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Review

Endophytic Entomopathogenic Fungi: A Valuable Biological Control Tool against Plant Pests

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Abstract: Among the non-chemical insect control methods, biological control is one of the most effective human and environmentally friendly alternatives. One of the main biological control methods is the application of entomopathogenic fungi (EPF). Today, biological crop protection with EPF plays a key role in projects for the sustainable management of insect pests. EPF have several advantages over conventional insecticides, including cost-effectiveness, high yield, absence of harmful side-effects for beneficial organisms, fewer chemical residues in the environment and increased biodiversity in ecosystems. Apart from direct application as contact bioinsecticides, EPF are able to colonize plants as endophytes acting not only as pest and disease control agents but also as plant growth promoters. The present paper presents an outline of the biocontrol potential of several EPF, which could be harnessed for the development of new integrated pest Management (IPM) strategies. Emphasis is given on benefits of endophytic EPF, on issues for practical application and in fields in need of further research. Our findings are discussed in the context of highlighting the value of entomopathogenic fungal endophytes as an integral part of pest management programs for the optimization of crop production.

Keywords: entomopathogenic fungi; endophytes; biological control; plant colonization

1. Introduction

Insect pests are responsible for a loss of 18–26% of worldwide annual crop production, which corresponds to an estimated value of $470 billion [1]. The greatest part of the losses (13–16%) occurs in the field, before harvest [1]. Furthermore, post-harvest pests constitute a major part of storage losses of agricultural products. About 50–60% of stored grains can be lost during the storage period due to insufficient control measures [2]. The intense use of chemicals has led to more than 500 species of arthropod pests becoming resistant to one or more insecticide classes [2]. Additionally, environmental and food regulations represent a barrier for the development of new insecticides, in terms of both time and cost. Approximately 140,000 insecticidal compounds need to be screened in order to find one successful compound that would be in line with the regulations, and it could take more than $250 million and 8–12 years before an insecticide is developed and registered [3].

Crop protection by agrochemicals has been responsible for maintaining and increasing the quality and quantity of crop production worldwide. However, their extensive and often irresponsible use has resulted in pest resistance, resurgence of secondary pests and a disruption or elimination of natural enemy complexes, thus reducing the efficacy of natural control processes. These factors, coupled with concerns about the impact on environment and human safety, have provided the momentum to develop more environmentally safe strategies that are both cost-effective and reliable.

Integrated pest management (IPM) is a comprehensive approach to crop production, combining a broad array of compatible techniques such as sanitation, survey and detection, use of resistant varieties, cultural manipulation, trap and companion cropping, and biological control, as well as agricultural chemicals when appropriate, in order to maintain pests below economic damage levels. This approach represents a shift from the traditional, individual, pest-centered strategies that rely heavily on chemical pesticides to a more holistic approach, viewing the crop production system as a whole for the management rather than eradication of pests [4,5].

Among the non-chemical pest control methods, biological control by entomopathogenic microorganisms represents one of the most effective options [6–9]. The use of entomopathogenic fungi (EPF) to reduce pest population density and, consequently, crop damage plays a key role in sustainable pest management programs. EPF have several advantages when compared with conventional insecticides, including cost-effectiveness, high yield, Absence of harmful side-effects for beneficial organisms, fewer chemical residues in the environment and increased biodiversity in human-managed ecosystems [10–13]. However, only a few genera have been applied as entomopathogens, including Beauveria, Metarhizium, Isaria, Lecanicillium and Hirsutella. These are used in fungal-based products, which have been formulated for use against a wide range of pests in forest, field and greenhouse environments, as well as against structural, household and storage pests.

Approximately 750 EPF species have been discovered to cause infection in a wide array of insects and mites, although individual fungal species and strains are very target specific [13]. Fungi act by producing spores that germinate and grow on the body of the insect host. Infection is initiated when spores attach to the insect integument, where the formation of the germinative tube and enzyme excretion begin. Penetration of the insect's cuticle is achieved not only by the mechanical pressure of a specialized structure formed in the germinative tube, the apresorium, but also by the action of degradative enzymes. Inside the insect haemocele, fungal hyphae are developed and invade tissues and organs. The timeframe of death (between 3 and 7 days) depends on the type of fungus and number of infecting spores. Following the death of the host, the fungus produces thousands of new spores on the cadaver, which then disperse and multiply on new hosts. EPF occupy a significant place in the microbial control of insect pests as virtually all insect orders are vulnerable to fungal diseases. Fungi have several significant properties, such as high reproductivity, target-specificity, short generation time, and a saprobic phase, all of which ensure that they survive longer even in the absence of a host.

