

Entomopathogenic Fungi as Endophyte: An Emerging Tool for Biological Pest Control

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Abstract

Biological control using fungal entomopathogen is an effective and sustainable alternative to chemical control of insect pests. However, despite enormous potential, they have not been fully utilized due to their susceptibility to unfavorable abiotic factors such as ultraviolet (UV) light and low humidity. An increasing number of studies in the last decade demonstrates that entomopathogenic fungi have wider ecology than previously thought. They have been found to colonize various plant naturally as endophyte as well as they have been successfully established in plants with various inoculation methods. In planta presence of these fungi can overcome the impediments arise from inundative application of fungal suspension as they have been found not only protect the host plant from pest and disease but also act as a plant growth promoter. In this review, we discussed the multiple benefits provided by fungal entomopathogens following their association with the host plant as an endophyte and highlights the prospects of incorporating fungal endophytes as an integral part of pest management programs towards sustainable crop production.

Keywords: Fungal endophyte, Plant colonization, *Beauveria*, *Metarhizium*, *Lecanicillium*

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1. Introduction

Insect pests cause 18–26 % crop loss worldwide, with a value of more than \$ 470 billion and the major part (13–16 %) occurs in the field (Culliney 2014). Agrochemicals have been the foremost choice to protect crops from pests for several decades. They have been responsible for increasing the quantity and quality of crops worldwide (Skinner *et al.* 2014). However, their extensive use has resulted in several unwanted consequences, such as the development of resistance in insect pests, secondary pest outbreak or resurgence of pests, residue in crop commodities and disruption of natural enemy population reducing the overall natural control of pests in agroecosystems (Skinner *et al.* 2014). As a consequence, concern about environmental impacts and human hazards from agrochemicals, have provided force scientists to develop safe and eco-friendly pest management approach alternatives to chemical pesticides.

Biological control is a viable and sustainable pest management technique that relies on using a living organism to manage insect pests which includes predator, parasitoid and microorganism such as virus, bacteria and fungus (van Lenteren *et al.* 2018). Among the microorganism, fungi, especially entomopathogenic fungi (EPF) has been used as an inundative approach for more than 100 years (Lacey *et al.* 2015). Over 700 different species of fungi from at least 90 genera are known to be pathogenic to insect pests (Khachatourians & Qazi 2008). However, only a few of them are well-recognized as insect pathogens including *Metarhizium*, *Beauveria*, *Lecanicillium*, *Isaria*, and *Hirsutella* etc. More than 170 entomopathogenic fungal strains are now commercially available as mycopesticides, especially *Beauveria* spp. and *Metarhizium* spp. (Clavicipitaceae) (de Faria and Wraight, 2007). Despite of its potential, EPF are mostly underutilized because they are generally applied as inundative approach which expose them to various biotic and abiotic factors. Temperature, humidity and solar radiation are abiotic factors affecting persistence and efficacy of entomopathogenic fungi (Jaronski 2010).

An increasing number of studies in the last decade demonstrate that entomopathogenic fungi, besides insect pathogen, they have wider ecology than previously thought (Vega *et al.* 2009; Barelli *et al.* 2016). They have been reported to play an additional role in nature, including endophytism (Vega *et al.* 2009), rhizosphere colonizer (Hu & St. Leger 2002; St. Leger 2008; Pava-Ripoll *et al.* 2011), plant disease antagonists (Ownley *et al.* 2004; Kim *et al.* 2008; Ownley *et al.* 2010; Jaber & Ownley 2018) and plant growth promoter (Kabaluk & Ericsson 2007; García *et al.* 2011; Sasan & Bidochka 2012; Liao *et al.* 2014; Lopez & Sword 2015; Jaber & Enkerli 2017). Various EPF have been reported to colonize an increasing number of plants naturally, including many agriculturally important crop such as coffee, maize, cotton etc. (Jones 1994; Arnold & Lewis 2005; Vega *et al.* 2008; Reay *et al.* 2010; Khan *et al.* 2012; Lefort *et al.* 2016) as well as their artificial inoculation and re-isolation have been successful in several important crops with various inoculation methods (Vega *et al.* 2009; Bamisile *et al.* 2018; Vega 2018) such

as banana, tomato, cotton, rice, sugarcane and many others (see table 1) (Bamisile *et al.* 2018). In this review, we provide a summary of multiple benefits provided by EPF following their endophytic association in plants and highlight the prospects of including fungal endophytes as biocontrol agents in integrated pest management program.

