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Entry

Entomopathogenic Fungi: Interactions and Applications

Spiridon Mantzoukas [1,*], Foteini Kitsiou [1,2], Dimitrios Natsiopoulos [2] and Panagiotis A. Eliopoulos [2,*]

[1] Department of Agriculture, University of Ioannina, 45100 Ioannina, Greece; kitsioufot@gmail.com
[2] Lab of Plant Health Management, Department of Agrotechnology, University of Thessaly, 45100 Larissa, Greece; dimnatsiopoulos@uth.gr
* Correspondence: sdmantzoukas1979@gmail.com (S.M.); eliopoulos@uth.gr (P.A.E.)

Definition: Entomopathogenic fungi are a special group of soil-dwelling microorganisms that infects and kills insects and other arthropods through cuticle penetration. They are currently used as biocontrol agents against insect plant pests and play a vital role in their management. Regardless that entomopathogenic fungi are currently on the agriculture market, their full potential has not yet been utterly explored. Up to date substantial research has covered the topic revealing numerous uses in pest management but also on their ability as endophytes, assisting the plant host on growth and pathogen resistance. This article addresses the literature on entomopathogenic fungi through the years, noting their mode of action, advantages, potential applications, and prospects.

Keywords: entomopathogenic fungi; insects; plants; endophytes; pest management; biopesticides

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1. Introduction

Interestingly, the idea of implementing microorganisms for pest control is not a modern application. The first entomopathogenic fungus was discovered and described by Agostino Bassi (1773–1856) in 1835, causing white muscardine disease in insects and was later named *Beauveria bassiana* (Balsamo) Vuillemin (Hypocreales, Cordycipitaceae) [1]. Some years later, Elias Metschnikoff (1845–1916) discovered the green muscardine, a fungal disease attacking insects, induced by *Metarhizium anisopliae* Metschnikoff Sorokin (Hypocreales, Clavicipitaceae) [2]. In the late 19th century, the combination of these discoveries and the groundbreaking knowledge obtained by the father of microbiology Louis Pasteur (1822–1895), led to assays experimenting on fungi as potential microbial control agents [3]. Later, the entrance of chemical insecticides in the market held back the establishment of fungi in pest management. Also, the development of *Bacillus thuringiensis* (Baciliales, Bacillaceae) Berliner against insects, played an important role on the biological protection research. While it assisted acknowledging the potential use of exploiting microorganisms as pest control agents, it may have detained the advance of biological protection studies, as the scientific community focused on bacterial entomopathogens [4]. Nonetheless, to present, even though entomopathogenic fungi (EPF) have been commercialized in the last years, their broad potential applications have not yet been fully discovered.

The advances in molecular biology and DNA sequencing allowed the collection and classification of organisms and along with the symbiosis theory, provided a better comprehension on the interactions between plants, fungi, and insects. During the last years, because of the concerning environmental implications of the extensive use of synthetic substances, the interests of research was rotated on alternatives of chemical pest management and so the EPF came back on the scene. Up to date, numerous studies and reviews have documented the multifaceted roles of EPF as endophytes that antagonize plant diseases [5–10], promote plant growth [11–14], and benefit the rhizosphere through colonization [15–17]. The use of EPF so far has been limited to utilization as inundate biopesticides against insects [18], although the newly emerging attributes open the way to complementary roles as dual agents against both arthropods and plant diseases, as vertically transmitted endophytes, and as biofertilizers [12,19,20]. Some fungal endophytes establish themselves in plants naturally while others are introduced therein artificially [21] (Figure 1).

