manage aphids. (Hanan et al. 2020). Different EPF strains have different optimal conditions for enzyme production. Therefore, optimization of EPF culture is mandatory to produce extracellular enzymes (Shah et al. 2005). Kim et al. (2010) reported that enzymes (chitinases and proteases) produced from *B. bassiana* (SFB-205) exhibited aphicidal activity against the cotton aphid *Aphis gossypii* that caused degradation of insect's cuticles. Chitinases from supernatant of *Metarhizium anisopliae* (M408) was tested against *Plutella xylostella* larvae that reduced the pupation and enhanced lethality (Wu et al. 2010). Alves et al. (2020) reported that that a purified cocktail from *B. bassiana* (IBCB 66) containing exocellulase, endocellulase, β1, 3-glucanase, and chitinase led to increased mortality rates, reaching 100% for first instar larvae and 40% for developed larvae after 24 h that demonstrating the potential of enzymatic cocktails for effective pest control.

Different G-protein-coupled receptors (GPCRs) recognize insects, with a core one sensing many species. MAPK pathway directs appressoria formation, PKA pathway matures them. Membrane proteins Tspan and OPY2 help in sensing and penetration. COH1 and COH2 control cuticle to hemocoel transition. Abbreviations: AC (adenylyl cyclase), CaMK (calcium/calmodulin-regulated kinase), CN (calcineurin), CREB (cAMP response element-binding protein), IP3 (inositol 1,4,5-triphosphate), MAPK (mitogen-activated protein kinase), PKA (protein kinase A), PLC (phosphatidylinositol-specific phospholipase C), RAP (Ras superfamily guanine-nucleotide-binding protein), Tspan (tetraspanin) (Hong et al. 2023).

The emerging role of RNA in pest management as a complement to EPF

RNA interference (RNAi), a mechanism of post-transcriptional gene silencing, holds promise as a pest control strategy (Zhu and Palli 2020). The delivery of double-stranded RNA (dsRNA) has been assessed in aphids using different techniques such as injection, feeding, topical application, and integration into transgenic plants (Hou et al. 2019). The complementary effects were explored using application of RNAi along with other pest management techniques (Ding et al. 2020). EPF (*B. bassiana*) produced a high mortality rate in aphids when the silencing of immune-associated genes in aphids was described (Ye et al. 2021). Aphid mortality was also increased when RNA interference with *B. bassiana* (Bb07) offering a promising way for minimizing the need for chemical pesticides (Zhang et al. 2023a, b).

Contributions of entomopathogenic fungi spores in pest control

Previous studies revealed the importance of EPF spores in pest management and have a central position regarding the efficiency of EPF as biocontrol agents (Sharma et al. 2023). Therefore, long time sustained spores have started infection and regulate the insect's papulation because of viability guarantees (Mei et al. 2021). These spores produced appressorium after attachment with insect cuticle (Mannino et al. 2019). The amalgamation of adhesion and subsequent penetration into the insect host amplifies the potency of entomopathogenic fungi in governing pest populations (Bava et al. 2022). In conjunction with their infectivity, entomopathogenic fungal spores showcase a comprehensive host range, a trait of paramount importance in crop pathogen control. This versatility assumes significance by enabling these fungi to effectively target and regulate various insect pests (Selvaraj and Thangavel 2021).

The production and extensive distribution of significant spore numbers by EPF enhances their efficacy in disease control (Santos et al. 2022). EPF could produce large numbers of spores, which makes it easier for them to spread over the surroundings (Rajula et al. 2020). The abundance and wide dispersal of spores increases the contact with and infecting desired pest targets, hence maximizing the effectiveness of pest control measures (Cafarchia et al. 2022).

EPF derived bioactive metabolites

Secondary metabolites have remarkable potential to penetrate host cells, also facilitate EPF to invade or inhibit the immune system of pathogens (Table 1). Different forms of toxins such polyketides and nonribosomal peptides help EPF to attack pathogens (Wang et al. 2021). EPF produce a vast variety of secondary metabolites that can either be released or kept in developmental structures, such as conidia (Fig. 4). Some secondary metabolites, including pigments, polyols, and mycosporines, are connected to fungal pathogenicity and/or tolerance to a variety of environmental stressors, such as temperature and sun radiation extremes (Carollo et al. 2010). According to previous study, metabolites (propanoic acid, ethyl ester, acetic acid, propyl ester, isopentyl acetate, acetic acid, 2-methylpropyl ester, behenic alcohol, 1-hexadecene, 1-octadecene, 1-hexacosanol, n-hexadecanoic acid, 1-tetradecanol, 1-dodecene, tetrydamine, and octadecanoic