2. What is an endophyte?

The term “endophyte” was introduced by de Bary (1866), to define any organism found within living plant tissues. Carroll (1988) excluded pathogenic fungi and mycorrhizal fungi and redefined endophyte as “organism that causes asymptomatic infections within plant tissues.” Since then, several definitions have been proposed for endophyte (see Box 1. in Hyde and Soyong, 2008). However, we use the amended definition proposed by Le Cocq *et al.* (2017) that ‘Endophytes are microbes which occur within plant tissue for at least part of their life cycle without causing disease under any known circumstances’. Now a days, endophyte research mainly focuses on endophytic fungi that live within plants for at least part of their life cycle without any visible symptoms (Hyde and Soyong 2008; Bacon and White 2016).

3. Endophytic insect pathogenic fungi as plant growth promoters

A growing number of studies have demonstrated the ability of EPF to promote plant growth when colonized artificially with various inoculation methods (Kabaluk & Ericsson 2007; García *et al.* 2011; Sasan & Bidochka 2012; Liao *et al.* 2014; Lopez & Sword 2015; Jaber & Enkerli 2016; Jaber & Enkerli 2017; Dash *et al.* 2018; Bamisile *et al.* 2020). In a field study, Kabaluk and Ericsson (2007) found an increased yield of corn when seeds were treated with *Metarhizium brunneum*. Similarly, Lopez and Sword (2015) observed improvements in growth and biomass of cotton when colonized by *Beauveria bassiana* and *Purpureocillium lilacinum*. Significantly greater number of lateral roots and root hair formations were recorded from plants colonized by *Metarhizium* compared to untreated counterparts (Sasan & Bidochka 2012). In another study, increased foliar biomass and leaf collar formation were reported in corn seeds when colonized with different *Metarhizium* strains (Liao *et al.* 2014). In addition, significantly greater plant height, shoot and root dry weight, root length was recorded from tomato plants colonized by *Metarhizium* (Elena *et al.* 2011).

Improvement in the stand counts and yield was recorded in wheat when plants were treated with *Metarhizium roberstii*, *M. brunneum*, and *B. bassiana* (Reddy *et al.* 2014). In another study, foliar treatment of faba bean (*Vicia faba*) plant with *Beauveria brongniartii*, *B. bassiana*, and *M. brunneum* improved the plant height, fresh shoot and root weight (Jaber & Enkerli 2017). In a recent study, Liao *et al.* (2017) found that *M. robertsii* produces the plant growth regulator indole-3-acetic acid (IAA; an auxin). This is the first report of plant growth regulator production by any EPF. Other *Metarhizium* and *Beauveria* strains were also found to produce IAA (Liao *et al.* 2017). In a recent study, Dash *et al.* (2018) found that besides *B. bassiana*, *I. fumosorosea* and *L. lecanii* also increased the plant height, shoot and root weight of common bean when the seed was inoculated with fungal suspension.

The mechanism of plant growth enhancement by endophytic entomopathogenic fungi is not fully elucidated yet; however, several hypotheses have been proposed. It has been found that EPF produces siderophores and organic acids, which can change the bioavailability of several nutrients (Jirakkakul *et al.* 2014). Furthermore, studies on endophytic fungus-plant interactions demonstrated that the positive plant growth effects could be due to the fixation of nutrients, bioactive metabolite production or up-regulation of plant growth hormone such as auxin, ethylene etc. (Berg 2009; Behie *et al.* 2012; Behie *et al.* 2017).