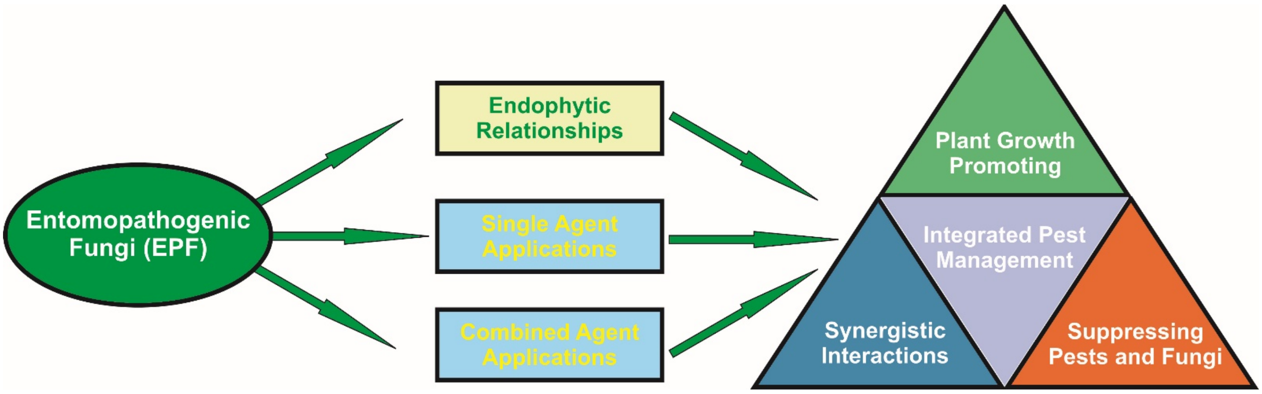

Figure 1. Applications of entomopathogenic fungi and the main effects.

Many EPF isolates have been recorded and tested throughout the years, some of them with thriving results. The ubiquitous soil-borne fungus, *B. bassiana* is recorded to infect more than 700 insect species. [22] Other examples of artificially inoculated endophytes are *Metarhizium brunneum* Petch (Hypocreales, Clavicipitaceae) in broad bean by [12], *M. anisopliae* in broad bean by Akello and Sikora (2012) [23] and cassava by Greenfield et al. (2016) [24]. *Beauveria brognartii* Sakkaro Petch was also tested in broad bean by Jaber and Enkerli (2017) [12]. Lastly, *Metarhizium robertsii* Metschnikoff Sorokin (Hypocreales, Clavicipitaceae) and *Isaria fumosorosea* Wie Brown and Smith (Hypocreales, Cordycipitaceae) was examined in sweet sorghum by Mantzoukas et al., 2015 [25].

Studies have provided data suggesting that fungal endophytes may act antagonistically against plant diseases, such as *Fusarium oxysporum* Snyder & Hansen (Hypocreales, Nectriaceae), *Botrytis cinerea* Pers. (Helotiales, Sclerotiniaceae), *Alternaria solani* Sorauer (Pleosporales, Pleosporaceae) [26] *Fusarium solani* f. sp. *phaseoli* Sacc. (Hypocreales, Nectriaceae) [7] and others. Fungal endophytes effects include mycoparasitism, antagonistic race for nutrition, and antibiosis. The effect on insects occurring upon infection includes physiological and behavioral changes, such as feeding deterrence, inertia, changes in oviposition etc., as possible consequences of the secondary metabolites secreted by fungi themselves [27].

2. Interactions and Applications

2.1. Plant—EPF Interactions

As mentioned above, apart from their role as regulators of pests by causing epizootics, EPF have been found to carry complementary multitrophic attributes: as endophytes, colonizers of internal plant tissues [21,28], as colonizers of the rhizosphere [15–17], as promoters of plant growth and plant fitness [12]. They have also been reported to act as enhancers of tolerance to environmental challenges, like drought tolerance, and promoting overall growth as biofertilizers [21]. Another important benefit is the ability to play an antagonistic role against plant pathogens [8,9], by taking up vital nutrient space [29] and inducing the plant's systemic resistance [8] as in the case of cotton and *B. bassiana* against *Xanthomonas axonopodis* pv. *malvacearum* [5]. *B. bassiana* is found in a wide range of plant hosts (Table 1), while the list of hosts for other fungal endophytes keeps growing.

Table 1. List of host plants in which *B. bassiana* has been reported as an endophyte which include insecticide and fungicide activity.