Table 1 Examples of bioactive metabolites from entomopathogenic fungi

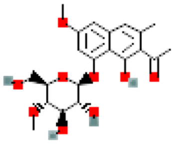
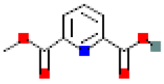
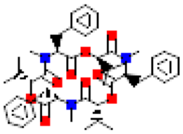
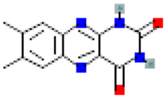
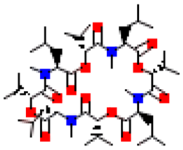
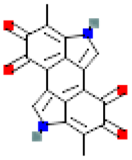
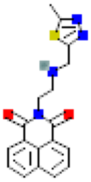
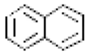
Fungal Species	Bioactive Compounds	Chemical structure	Characterization Technique	References
Aschersonia confluens	4′-O-methyltorachrysone 8-O-Glucoside	 PubChem CID: 156,582,430	HPLC	Sadorn et al. (2020)
Beauveria asiatica	6-(methoxycarbonyl) Picolinic acid	 PubChem CID: 4,019,172	Mosher's method and ECD calculation	Kornsakulkarn et al. (2021)
Beauveria bassiana	Beauvericin	 PubChem CID: 3,007,984	GC–MS	Al-Khoury et al. (2022)
	Lumichrome	 PubChem CID: 5,326,566	GC–MS	Andrioli et al. (2017)
	Bassianolide	 PubChem CID: 89,254,632	HPLC	Xu et al. (2009)
	Melanin	 PubChem CID: 6,325,610	LC–MS	Fuguet and Vey (2004)
	Chitinase	 PubChem CID: 86,223,063	LCMS-QTOF	Bhadani et al. (2021)
	Xylanase and Endoglucanase	 PubChem CID: 9394	GC–MS	Amobonye et al. (2021)
	Sphingomyelins Phenolic/glycolipids, Phosphatidylcholines	 PubChem CID: 9,939,941	HPLC	Tsoupras et al. (2022)
	Naphthalene	 PubChem CID: 931	SPME–CGC–MS	Crespo et al. (2008)

Table 1 (continued)

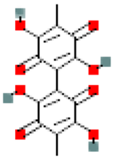
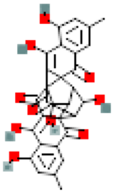
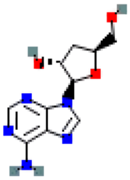
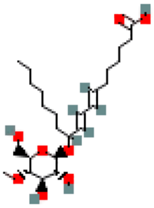
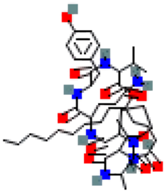
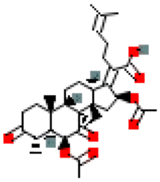
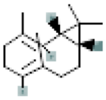
Fungal Species	Bioactive Compounds	Chemical structure	Characterization Technique	References
Beauveria caledonica	Oosporein	 PubChem CID: 135,426,831	RP-HPLC	Mc Namara et al. (2019)
Chrysoporthe sp.	Rugulosin	 PubChem CID: 62,769	HPLC	Nirma et al. (2015)
Cordyceps militaris	Cordycepin	 PubChem CID: 6303	HPLC	Woolley et al. (2020)
Cordyceps sp.	Cordyglycoside	 PubChem CID: 156,582,401	NMR,HRESIMS, HPLC,X-ray crystallography	Fan et al. (2023)
Lecanicillium sp.	Verlamelin	 PubChem CID: 139,588,823	HPLC	Ishidoh et al. (2014)
Metarhizium anisopliae	1,2-dihydrohelvolic acid	 PubChem CID: 23,844,015	HPLC	Lee et al. (2008)
	Bicyclogermacrene	 PubChem CID: 13,894,537	GC–MS	Bitencourt et al. (2022)
Metarhizium brunneum	3-octanone	 PubChem CID: 246,728	GC–MS	Hummadi et al. (2021)

Table 1 (continued)

Fungal Species	Bioactive Compounds	Chemical structure	Characterization Technique	References
Ophiocordyceps sinensis	Meso-erythritol	 PubChem CID: 222,285	GC–MS	Zhang et al. (2020a, b)