4. Endophytic insect pathogenic fungi as plant disease antagonists

There is now a plethora of evidence that some endophytic entomopathogenic fungi, particularly *Beauveria bassiana* and *Lecanicillium lecanii* (formerly *Verticillium lecanii*) may also exhibit antagonistic activity against plant pathogens besides their well-known biological control potential (Ownley *et al.* 2004; Ownley *et al.* 2008; Vega *et al.* 2009; Ownley *et al.* 2010; Jaber & Ownley 2018; Vega 2018).

Antagonistic activities of *B. bassiana* on plant pathogens have been reported in many studies (Kim *et al.* 2008; El-Deeb *et al.* 2012; Sasan & Bidochka 2013; Jaber & Salem 2014; Jaber 2015; Barra-Bucarei *et al.* 2020; Canassa *et al.* 2020). For example, *B. bassiana* strain 11-98, when applied as a seed treatment, was found to suppress damping-off disease caused by *Rhizoctonia solani* and *Pythium myriotylum* in tomato (Ownley *et al.* 2004) and cotton seedlings (Ownley *et al.* 2008). Using several strains of *B. bassiana*, Jaber and Salem (2014), were able to reduce the incidence of Zucchini yellow mosaic virus (ZYMV; genus *Potyvirus*, family Potyviridae) in squash. Similarly, using *Beauveria bassiana* strain 11-98, pre-treatment of cotton seedlings reduced the incidence of *Xanthomonas axonopodis* pv. *malvacearum* (Xam) causal organism for bacterial blight disease (Griffin *et al.* 2006). In addition, foliar inoculation of grapevine with conidial suspensions of *B. bassiana* reduced the prevalence of downy mildew disease caused by *Plasmopara viticola* (Berk. and Curt.) (Oomycota: Peronosporaceae) (Jaber 2015).

Recently, seed treatment of wheat with *Beauveria bassiana* (NATURALIS) and *Metarhizium brunneum*

(BIPESCO5) reduced crown and root rot (CRR) in wheat (Jaber 2018) and sweet pepper (Jaber & Alananbeh 2018) a disease caused by *Fusarium culmorum*. Although not fully elucidated, multiple but not mutually exclusive mechanisms have been proposed (Ownley *et al.* 2008; Gao *et al.* 2010; Ownley *et al.* 2010; Jaber 2018; Jaber & Ownley 2018). Disease suppression by endophytic entomopathogenic fungi has been described as both direct effects including mycoparasitism, competition and antibiosis, as well as indirect effects such as secondary metabolites, promotion of plant growth and induction of systemic plant resistance as possible mechanisms (Ownley *et al.* 2010; Jaber 2018; Jaber & Ownley 2018). Mycoparasitism has been observed for *Pythium myriotylum* by *B. bassiana* in vitro (Ownley *et al.* 2008) as well as by *Lecanicillium* against *Pythium ultimum* both in vitro and in planta (Benhamou & Brodeur 2001). Antibiosis (production of secondary metabolites), another mechanism was demonstrated by *Beauveria bassiana* (NATURALIS) and *Metarhizium brunneum* (BIPESCO5) against *Fusarium culmorum* when these two fungi were co-cultured with the pathogen in dual plate assays (Jaber & Alananbeh 2018). In this study, competition for the resource was also observed with clear zones of inhibition that occurred at the interface with the pathogenic fungus (Jaber & Alananbeh 2018).

Entomopathogenic fungi are well-known to produce an array of secondary metabolites of antibacterial, antifungal and insecticidal origin (Gibson *et al.* 2014) which has been an important mechanism involved in controlling plant pathogenic fungi (Gibson *et al.* 2014). Another indirect mechanism is the induction of systemic resistance in the plant; a mechanism has been found to be used by *B. bassiana* against *Xanthomonas axonopodis* pv. *malvacearum* in cotton (Ownley *et al.* 2008) and zucchini yellow mosaic virus in pumpkin (Jaber & Salem 2014). The above studies indicate that fungal entomopathogens have a great potential to be developed as biopesticides for multi-purpose functionality in integrated pest management programs (Goettel *et al.*, 2008, Vega *et al.*, 2009 and Ownley *et al.*, 2010).