Apart from their use as biological insecticides, there is growing evidence that many EPF species can colonize the tissues of certain plants [14,15]. Although only a few EPF species have been reported as naturally occurring endophytes, there have been many successful attempts to artificially introduce EPF into plants using different techniques [14,15]. This natural or artificial colonization could be beneficial for the plant as it has been reported to improve plant growth and reduce pest infestation in numerous economic crops [16–21].

Endophytic fungi may have significantly longer periods of efficacy than non-endophytic organisms since many are able to survive at least for the whole growing season of an annual crop [22,23]. Fungal endophytic strains, which colonize trees, may settle in the shoots, roots, or stems of perennial plants [24,25]. Fungi directly affect plants more than most chemical pesticides. EPF endophytes have been identified in hundreds of plants, including several important agricultural crops such as wheat, bananas, soybeans and tomatoes [26–31] as plant growth promoters [18,28,32–36] and beneficial rhizosphere colonizers [37–40]. However, the multifaceted roles played by fungal entomopathogens could also be used indirectly and cost-effectively in sustainable agriculture, for instance, as biofertilizers [18,29,33,36], vertically-transmitted fungal endophytes [41,42] and microbial control agents against both plant diseases and arthropod pests [11,28,43–45].

The present review provides a summary of the information available on the extent to which EPF colonize different crop plants. It also examines the insecticidal effect of such colonization on major plant insect pests, the potential for effective pest control, case studies, problems, limitations and future prospects of the application of these endophytic EPF within IPM strategies.

2. Ecology and Mechanisms of EPF as Endophytes

The term endophyte includes fungi and bacteria that develop within plant tissues without causing any noticeable symptoms of disease in the plant [46]. It is worth noting that endophytic fungi are abundant in plant species, while the characteristics and the level of the endophytic colonization differ depending on the plant tissue.

The ecological functions of these fungi, which are related to their endophytic behavior and their competence in the rhizosphere, may hold enormous significance for crop protection and agronomy [47]. Numerous investigations revealed that EPF are not only effective against insect and mite pests but they also improve the plant's response to other biotic stresses. The latter happens through the induction of systemic resistance or through the production of compounds such as insecticides, antifungals, herbicides and antivirals, during multiple biocide activities. The benefits of these processes involve the promotion of plant growth [32,48–50], plant nutrition [51,52], root development [14,53,54], and relief from abiotic stresses such as salinity [55] or Fe deficiency [15,32].

Reduced plant damage is achieved by endophytic EPF through many mechanisms. The most common cases that have been recorded are the retardation of the developmental rate of the pest [16,56,57], inhibition of insect food consumption rate [58–61], reduction of larval survival [62–64] and decreased reproduction rate [65,66]. However, it should be mentioned that many hidden and unexplored mechanisms may exist in these complicated tritrophic (EPF-plant-insect) interactions.

Endophytic EPF colonization is not an incidental opportunity given that, upon colonization, specific chemicals are secreted by both the host plant and the endophytes. Various types of secondary metabolites, including alkaloids, flavonoids, phenolics and others, are produced by plants as a defense mechanism against pathogen infections, as well as in response to probable endophytic colonization, which is perceived, at least in its early stages, as a potential pathogenic threat [67]. Secondary metabolites thus represent obstacles for the colonization of endophytic fungi. To overcome this, endophytic fungi produce detoxification and degradation enzymes, including β-1,3-glucanases, chitinases, amylases, laccases, and cellulases. In addition, fungal metabolites play an important role in pathogenicity-related and other interactions between the fungus and its insect host. They mediate inter- or intraspecific communicative functions or aid in mitigating abiotic and biotic stresses [10].

Moreover, endophytes produce various secondary metabolites, which have a unique species-specific bioactive structure (i.e., benzopyranones, phenolic acids, quinones, and steroids) [53], and which are widely applied as agrochemicals, antibiotics, antiparasitics, and antioxidants [54]. The production of metabolites in host plants creates opportunities for the production of plant-based drugs. Although this has given a new impetus to natural-product-based drug discoveries, no endophyte has thus far been used as an alternative source of plant metabolites, as their production by the fungi rapidly diminishes in vitro. Studying the interaction between endophytes, and plant hosts and endophytes, would aid the sustained production of plant metabolites by endophytes, thereby alleviating the dependence on plants for such bioactive compounds [19,40].