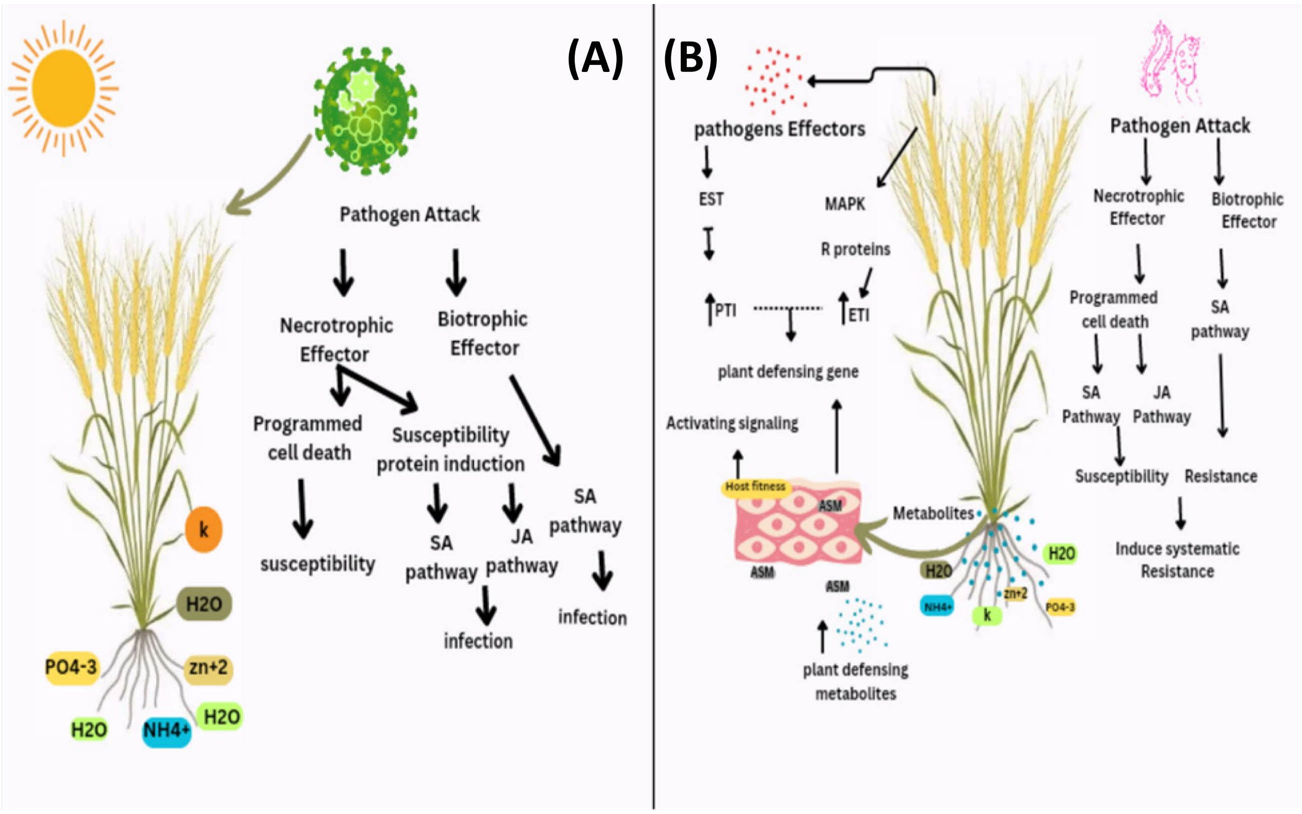


Fig. 4 Showing plant responses against phytopathogens in (**A**), absence and (**B**), presence of EPF based metabolites

acid) from EPF *Penicillium sp*. were tested for larvicidal activity against *Spodoptera litura* and *Culex quinquefasciatus*. The mortality rate after 48 h was checked and 90% mortality occurred at 282.783 mg/mL against *Spodoptera litura* and 475.049 mg/mL concentration against *Culex quinquefasciatus* (Arunthirumeni et al. 2023). Similarly, Qasim et al. (2020) used EPF based on classes of mycotoxins alkaloids, peptides, and polyketides to manage *Diaphorina citri*. After two days of application of mycotoxin (bassianolide) caused more than 70% and 80% mortality of *D. citri* nymphs and adults. Bioactive metabolities have ability to mitigate resistance development within pest populations, disrupting the physiological processes in insect's pests, and leading towards their death (Mantzoukas and Eliopoulos 2020). Bioactive metabolities such as destruxins, beauvericin, and metarhizins have been identified as remarkable potent entities having insecticidal potentials. Destruxins affect the insect immune system, inducing immune suppression and subsequent fatality, conversely, beauvericin manifests dual insecticidal and antifungal activities, interfering with essential cellular mechanisms in insects while also perturbing fungal cell membranes (Paschapur et al. 2021). Metarhizins enact their impact by targeting the insect cuticle, facilitating host penetration and subsequent infection. Beyond their insecticidal properties, these bioactive compounds can also demonstrate antimicrobial effects, hindering the growth of secondary pathogens that might exploit the insect postmortem (Paschapur et al. 2021).

In the absence of metabolites, severe damage of plants occurs due to increased susceptibility to necrotrophic and biotrophic pathogens. Underdeveloped root systems result in poor nutrient uptake, leading to plant death. In the presence of EPF metabolites, enhanced plant growth due to improved nutrient acquisition occurs. Increased tolerance to various stresses (drought, salt, herbivory) through complex signal communications and increased photosynthetic rates also changes in root exudates, altering the soil microbial community and suppressing pathogens occurs. Reduced incidence of soilborne pathogens through priming of plant defense mechanisms, mediated by phytohormones such as JA and ET, leading to enhanced Induced Systemic Resistance (ISR).

Biological activities

Controlling phytopathogens is becoming a major concern world-wide, mainly due to usage of different pesticides, and phytopathogens are gaining resistance to pesticides. Considering this, more research has been done about a sustainable method of controlling plant diseases and increase crop protection (Keshmirshekan et al. 2024). Thus far, several EPF have been extensively investigated for their biological activities (Table 2). Among these, EPF such as *Beauveria*, *Metarhizium*, *Akanthomyces,* and *Cordyceps* fungi are the most studied in the context of their antimicrobial activity (Zhang et al. 2024).

Phytopathogen control

Plant pathogenic bacteria (PPB) represent a significant group of phytopathogens that inflict substantial harm on a wide range of both cultivated and wild plants worldwide (Abdelsattar et al. 2023). To mitigate the damage caused by PPB, various control strategies are frequently employed, including the cultivation of resistant or tolerant plant varieties and the use of chemical treatments (Kumawat et al. 2023). Plant viruses constitute a major group of pathogens for crops. Despite their simple structural makeup, they exhibit intricate mutations and possess a broad host spectrum, posing a significant peril to agriculture and leading to substantial economic losses (Spechenkova et al. 2023). Plant-parasitic nematodes (PPNs), constituting one of the three prevalent crop infestations, are parasitic worms that infest plants. With over 4100 identified PPN species (Khan et al. 2023), four among them stand out as particularly perilous. Root-knot nematodes (RKN) belonging to the *Meloidogyne* genus exhibit a wide-ranging host preference and predominantly inflict damage on vegetable crops (Chen et al. 2023). The presence of nematode diseases exerts a substantial adverse influence on both agricultural and horticultural production, resulting in annual losses amounting to a staggering $173 billion (Fan et al. 2023). *Beauveria alba* displayed significant antibacterial activity against *Bacillus subtilis* in vitro (Fabelico 2015). *B. bassiana* exhibited antiviral activity against Squash Leaf Curl Virus (SLCV) in vivo, reducing transmission by *Bemisia tabaci*. Whiteflies from EPF-treated squash plants showed only 33.4% transmission effectiveness, compared to 100% in untreated plants (Abd El-Wahab et al. 2023). Karabörklü et al. (2022) reported that *B. bassiana* and *M. anisopliae* have excellent nematicidal activity against *Meloidogyne incognita* in both tomato and cucumber, resulting in gall index reductions to 3.2, 2.0, and 2.2 for *B. bassiana, M. anisopliae*, and *P. lilacinum*, respectively. The highest decrease in gall formation (75.2%) occurred with *M. anisopliae* treatment in tomato, while in cucumber, the highest control index (71.7%) was achieved with *M. anisopliae* as mentioned in Table 3.