Host Plants	Insecticide Activity	Fungicide Activity	References
Brassica napus L. (Brassicaceae)			[30]
Brassica oleracea L. (Brassicaceae)	*Aphis fabae*		[31,32]
Capsicum spp. (Solanaceae)	*Myzus persicae*		[31,33]
Carpinus caroliniana Walter (Betulaceae)			[34]
Cicer arietinum L. (Fabaceae)			[31]
Citrus spp. (Rutaceae)			[31]
Coffea arabica L. (Rubiaceae)			[35]
Corchorus olitorius L. (Malvaceae)			[36]
Corchorus capsularis L. (Malvaceae)	*Apion corchori*		[37]
Cucurbita maxima L. (Cucurbitaceae)	*Aphis gossipii*		[32]
Cucurbita pepo L. (Cucurbitaceae)			[8]
Cynara scolymus L. (Asteraceae)			[38]
Datura stramonium L. (Solanaceae)			[39]
Glycine max (L.) Merr. (Fabaceae)			[40]
Gossypium hirsutum L. (Malvaceae)	*Aphis gossipii*	*Pythium myriotylum*	[32,39,41]
Helianthus annuus L. (Asteraceae)			[31]
Manihot esculenta Crantz (Euphorbiaceae)			[24]
Musa spp. (Musaceae)	*Cosmopolites sordidus*		[31,42]
Nicotiana tabacum L. (Solanaceae);			[39]
Papaver somniferum L. (Papaveraceae).	*Iraella luteipes*		[43]
Phaseolus vulgaris L. (Fabaceae)	*Helicoverpa armigera*		[30–32]
Phoenix dactylifera L. (Arecaceae)			[44]
Pinus monticola Dougl. ex. D. Don (Pinaceae)			[45]
Pinus radiata D. Don (Pinaceae)			[46]
Punica granatum L. (Lythraceae)			[31]
Saccharum officinarum L. (Poaceae)			[47]
Solanum lycopersicum L. (Solanaceae)	*Aphis gossipii*, *Tuta absoluta*, *Helicoverpa zea* *Helicoverpa armigera*	*X. axonopodis* pv. *Malvacearum*. *Rizoctonia solani*, *Pythium myriotylum*	[5,32,40,48–50]
Solanum melongena L. (Solanaceae)			[31]
Solanum tuberosum L. (Solanaceae)	*Phthorinaea operculla* *Trialeurodes vaporariorum*		[39,51]
Sorghum bicolor L. (Poaceae)	*Sesamia nonagrioides*, *Chilo partelus*		[25,52]
Theobroma cacoa L. (Malvaceae)			[53]
Theobroma gileri Coatrec (Malvaceae)			[54]
Triticum aestivum L. (Poaceae)	*Aphis gossipii*		[32]
Vicia faba L. (Fabaceae)	*Helicoverpa armigera*		[30,55]
Vigna radiata (L.) Wilczek (Fabaceae)			[31]
Vitis vinifera L. (Vitaceae)		*Plasmopara viticola*	[56]
Xanthium strumarium L. (Asteraceae)			[39]
Zea mays L. (Gramineae)	*A. gossipii*, *Sesamia calamistis*, *Ostrinia nubilalis*		[31,32,57,58]

Failure of some fungal isolates to colonize their plant hosts has also been recorded [23,33,59] provoked by an interplay of factors, including plant genetics, fungal-related specifics, chemistry of the leaf surface, and antagonism with other natural endophytes [35,60]. The impact of fungal entomopathogens on plant herbivores has been explored, with encouraging results, highlighting the possibility of recruiting them in this role to reduce plant damage. Studies have described the successful plant colonization by *B. bassiana* capable of limiting damage induced by the lepidopteran cob- and stemborers *Ostrinia nubilalis* and *Sesamia calamistis* Hampson (Lepidoptera: Noctuidae) in maize [57,58]; the South American tomato pinworm, *Tuta absoluta* (Lepidoptera: Gelechiidae) [49], the tomato fruitworm *Helicoverpa zea* Boddie

(Lepidoptera: Noctuidae) in tomato [50]; the tom ato fruit worm, *Helicoverpa armigera* Hübner (Lepidoptera: Noctuidae) [51]; the banana weevil, *Cosmopolites sordidus* Germar (Coleoptera: Curculionidae) in banana [42,61]; the poppy stem gall wasp, *Iraella luteipes* Thompson (Hymenoptera: Cynipidae) in opium poppy [43]; and the stem weevil *Apion corchori* Marshall (Coleoptera: Curculionidae) in white jute [37]. Thus, foliar application coupled with endophytic colonization could serve the dual role of enhancing plant protection as well as overcoming the hurdles of exposure of conidia to adverse environmental conditions that topical application entails [9].