Initially, the conidia of EPF form germ tubes, which gradually become hyphae. EPF enter the plants either through natural openings or directly through the epidermal cell walls with the help of enzymes and/or mechanical pressure. Upon entering the plant, the hyphae grow in the space between the parenchyma cells or even in the xylem vessels.

In most cases, evidence of endophyte-host mutualism has not been conclusive. Nevertheless, plant communities would likely not overcome many environmental stresses without this symbiosis. During the last decade, research has identified several benefits of endophytic microorganisms for plant growth and development. The fact that some entomopathogens have been isolated from surface-sterilized plant materials points to their ability to have an endophytic phase in their life cycle. However, although entomopathogenic endophytes might not be ubiquitous in specific plant species, some, like *B. bassiana*, have a wide range of plant hosts. Moreover, the fact that EPF can be found as natural endophytes suggests that these fungi have complex life cycles that can be completed in plants, soil, or invertebrates [43,45,57,60,61,63,65].

3. Artificial Plant Inoculation with Endophytic EPF

The artificial establishment of EPF in plants for endophytic colonization has also been examined for pest control [3,68,69]. More specifically, endophytic colonization can offer systemic plant protection against pests as the latter are negatively affected by the chemical changes triggered in the plant by the endophyte as well as by the secondary chemicals secreted by the fungus [56,70,71]. However, not all fungi are able to colonize plants—at least not for their whole life cycle—because they cannot adapt to the nutrient content inside the plant [72]. Nevertheless, a transient fungal/plant association can exist for a few days following a spray application because of the abundance of propagule on the leaves [44,73].

Endophytic EPF colonization in plants is influenced not only by soil microorganisms but also by environmental factors such as temperature and relative humidity [74]. Other factors that have been proven to play a vital role in the inoculation of EPF into plant tissues are the age and species of the plant, the growth medium, the conidial density and species of the EPF and the applied inoculation method [74–79].

Various methods and experimental protocols have been used to artificially inoculate endophytic EPF into crop plants. These methods can be categorized as: (a) spraying leaves with conidial suspension, (b) soaking seeds in conidial suspension, (c) injecting fungi inoculum into stems, (d) dipping of seedling roots in conidial suspension, and (e) soil drenching with conidial suspension. Table A1 in Appendix A summarizes previous studies where EPF have been successfully inoculated into the plant tissues of major crop plants.

The foliar application is the most common method, with many promising results (Table A1). However, certain drawbacks have been reported and must be taken into serious consideration. The foliar endophytes can reduce the insect population by producing alkaloids that are toxic [53,54]. The major concern of this method is the extremely localized colonization that is often limited to the foliar parts of the plant, with EPF being absent from stems and roots [77,80]. Apart from that, poor efficiency of hyphal penetration into leaf tissues has been reported [76,79], possibly due to the low density of stomata (natural entries for fungal infection), leaf surface structure and specific cuticular components.

Soaking seeds in conidial suspension before propagation is another inoculation method that has been successfully applied to many major crops (Table A1). However, there have been reports where inoculation through the seed resulted in some or no colonization of the stem or leaf [77,81]. This was attributed to the negative effect of soil microorganisms that may act antagonistically toward the EPF.

Stem injection has also been evaluated as an inoculation method of EPF on various plants [74,76]. When *B. bassiana* was inoculated with this method, the highest post-inoculation recovery was yielded in coffee seedlings, compared with foliar spraying or soil drenching [76], and efficient *H. armigera* control was provided for tomato plants [81].

Dipping roots in conidial suspension has proven an effective inoculation method, although results were often contradictory when compared with other methods such as foliar application or seed treatment [79,82]. The success of this method has been reported to be greatly dependent on the plant species.

The soil drenching technique includes the watering of seedlings with conidial suspension. Similar to root dipping, the low colonization rate that is often recorded with this method has been linked to the interaction between EPF and other competing soil microorganisms. The use of sterile growth media instead of non-sterile soil significantly enhanced the success of this method [77].

4. Endophytic EPF as Biocontrol Agents

EPF endophytes have been recorded to provide effective protection to host plants against pest infestation and have been evaluated as biocontrol agents in numerous studies (Appendix A Table A2). Many commonly applied EPF species, such as *Beauveria bassiana*, *Isaria fumosorosea* and *Metarhizium anisopliae*, naturally occurring as endophytes, have been recorded to provide effective protection against herbivores [16,17,57–60,62–65,71–74,83–106].