Diverse entomopathogenic fungal species have demonstrated their multifaceted roles within natural ecosystems, serving as endophytes, antagonists against plant pathogens, and stimulators of plant growth (Ownley et al. 2010). Moreover, the well-known entomopathogenic fungus *Metarhizium roberstsii* establishes beneficial interactions by forming endophytic associations with plant roots, imparting advantageous effects to the plant (Sasan and Bidochka 2012). Recent studies have unveiled the potential of entomopathogenic fungi to exert antimicrobial effects against various microorganisms (Lee et al. 2005; Goettel et al. 2008; Lozano-Tovar et al. 2013). Dual action against insect pests and plant pathogens were studied in *Beauveria spp*., *Metarhizium spp*., *Lecanicillium spp*. and *Clonostachys rosea* with good results (Kim et al. 2007). Saidi et al. (2023) described the antifungal activity of *Akanthomyces muscarius* against the tested phytopathogenic fungi resulted in inhibition rates ranging from 39.61% to 52.94%. Ajvad et al. (2020) reported the antifungal activity of entomopathogenic fungi *Metarhizium anisopliae* against *Lycoriella auripilla* and concluded that *M. anisopliae* at 10^8 spores/mL improved compost-to-mushroom conversion. Chairin and Petcharat (2017) reported that the crude extract from fruit peel of *Metarhizium guizhouense* exhibited antifungal activity, inhibiting the mycelial growth of *Botrytis sp*. (34.9 ± 3.1%) and *Fusarium sp*. (29.3 ± 5.0%). Lozano-Tovar et al. (2013) demonstrated the antifungal activity of *Metarhizium brunneum* and *B. bassiana* against olive pathogens, with inhibition rates of 42–62% for *Phytophthora spp*. and 40–57% for *V. dahliae*. Boguś et al. (2010) also reported the antifungal activity of entomopathogenic fungi and concluded that applied concentrations (ranging from 0.1% to 0.0001% w/v), of the entomopathogenic fungi inhibited the growth of the parasitic fungus *Conidiobolus coronatus*.

Yang et al. (2023) reported that *Beauveria bassiana* and *Isaria fumosorosea* exhibited larvicidal activity against *Rhynchophorus ferrugineus*. Five fungal strains, comprising four strains of *Beauveria bassiana* (JEF-484, 158, 462, 507) and one of *Isaria fumosorosea* (JEF-014), caused 100% mortality in last stage *R. ferrugineus* larvae within

Table 2 Insecticidal activity of selected EPF

Fungi	Targeted Pathogen	Mode of study	Effect	References
Beauveria bassiana (Bals.-Criv.) Vuill	*Duponchelia fovealis*	In vitro	*B. bassiana* strains (4485) showed a reduction to 8.31% and 32% and *B. bassiana* strains (4488) showed 6.74% and 33% reduction in eggs and pupae, respectively	Da Rocha et al. (2024)
	Plagiodera versicolora	In vitro	Mortality increased	Tu et al. (2023)
	Aedes albopictus and *Culex pipiens*	In vitro	Mortality rates were 93% or 89% in adult mosquitoes	Lee et al. (2023)
	Spodoptera frugiperda	In vitro	Reduced enzyme activities in larvae at 60 h	Zhang et al. (2023a, b)
	Ips typographus	In vitro and In vivo	Mortality (83–93%) and mycosis rates (75–93%)	Kreutz et al. (2022)
	Conogethes punctiferalis	In vitro	Decreases in hemocyte counts in larvae over time	Li et al. (2022)
	Myzus persicae	In vitro	*B. bassiana* (KTU-24) stood out as the most promising strain to control *Myzus persicae*	Eski et al. (2022)
	Sarcoptes scabiei	In vitro	The highest hatching inhibition (28.75%) was achieved with a commercial strain of *B. bassiana*	Al-Khoury et al. (2021)
	Helicoverpa armigera	In vitro	Suppressed the host insect's immune response	Liu et al. (2021)
	Bemisia tabaci	In vitro	Highest mortality and lowest LC_{50}	Bhadani et al. (2021)
	Thrips palmi	In vivo	Reduced thrip population	Li et al. (2021)
	Raoiella indica	In vitro	Reduced mite survival	Freitas et al. (2021)
	Dysdercus cingulatus Fab. and Phenacoccus solenopsis	In vitro	174 kDa entomotoxic protein (BBF2) controlled pest	Tomson et al. (2021)
	Diaphorina citri	In vitro	High conidial production and increased virulence against *D. citri*	Awan et al. (2021)
	Hypothenemus hampei	In vitro and In vivo	Coffee berry borer controlled	Bayman et al. (2021)
	Bactericera cockerelli	In vitro	*B. bassiana* effectively controlled	Liu e al. (2020)
	Bombyx mori	In vitro	Exhibited enzyme activity and contributed to the virulence of the fungus against silkworms	Gu et al. (2020)
	Drosophila	In vitro	Inhibits insect immunity, attenuates fungal virulence, and enhances bacterial pathogenicity	Yuan et al. (2020)
	Phereoeca uterella	In vitro	Increased enzyme activities	Alves et al. (2020)
	Chironomus riparius	In vitro	Showed sublethal effects on larvae	Bordalo et al. (2020)
	Carya illinoinensis	In vitro	Reduced populations of *M. caryaefoliae* and *M. caryella* in a leaf-disc assay, compared to control leaves	Ramakuwela et al. (2020)
Beauveria bassiana and *Cordyceps javanica (Frieder. and Bally)*	*Duponchelia fovealis*	In Vitro	Strain Bea111 and Isa340 exhibited differential efficacy against *D. fovealis* larvae and pupae	Baja et al. (2020)