The application of EPF through inoculation of some plant parts rather by means of inundation which is contingent upon exposing spores to unfavorable environmental conditions, could minimize the risks of abiotic factors [62]. In fact, Basimile has reported the lasting protective effect of *B. bassiana* as an endophyte of citrus, 2 months post inoculation of seedlings [63]. Using different artificial inoculation methods, EPF can be successfully established as endophytes in the entirety of the plant and endow it with systemic resistance against herbivores, even when only an individual part or organ of the plant is initially treated [25].

Occurrence of EPF in the soil depends on soil type, plant species and cultivation practices. The soil generally protects EPF from UV light, high temperatures and other biotic and abiotic factors that may hinder their distribution [64,65].

The fact that EPF are microorganisms existing extensively in natural habitats indicates that they do not pose a threat to the environment. Although fungal entomopathogens require more time to cause death in comparison with chemical pesticides, they have low mammalian toxicity [66–68], they are environmentally friendly, and these are attributes that render them appealing within the new framework of IPM. When the prerequisites of containment of plant damage and pest mortality are met, while plants remain unaffected, fungal pesticides are considered as effective [25,69,70]. Entomopathogenic fungi persist in the environment as they can develop on cadavers and thus recycle inoculum. Residual persistence is a desirable characteristic of EPF in contrast to the perseverance of chemical residues in the environment [71].

Fungus induced insect infections are part of nature's mechanics, and epizootics function to manage pest populations. In fact, 60% of insect diseases are attributed to fungal infections. However, in crops, fungal infections of pests do not occur naturally at an efficient mortality speed or in a large scale to prevent crop damage. Virulent fungi such as *B. bassiana*, *M. anisopliae* and *I. fumosorosea* occupy the largest share in the mycopesticide market. However, to this day, these biological control products remain underutilized. This is partly linked to the practical hurdles of their application such as the high cost of formulations, the short shelf life of the inoculum, the high humidity needed on their application, and the long period required until mortality occurs. Within the framework of IPM, biological control of pests has become a more than necessary control approach as chemicals overburdens the environment and products with harmful residues, and consumers are conscious of the safety of their products [72].

2.2. Single Agent Applications—Mode of Action

Insects are infected as fungal spores attach to the insect cuticle. The fungus germinates as it receives cues from the cuticle surface. A variety of cuticle degrading enzymes are produced by the germ tubes. The combined function of enzymes and germ tube mechanical pressure breach the cuticle and as soon as fungal hyphae reach the hemolymph, blastospores are produced and dispersed in the insect organism. Death results from nutrient depletion, fungus related toxicity, disruption of circulatory system and organ disruption. Upon death, fungal hyphae emerge and may remain in tall tissues of the insect body and sporulate once again when environmental conditions allow. The new aerial conidia are then dispersed into the environment by air or water [73].

Upon infection, insects activate a series of immune responses that are distinguished between humoral and cellular in terms of their mode of action. The first consists of the activation of phagocytosis, encapsulation, or nodulation of pathogens, while the latter stimulates the production of antimicrobial peptides (AMPs) or triggers melanization and coagulation in the host. Immune signaling pathways are activated upon recognition of molecular pathogen traits. *B. bassiana* activates the cellular and humolar responses in insect hosts and induces death. In a study examining differences in the immune response between *Monochamus alternatus* Hope (Coleoptera: Cerambycidae) exposed to the symbiont *Sporothrix* sp. and the entomopathogen *B. bassiana*, it was discovered that exposure to the ectotrophic symbiont, triggered an acuter immune response but *M. alternatus* individuals maintained a normal state of body and the immune genes were inactivated at 48 h. *M. alternatus* not only tolerated infection with the ectotroph, but also benefited in terms of its growth. The opposite occurred with *B. bassiana* whereby at first the immune signaling pathways remained unstimulated but entered an acute alarm at 48 h, resulting in the death of the host after some days. At 72 h post infection, the already dead individuals became melanized [74].