The best-studied EPF, *B. bassiana*, was reported to colonize numerous crops, such as corn, wheat, cotton, soybean, tomato, grapevine, sorghum, and citrus, and to reduce infestation by serious pests, mainly moth larvae and aphids. The presence of endophytic EPF resulted in the significant reduction of both pest population and plant damage in most cases. However, there have been reports of poor performance, indicating the complexity of these EPF insect–plant interactions [17,56,88,91].

The combination of endophytic EPF with other biocontrol agents, such as predators and parasitoids, has been proposed in previous studies [16,57,65,66]. For instance, a study was recently carried out to explore the effectiveness of the combined use of *B. bassiana*, *M. brunneum,* and the aphid endoparasitoid *Aphidius colemani* Viereck (Hymenoptera: Braconidae) against the green peach aphid *Myzus persicae* Sulzer (Homoptera: Aphididae) in sweet pepper [53]. Similar research has documented successful combinations of endophytic EPF species with entomophagous insects against leafminers in beans [16].

5. Future Prospects

The present article reviewed the literature currently available on the endophytic EPF colonization of different host plants and provided an overview of the colonization effects against insect pests known to date. It also addressed the possible ways in which endophytic fungal entomopathogens contribute to the protection of the plant, and discussed the potential use of these fungi as control agents against insect pests. Future research should explore entomopathogenic fungi in terms of their role as endophytes. The development of novel EPF-based biological control methods is anchored in comprehending the interactions between fungal endophytes and plants. To this end, it is crucial that several aspects are investigated, i.e., (a) the physiological mechanisms endophytes use to colonize the plant and whether these mechanisms differ according to the entry point in the plant; (b) whether some fungal isolates are more successful as endophytes than others and the degree to which their strain determines their survival rate inside the plant; (c) how endophytic fungi travel to the plant, be it via seeds, soil conidia, etc.; (d) the ways plants and feeding insects are affected by endophytes; and (e) the ways endophytes benefit from plants.

Moreover, the practical implementation of EPF into the IPM programs demands an in-depth understanding of the abiotic and biotic factors that influence the insecticidal action of EPF and their endophytic behavior. Apart from this, the evaluation of inoculation methods for extended colonization is crucial in order to develop effective management strategies. Although foliar and stem applications are often more effective than root or seed treatments, identifying the soil characteristics that enhance or inhibit EPF endophytic action will help improve the efficiency of EPF applications in the soil.

Despite the numerous studies on endophytic EPF, it is true that only very few species have been studied. It is strongly believed that there are still thousands of unexplored endophytes due to limited research in this field. Therefore, there is an urgent need to discover and evaluate these unknown endophytic strains of EPF.

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Appendix A

Table A1. Successful cases of artificial plant inoculation with endophytic EPF in major crop plants.

EPF Endophytic Species	Plant Species	Inoculation Method	Ref
Beauveria bassiana	sorghum	FA	[73,77]
		SD	[77]
	tobacco	FA	[82]
		ST	[82]
		RD	[82]
	wheat	FA	[82,94]
		SD	[96,97]
		ST	[94]
		RD	[82]
	soybean	FA	[82]
	corn	FA	[95]
	maize	FA	[74,84,98]
		SI	[74]
		RD	[82]
		ST	[32]
	potato	FA	[99]
	coffee	FA	[76,100]
		SI	[76]
		SD	[76]
	tomato	FA	[81,101]
		SD	[17,27,34,103]
		SI	[104]
		RD	[81]
		ST	[103,104,107]
	grapevine	FA	[31,90]
	banana	SI	[108]
		RD	[108]
	fava bean	ST	[56]
	common bean	ST	[16]
		SD	[78]
	cotton	ST	[27,70]
	soybean	RD	[82]
	cassava	SD	[109]
	sweet pepper	SD	[57]
	rice	FA	[110]

Table A1. *Cont.*

EPF Endophytic Species	Plant Species	Inoculation Method	Ref
Metarhizium anisopliae	maize	ST	[33]
	tomato	ST	[27]
		SD	[34]
	cassava	SD	[109]
	common bean	ST	[111]
	sorghum	FA	[73]
Metarhizium brunneum	sweet pepper	SD	[57]
	wheat	SD	[96]
Metarhizium pingshaense	maize	ST	[105]
Metarhizium robertsii	cowpea	ST	[106]
	wheat	SD	[96]
	sorghum	FA	[73]
Purpureocillium lilacinum	cotton	ST	[72]
Isaria fumosorosea	sorghum	FA	[73]

FA: foliar application, SI: stem injection, ST: seed treatment, RD: root dipping, SD: soil drenching.