Table 2 (continued)

Fungi	Targeted Pathogen	Mode of study	Effect	References
Beauveria bassiana and Metarhizium anisopliae (Metschn.) Sorokin	*Culex pipiens*	In vitro	Mortality increased	Salem et al. (2023)
	Kuschelorhynchus macadamiae	In vitro	Both strains caused 97.5% and 92.5% mortality in adult weevils	Khun et al. (2020)
	Cosmopolites sordidus	In vitro	Weevil mortality achieved 4.63% to 53.3%	Membang et al. (2021)
	Ceratitis capitata	In vivo	*BbLCB289* in sandy soil had higher mortality, while *MaLCB255* showed reduced percolation; residual effect lasted 27–34 days	Gava et al. (2021)
	Monochamus alternatus	In vivo	Showed 67% mortality	Kim et al. (2020)
Beauveria pseudobassiana (Vuill.), and Akanthomyces muscarius (Petch)	*Lucilia sericata*	In vitro	*B. bassiana, A. muscarius,* and *B. pseudobassiana* exhibited median lethal times (LT50) of 5.3, 5.9, and 6.2 days, respectively	Muniz et al. (2020)
Purpureocillium lilacinum (Thom), and *Isaria javanica (Frieder. and Bally)*	*Duponchelia fovealis*	In vitro	Increased mortality of *D. fovealis*, along with enhanced chitinase and lipase activities	Da Costa Stuart et al. (2020)
Clonostachys rosea (Link: Fries)	*Diaphorina citri*	In vitro	Mortality rate of 46.67%	Yang et al. (2021a, b)
Cordyceps fumosorosea (Wize) Kepler)	*Myzus persicae*	In vitro	Mortality of adults after injection and ingestion was 81.85% ± 13.45% and 85.45% ± 11.88%,	Diao et al. (2022)
	Asian citrus psyllid	In vitro	Reduced ACP resistance	Qasim et al. (2021)
	Diaphorina citri	In vitro	Showed high mortality against *Diaphorina citri* nymphs and adults	Qasim et al. (2020)
Cordyceps nidus (T. Sanjuan and Chir)	*Pleurotus ostreatus*	In vitro	Supplementing *C. nidus* extracts enhances laccase activity of *P. ostreatus* fourfold compared to the control	Durán-Aranguren et al. (2020)
Isaria javanica (Friedrichs and Bally)	*Sogatella furcifera*	In vitro and In vivo	Effectively controlled *S. furcifera*	Zhou et al. (2023)
Lecanicillium lecanii (Zare and Gams)	*Myzus persicae*	In vivo	*L. lecanii* protein reduced aphid survival and fecundity	Hanan et al. (2020)
Metarhizium anisopliae (Metschn.) Sorokin)	*Spodoptera litura, Aphis craccivora*	In vitro	Showed potency against S. *litura* and *A. craccivora* in the lab	Kumar et al. (2023)
	Blattella germanica	In vitro	*Metarhizium anisopliae* + boric acid-controlled cockroaches	(Yang et al. (2021a, b)
	Rhipicephalus microplus	In vitro	Improved the insecticidal activity	Coutinho-Rodrigues et al. (2021)
	Schistocerca gregaria	In vitro	Exhibited additive and synergistic effects, influencing behavior, immune response, and biochemical parameters	Abdellaoui, et al. (2020)
	Psoroptes ovi	In vitro and In vivo	Showed 83.33% mortality in vitro at day 9 and achieved 100% efficacy in vivo within 3 days	Gu et al. (2020)
Metarhizium brunneum, Metarhizium pemphigi (Driver and R. J. Milner)	*Ixodes ricinus*	In vitro	Encapsulation of blastospores resulted in the highest concentration with *M. brunneum* Cb16II. Encapsulated *M. pemphigi* X1c demonstrated the highest nymph mortality of *I. ricinus*	Lorenz et al. (2020)

Table 2 (continued)

Fungi	Targeted Pathogen	Mode of study	Effect	References
Metarhizium guizhouense (Sorokīn)	*Cossus chloratus*	In vitro	Effectively controlled longkong bark eating caterpillars, achieving 0.0–18.0% larval survival	Thaochan et al. (2020)
Metarhizium lepidiote (Driver and Milner)	*Chaetanaphothrips signipennis*	In vitro and In vivo	Reduced thrips damage and improved marketability of treated banana bunches	McGuire and Northfield (2021)
Metarhizium pinghaense (Chen and Guo)	cotton aphids	In vitro	100% mortality at 3rd day	Heo et al. (2023)
Pandora sp. (Remaud and Henn)	*Psyllid*	In vitro	Effectively controlling vectors	Görg et al. (2021)

5–10 days post inoculation. The combination of JEF-484 and JEF-158 offers a promising microbial control approach against *R. ferrugineus* at different life stages in palm trees under fields. The ethyl acetate extract derived from EPF *Penicillium sp*. exhibited larvicidal activity against *Spodoptera litura* and *Culex quinquefasciatus* larvae with LC_{50} values of 72.205 mg/mL and 94.701 mg/mL, and LC_{90} values of 282.783 mg/mL and 475.049 mg/mL respectively.