Adhesion of conidia to insect cuticle, penetration, infection of hemolymph and eventual death constitute successive steps which presuppose a series of metabolic and chemical processes. The mortality rate depends on the fungal strain, host-pathogen interaction, fungal specificity for the host and other factors. Infection process by a fungus also manifests a range of symptoms from changes in behavior and growth parameters of the insect to its eventual death and morphological markers of infection [59]. Variation in insect mortality caused by EPF should not be attributed solely to differences in applied fungal concentrations. Other factors, such as insect behavior, density of population, vulnerability to biological control agents, insect age, nutrition, and others play important role to the efficiency of EPF and should be considered [70,75–78].

The degree of fungal virulence depends on several factors that stretch from the premise of the infection of the host, the length of the incubation period, the rate at which the fungus spreads and other environmental factors that are favorable or detrimental to the development of epizootics [79,80]. The occurrence and virulence of epizootics depend on a series of factors which extend beyond the favorability of the habitat and the abiotic conditions (i.e., soil pH, UV light, high temperatures, inappropriate relative humidity), to biotic factors which include the fungal species and strain, host's vulnerability to it, the spore density etc. [81]. A plethora of studies testify to the fact that high spore density increases mortality of insect pests because the production of infective propagules is increased [82].

Moreover, a set of morphological, physiological, and behavioral parameters determine insect susceptibility to an EPF. To these, poor insect diet, pesticide induced weakness and stress are conducive to insect vulnerability. Abiotic environmental factors also vary in their impact on the EPF virulence which correlates with the fungal species and strain and its plateau of temperature and humidity tolerance. Species from warmer climates tolerate higher temperatures than those coming from cooler climates [22]. *B. bassiana*, for instance, is an environmental fit and ubiquitous species that can thrive in a wide range of temperatures, from 8 to 35 °C [83], while other fungal isolates tolerate between 25 and 30 °C [84].

2.3. Combined Agent's Applications

Another potential implementation of EPF could be on post-harvest pest management, to circumvent the use of chemical and residual fumigants [28,75,85]. According to Batta [86], control of stored-grain insects in many countries is irregularly practiced decreasing their damage in storage facilities during warm months by chemical control with various types of contact insecticides such as, Bioresmethrin, Deltamethrin and Pirimiphos-methyl [87,88] and fumigants such as Phosphine [89–91].

Stored products that have been treated with EPF showed less damage and underwent lower mean fresh loss in comparison with untreated products. An additional factor of fungal virulence in stored product protection is the grain or product type. This abiotic parameter has been understudied in laboratory testing. However, the type of the grain is a factor that should be accounted for when selecting a virulent fungal strain, to reinforce control of harmful post-harvest insects [92]. Potential for this use has been reported by some investigators for the entomopathogenic fungus *B. bassiana* against the following stored-grain insects: rice weevil (*Sitophilus oryzae* L. (Coleoptera: Curculionidae)), corn weevil (*Sitophilus zeamais* L. (Coleoptera: Curculionidae)), granary weevil (*Sitophilus granarius* L. (Coleoptera: Curculionidae)), lesser grain borer (*Rhyzopertha dominica* Fabricius (Coleoptera: Bostrichidae)), red and confused flour beetles (*Tribolium castaneum* Herbst (Coleoptera: Tenebrionidae) and *T. confusum* Jacquelin du Val (Coleoptera: Tenebrionidae)), *Oryzaephilus surinamensis*, and *Prostephanus truncatus* (Horn) (Coleoptera: Bostrichidae) [93–104].

Moreover, the potential synergism between *B. bassiana* and diatomaceous earth dust types has been successfully examined against coleopteran storage insects. Promising results were shown on *S. oryzae*, *R. dominica*, [102] *S. granarius* [103], and *T. castaneum* [104]. The mean percentage mortality of adults exposed to the formulation of fungi with the earth dusts was considerably higher than those of the control or those which had been exposed to either earth dusts or unformulated fungi alone.

The combined use of *Chromolaena odorata* leaf powder and *B. bassiana* showed a dose-dependent insecticidal effect against *S. oryzae* L. and *T. castaneum* [105].