Table A2. Entomopathogenic fungal endophytes evaluated as biocontrol agents against insect pests on various plants.

EPF Endophytic Species	Plant Species	Target Pest	Conclusion	Ref
Beauveria. bassiana	coffee	*Hypothenemus hampei*	Pathogenic action verified	[14]
	maize	*Ostrinia nubilalis*	Suppression of pest population	[74]
		Sesamia calamistis	Reduction of larval tunneling	[83,84]
	banana	*Cosmopolites sordidus*	Reduction of larval survival	[85]
	tomato	*Helicoverpa zea*	Insignificant effect on larval mortality	[17,102]
		Helicoverpa armigera	Reduced infestation	[81]
	sorghum	*Chilo partellus*	Reduction of larval tunneling	[86]
		Sesamia nonagrioides	Reduced infestation	[45,73]
	opium poppy	*Iraella luteipes*	Reduction of larval survival	[62]
	cotton	*Aphis gossypii*	Reduced reproduction	[70,71,89]
		Chortoicetes terminifera	Reduced growth rate	[71]
		Rachiplusia nu	Reduced larval feeding	[58]
	melon	*Aphis gossypii*	Reduced reproduction, no effect on natural enemies	[65,66]
	fava bean	*Helicoverpa armigera*	Reduction of larval survival	[63]
		Liriomyza huidobrensis	Reduced population	[16]
		Acyrthosiphon pisum	Reduced population	[56]
		Aphis fabae	Reduced population	[56]
			Increased population	[91]
	common bean	*Helicoverpa armigera*	Reduction of larval survival	[63]
		Liriomyza huidobrensis	Reduced population	[16]

Table A2. *Cont.*

	white jute	*Apion corchori*	Reduced infestation	[87]
	Soybean	*Aphis glycines*	Insignificant effect on pest population	[88]
		Helicoverpa gelotopoeon	Decreased larval food consumption	[59]
	grapevine	*Planococcus ficus*	Reduced infestation	[90]
		Empoasca vitis	Reduced infestation	[90]
	pepper	*Myzus persicae*	Increased pest mortality	[44]
			Reduced development and fecundity	[57]
	strawberry	*Myzus persicae*	Reduced feeding	[60]
	cauliflower	*Bemisia tabaci*	Reduced pest survival	[93]
	pecan	*Melanocallis caryaefoliae*	Reduced pest population	[94]
		Monellia caryella		
	lemon	*Diaphorina citri*	Reduced reproduction and survival	[112]
Lecanicillium lecanii	cotton	*Aphis gossypii*	Reduced reproduction	[71,89]
Lecanicillium muscarium	cauliflower	*Plutella xylostella*	Increased larval mortality	[92]
Aspergillus parasiticus	cotton	*Chortoicetes terminifera*	Reduced growth rate	[71]
Metarhizium anisopliae	fava bean	*Acyrthosiphon pisum*	Insignificant effect on pest population	[56]
	pepper	*Myzus persicae*	Increased pest mortality	[44]
	rapeseed	*Aphis fabae*	Reduction of larval survival	[64]
		Plutella xylostella	Reduction of larval survival	[64]
	strawberry	*Myzus persicae*	Reduced feeding	[60]
Metarhizium brunneum	soybean	*Aphis glycines*	Increase of pest population	[88]
	cauliflower	*Bemisia tabaci*	Reduced pest survival	[93]
	melon	*Aphis gossypii*	Reduced reproduction and survival	[66]
Metarhizium robertsii	sorghum	*Sesamia nonagrioides*	Reduced infestation	[45,73]
Clonostachys rosea	coffee	*Hypothenemus hampei*	Pathogenic action verified	[14]
Purpureocillium lilacinum	cotton	*Aphis gossypii*	Reduced reproduction	[70]
Isaria fumosorosea	sorghum	*Sesamia nonagrioides*	Reduced infestation	[45,73]
	pepper	*Myzus persicae*	Increased pest mortality	[44]
	lemon	*Diaphorina citri*	Reduced reproduction and survival	[112]

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