Rocha et al. (2022) reported the larvicidal activity of *B. bassiana, Metarhizium humberi, M. anisopliae, Akanthomyces saksenae*, and *Simplicillium lamellicola* against *Aedes aegypti*. For this purpose, 21 strains (7 *Beauveria bassiana*, 7 *Metarhizium humberi*, 3 M. *anisopliae*, 2 *Cordyceps sp*., and one each of *Akanthomyces saksenae* and *Simplicillium lamellicola*) of EPF were used against *Aedes aegypti*. *M. anisopliae* and *M. humberi* were highly effective.

Michereff-Filho et al. (2022) described that *B. bassiana* strains showed larvicidal activity against *Neoseiulus* species, with mortality exceeding 70% under in vitro study. *Neoseiulus* mites, particularly *N. barkeri*, showed susceptibility to fungi, while low humidity hindered their feeding and reproduction. Combining *B. bassiana* and *Neoseiulus* compromised mite survival and offspring. Conidia of entomopathogenic were fungi applied against *Aedes aegypti* larvae with concentrations 10^5 10^6, 10^7, and 10^9 propagules mL^{-1} water suspension. Larvae survival rates were observed for 7 days, with median survival time (S50) determined. *Beauveria bassiana* and *Metarhizium anisopliae* reduced larval survival time to two days at 10^8 propagules mL^{-1} and three days at 10^8 conidia mL^{-1}, respectively (Bitencourt et al. 2021).

Metarhizium anisopliae was applied with concentrations of 1×10^6 conidia/mL against larvae of *Aedes albopictus* and *Aedes aegypti*. After 7 days, high larvicidal activity was observed by killing both larvae (Zuharah et al. 2021). Koodalingam Dayanidhi, (2021) reported the larvicidal activity of *B. bassiana* and *Metarhizium anisopliae* that increased mortality of *Culex quinquefasciatus* larvae by 60% and 50.59%, respectively. Wang et al. (2021) checked the larvicidal activity of *Metarhizium rileyi* against *Spodoptera litura* larvae and led to the identification of *M. rileyi*'s high-pressure appressorium, the vital function of the Mrpmk1 gene, blastospore formation within larvae, activation of host immunity, and stage-specific metabolic adjustments facilitating infection. Gamma irradiation (0.2 to 1 kGy) increased the enzymatic activity of *Metarhizium anisopliae*, optimizing activity at 0.4 kGy. TiNPs were synthesized from both irradiated and unirradiated fungi. The combination of irradiated *M. anisopliae* with TiNPs showed strong larvicidal activity against *Galleria mellonella* larvae, indicating a potential strategy against insect resistance (Yosri et al. 2018).

Kirubakaran et al. (2018) reported that *Metarhizium pingshaense* caused > 90% mortality in *Cnaphalocrocis*

Table 3 Antibacterial, antiviral, and nematicidal activity of EPF

Fungi	Targeted Pathogen	Activity	Mode of study	Effect	References
Beauveria alba	*Bacillus subtilis*	Antibacterial	In vitro	Displayed significantly high antibacterial activity against *Bacillus subtilis*	(Fabelico 2015)
Beauveria bassiana *Metarhizium anisopliae*	*Bacillus* and *Staphylococcus*	Antibacterial	In vitro	The entomopathogenic fungi (81%) produced antibacterial compounds, and a substantial portion (64%) produced compounds effective against *Staphylococcus*	(Lee et al. 2005)
Beauveria bassiana	Squash Leaf Curl Virus (SLCV)	Antiviral	In vivo	Reduced transmission of SLCV by *Bemisia tabaci*; whiteflies acquired from EPF-treated squash plants showed lower transmission effectiveness (33.4%) compared to untreated plants (100%)	(Abd El-Wahab et al. 2023)
	Barley yellow dwarf virus (BYDV)	Antiviral	In vitro	Direct killing of aphids and beneficial effect in delaying PLRV infection in plants	(Fingu-Mabola et al. 2021)
	Meloidogyne incognita	Nematicidal	In vivo	Improved tomato leaf count and root weights	(Karabörklü et al. 2022)
Isaria fumosorosea	Tomato yellow leaf curl virus (TYLCV)	Antiviral	In vivo	Significant reduction in TYLCV transmission by *Bemisia tabaci* pest	(Zhang et al., (2016)
Isaria javanica	Tomato yellow leaf curl virus (TYLCV)	Antiviral	In vivo	Decreased TYLCV levels in whiteflies; reduced disease index in tomato plants attacked by viruliferous whiteflies	(Sun et al. 2021)
Metarhizium brunneum	*Xanthomonas euvesicatoria*	Antibacterial	In vivo	Three days after inoculation, there was a 40% reduction in bacterial colony-forming units (CFU) when compared to plants that were not sprayed with EPF	(Gupta et al. 2022)
	Meloidogyne hapla	Nematicidal	In vivo	Increased nematode numbers on tomato plants with higher conidia doses	(Khoja et al. 2021)
Metarhizium majus	Novel dsRNA virus MmPV1	Antiviral	In vivo	Potential antiviral activity in the host	(Wang et al. 2023a, b)
Metarhizium rileyi	*Helicoverpa armigera*	Antibacterial	In vitro	Plasma antibacterial activity and AMP expression increased as a result of *M. rileyi* infection	(Wang et al. 2023a, b)
Phomopsis amygdali	*Pseudomonas aeruginosa*	Antibacterial	In vitro	MIC values 26 µg/mL to 58 µg/mL	(Ma et al. 2016)

medinalis larvae when subjected to the concentration of 1×10^8 conidia/mL. Similarly, *M. pingshaense* also exhibited *lower* LC_{50} (7.94×10^5 conidia/mL) against pupae.