Compatibility between *B. bassiana* at different concentrations with plant leaf extracts from Neem, Chinaberry, Lantana leaves and Mexican sunflower against the *Spodoptera litura* (Lepidoptera: Noctuidae) has been investigated by Afandhi et al. (2020) [106]. The combinatorial effect of the fungus with either plant extract was measured in terms of *B. bassiana* colony growth, conidia viability and density, and mortality of insect larvae. Results showed that the fungal colony growth decreased in all combinations while in terms of insect mortality, the most suitable combination was of the fungus with 0.25% Chinaberry whereby *B. bassiana* exhibited the best conidial viability and density as well as enhanced insect mortality (44%).

Depieri et al. (2005) [107] tested the compatibility of *B. bassiana* with emulsible neem oil (*Azadirachta indica* A. Juss) and with neem seeds and leaves aqueous extracts and found that the latter did not impact the viability of the fungal spores although conidia growth and production were reduced. The emulsible neem oil, by contrast, especially at higher concentrations, affected all conidia parameters to a high degree, thus leading to the conclusion of non-compatibility with the fungus.

Mantzoukas et al., 2019 [108] investigated the potential interaction between two potent entomopathogenic fungi, *B. bassiana* and *I. fumosorosea* against two important coleopteran stored product pests, *S. oryzae* and *S. granarius*. The combined application of the two fungi was additive against *S. granarius* in all nine combinations of the three different conidial suspensions, while it was effective in seven combinations and competitive in two combinations against *S. oryzae*. Moreover, another study showed that the synergistic action of *B. bassiana* and *Trichoderma asperellum* on corn (*Zea mays* L.) against the Asian corn borer *Ostrinia furnacalis* Guenne (Lepidoptera: Crambidae) proved to suppress the immune response of *O. furnacalis* and increased the lethal activity of *T. asperellum.* These studies indicate the advantage of exploring potential synergisms against pests than using a single pathogen [109].

Naturally, in mixed infections, one entomopathogen may enhance, improve, or suppress the entomopathogenic activity of the other. Several studies have delved into the insecticidal possibilities of the combined presence of entomopathogens. The results mostly point to the synergism between the agents. And while most studies have explored the coupling of fungal entomopathogens with other insecticidal agents such as bacteria [110,111], viruses [112], nematodes [113], diatomaceous earth dusts [114] etc., the simultaneous presence of fungal entomopathogens has not been sufficiently investigated [115,116]. Although fungal entomopathogens are supposed to have the same mode of action, they differ in their virulence depending on abiotic and biotic factors including insect species, fungal strain, secondary metabolites etc. *I. fumososrosea*, for example, was more virulent against *S. oryzae* and *B. bassiana* to *S. granarius*, but the effect of their combined action increased host mortality in both hosts [108].

3. Conclusions and Prospects

Entomopathogenic fungi are a specialized group of microbial organisms with traits and modes of action that render them effective as biopesticides. Hypocreales species are ubiquitous parts of the soil microbiota. Soil is important for protection against environmental extremes, for water availability, and, also as a source of insect hosts.

While the chemical pesticides are becoming obsolete, the urge for research and development of biopesticides is growing. While only a few species of *Beauveria*, *Metarhizium*, *Lecanicillium* and *Isaria* are commercially available, the recent surge in studies exploring the endophytical attributes of fungi paves the way to further research into their complex ecology. Acknowledging their ecology better, biopesticides can potentially develop to more efficient and more diversified applications. Better grasp of their compatibility with other microbial agents, natural arthropod enemies, or plant and/or chemical compounds could generate a richer and stronger pool of available tools for pest control. Also, research should be focused on discovering the most appropriate strains or isolates per plant host. Differential rates of endophytism and degrees of fungal colonization make the case for better research into the compatibility of fungal agents with their hosts and the persistence inside the plant. Inoculation method has been shown to influence the success of colonization. Inundative EPF releases as biological control agents against insects, mites and ticks is based on the action of the agent and not on successive generations of the fungi. Attention has predominantly focused on the technical logistics of mass production and formulation of fungal biopesticides. Mass production is concerned with creating products which are relatively cost efficient, consistently effective in the field and with a relatively long shelf life.

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