Metarhizium brunneum reduced western corn rootworm population without affecting plant yield (Rauch et al. 2017). *B. bassiana* strains (MS-8) showed high pathogenicity on *L. serricorne* eggs (Saeed et al. 2017). Liao et al. (2023) reported that *Metarhizium robertsii* promoted wheat plant growth by producing 1-aminocyclopropane-1-carboxylate deaminase (ACCD), leading to a 66.2% increase in root length and a 56.6% increase in plant biomass. It also enhanced shoot growth by 42.3%. Zitlalpopoca-Hernandez described that in tomato seedlings, combining entomopathogenic fungi (*Metarhizium spp.* and *Beauveria bassiana*) with arbuscular mycorrhizal fungus showed promise for boosting plant growth and controlling the foliar phytopathogen *Botrytis cinerea*. According to González-Pérez et al. (2022) entomopathogenic fungi *Metarhizium anisopliae* strains act as both biocontrol agents for insects and promote plant growth in *Arabidopsis*, tomato, and maize, offering promising applications in field production. Zitlalpopoca- Gonzalez-Guzman et al. (2021) reported that *B. bassiana* and *M. brunneum*, as entomopathogenic fungi, positively enhanced durum wheat growth, increasing aerial dry matter and root parameters during early and mid-crop growth stages in field experiments. Mantzoukas and Grammatikopoulos (2020) reported that entomopathogenic fungi (*Beauveria bassiana, Metarhizium robertsii*, and *Isaria fumosorosea*) significantly enhanced sorghum plant growth, while reducing *Sesamia nonagrioides* larval infestation (20–30%) and tunneling length (19–43%). Canassa et al. (2019) reported that seed treatment with entomopathogenic fungi *M. robertsii* and *B. bassiana* enhanced bean plant (*Phaseolus vulgaris*) growth and suppressed spider mite (*Tetranychus urticae*) populations. Russo et al. (2019) reported that entomopathogenic fungi, acting as endophytes, effectively colonize soybean plants, promoting growth parameters such as root, stem and leaves using different methods such as leaf aspersion, seed immersion and root immersion. The presence of entomopathogenic fungi was not observed in the non-inoculated controls. All inoculation techniques effectively introduced *B. bassiana* strain into soybean plants. However, the seed immersion technique failed to introduce *M. anisopliae* and *M. roberstii.s*

Espinoza et al. (2019) described that *B. bassiana* had minimal effects on chive plant growth, but significantly increased total alkaloid content in the leaves by approximately 52–91%. Krell et al. (2018) reported that *M. brunneum* enhanced plant productivity and vitality, particularly under nutrient-poor conditions in potato plants. EPF can be applied as seed treatment. For this purpose, cultivated cotton (*Gossypium hirsutum*) was subjected to *Beauveria bassiana and Purpureocillium lilacinum* as seed treatments. There was a significant increase in plant dry biomass and the number of flowers (Sword 2015).

Application methods for commercial EPF formulations

EPF can be applied to plants using various methods. These methods include leaf spraying, stem injection, seed treatment, and soil irrigation (Fig. 5) (Quesada-Moraga et al. 2006). A highly effective approach for controlling insect pests on the leaf surface (phylloplane region) is the application of EPF spore suspensions through spraying (Vega et al. 2009). EPF targets insects that feed on the leaves, roots, stems, seeds, and rhizomes (Resquín-Romero et al. 2016). Studies have demonstrated that foliar spraying of EPF strains like *Metarhizium brunneum* and *B. bassiana* can lead to temporary endophytic colonization of plants such as alfalfa, tomato, sweet pepper, and melons (Jaber and Araj 2018).

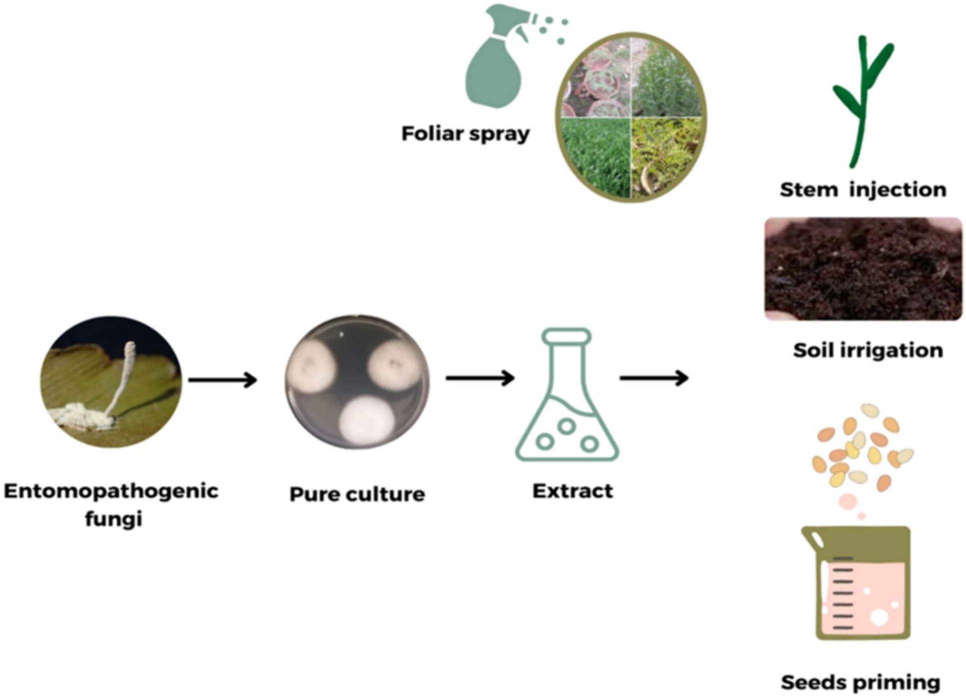


Fig. 5 Showing different methods to apply EPF for crop protection. EPF is initially isolated from sources such as insects or soil, then pure culture is obtained which can be used as extract for application. It can be applied as foliar spray directly on crops or injected into stem. Moreover, soil irrigation and seed priming also proved useful

Artificial inoculation of EPF in tomato plants has shown promising results in effectively controlling *Tuta absoluta* (Leaf miner) (Klieber and Reineke 2016). EPF formulations on the market generally have three to six months of shelf life. These formulations typically contain a concentration of fungal spores ranging from 10^9 to 10^{10} spores per gram, the appropriate dosage for application may vary depending on the specific formulation, the severity of the insect infestation, the type of insect targeted, and the prevailing environmental conditions. Recent research has concentrated on developing novel formulations and treatments to enhance the efficacy of entomopathogenic fungi as biopesticides with improved biopesticidal formulation with a shelf life of at least one year at temperatures from 0 to 38 °C. This formulation involves biphasic solid-state fermentation, followed by mixing the conidia with various additives and compressing them into tablets (Wakil et al. 2022). Additionally, microsclerotial granular formulations of entomopathogenic fungi have shown effectiveness against pests such as the annual bluegrass weevil, with combinations of microsclerotia and imidacloprid being particularly potent (Koppenhöfer et al. 2022). Moreover, biopolymer-based formulations have emerged as promising methods for delivering entomopathogenic fungi, enhancing their stability and effectiveness in pest control (Friuli et al. 2023).

Commercialization and future prospects

The use of EPF such as *Beauveria, Metarhizium, Lecanicillium*, and *Isaria* is upsurging in recent years to manage crop insect pests. EPF are considered better than synthetic insecticides as they are safe for humans, sustainable to the environment, and target specific. Many of these EPF are pathogenic to economically important insect pests and thus can control them. They are cheaper in long run, show lesser residual effects, and can overcome the problem of resistance (Sharma et al. 2023). In recent years, entomopathogenic fungi have emerged as a compelling substitute for chemical pesticides, offering environmentally sustainable solutions for pest control. Anticipated growth in the market for these fungi is fueled by rising demand for eco-friendly pest management options and heightened awareness of the adverse effects of chemical pesticides on human health and the environment (Bamisile et al. 2021). Approximately 200 commercial products of EPF are available globally, such as liquid formulation, wettable powder, and suspensible granules (Fig. 6A&B). These available formulations under different trade names can be used for several crops and pests at the recommended dosage to obtain optimum results (Jaronski 2023).

Challenges and future directions

Despite the evident potential of entomopathogenic microbes as biological control agents (BCAs), several obstacles need to be addressed to enable their effective and widespread application. These challenges can be broadly grouped into four key areas: bioassay procedures, production, formulation, and application strategies. Bioassay procedures are pivotal for evaluating the effectiveness of entomopathogenic microbes against targeted pests (Spescha et al. 2023). Current protocols are often intricate, labor-intensive, and lacking in standardization, which makes it challenging to make meaningful comparisons. Furthermore, results obtained in controlled laboratory conditions may not always accurately predict the performance of BCAs in natural field settings due to variations in environmental factors like temperature, humidity, and interactions with other living and non-living factors (Shukla et al. 2023). Consequently, refining and standardizing bioassay protocols to ensure consistent and replicable outcomes represent a crucial challenge. Scaling up the production of entomopathogenic microbes also presents significant difficulties. In the future, EPF products will last longer on the shelf, without causing allergies in humans and animals. There is a need to study how EPF interacts with insects and their surroundings to create better versions of insecticides (Siddiqui et al. 2022).

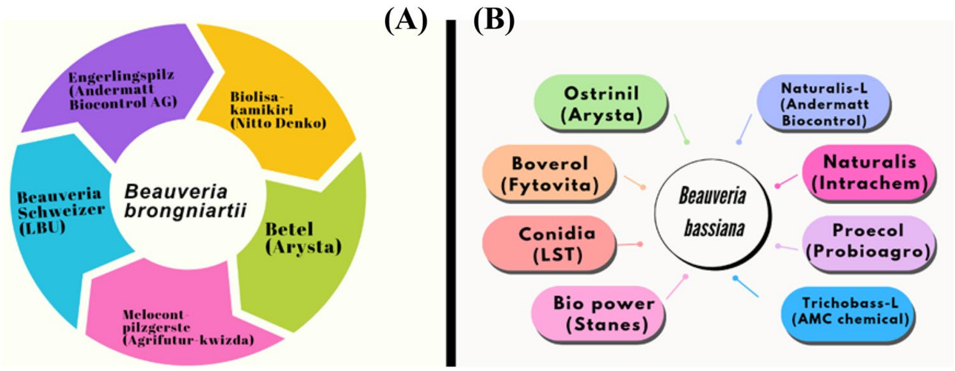


Fig. 6 A diagram of commercial products of two species of *Beauveria (B. brongniartii and B. bassiana).* EPF based different commercially available products **A** *B. brongniartii* and **B** *B. bassiana.* The name inside the brackets such stones, probioagro, arista are name of company but name out of brackets such ostrinil, betel, proceol etc. are different products

Conclusions

The utilization of EPF is a sustainable and eco-friendly strategy to control different phytopathogens such as fungi, bacteria, viruses, nematodes as well as insects' pests. Also, it has a significant role in improving crop growth and development. The biological activity and presence of bioactive metabolites of EPF indicates the nature-based solution for crop protection.

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Declarations

Competing interest The authors declare no competing interests.

Ethical approval The current study does not involve the use of animals.

Consent to participate Not applicable.

Consent to publication Not applicable.

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