5. Endophytic insect pathogenic fungi as insect antagonists

From the endophyte research in the last decades, there is now substantial evidence that entomopathogenic fungi can play multiple roles besides their well-known insect pathogenic activities especially association with the plant as an endophyte (Vega *et al.* 2009; Vega 2018). Endophytic presence of entomopathogenic fungi provides multiple benefits to the host plant in planta such as insect control, plant disease antagonist, plant growth promotion (Vega *et al.* 2009). There are a plethora of recent studies on insect control abilities of endophytic entomopathogenic fungi following their colonization in planta through various inoculation methods (Jaber & Ownley 2018; Vega 2018).

In a recent review, Vega (2018) reported that 39 out of 85 papers (46%) examined the effects of endophytism by EPF on 33 insect species from 17 families and 8 orders where negative effects on insect pests were reported in 38 studies. Endophytic colonization of crop plants by *B. bassiana* has been reported to reduce damage caused by stem and corn borers *Ostrinia nubilalis* and *Sesamia calamistis* (Lepidoptera: Noctuidae) in maize (Bing & Lewis 1991; Bing & Lewis 1992a, b); *Chilo partellus* (Lepidoptera: Pyralidae) in Sorghum (Reddy *et al.* 2009); *Plutella xylostella* (Lepidoptera: Plutellidae) in *Brassica napus* (Brassicaceae) (Batta 2013); fruitworm *Helicoverpa zea* Boddie (Lepidoptera: Noctuidae) in tomato (Powell *et al.* 2009; Qayyum *et al.* 2015); tomato pinworm *Tuta absoluta* (Lepidoptera: Gelechiidae) in tomato (Klieber & Reineke 2016); *Sesamia nonagrioides*, (Lepidoptera: Noctuidae) in sorghum (Mantzoukas *et al.* 2015); banana weevil, *Cosmopolites sordidus* (Coleoptera: Curculionidae) in banana (Akello *et al.* 2008a); stem weevil *Apion corchori* Marshall (Coleoptera: Curculionidae) in white jute (Biswas *et al.* 2013); the whitefly, *Bemisia tabaci* (Hemiptera: Aleyrodidae) in tomato (Wei *et al.* 2020); very recently the fall armyworm, *Spodoptera frugiperda* (J. E. Smith) (Lepidoptera: Noctuidae) in corn (Ramos *et al.* 2020); the two-spotted spider mite, *Tetranychus urticae* Koch (Acari: Tetranychidae) in common bean *Phaseolus vulgaris* L. (Fabaceae) (Dash *et al.* 2018); the Asian citrus psyllid, *Diaphorina citri* Kuwayama (Hemiptera: Liviidae) in *Citrus limon* (Bamisile *et al.* 2019).

Other than *B. bassiana*, several species of *Metarhizium* also exhibited negative effects against insects from different feeding guilds (Bamisile *et al.* 2020; Canassa *et al.* 2020; Ment *et al.* 2020). For example, endophytic strains of *Metarhizium robertsii* reduced relative growth rate of black cutworm, *Agrotis ipsilon* (Hufnagel) (Lepidoptera: Noctuidae) in maize (Ahmad *et al.* 2020); corn stalk borer, *Sesamia nonagrioides* Lefebvre (Lepidoptera: Noctuidae) in sweet sorghum (Mantzoukas *et al.* 2015). In addition, *M. anisopliae* was found to effect the performance of the bean stem maggot, *Ophiomyia phaseoli* Tryon (Diptera: Agromyzidae) in bean *Phaseolus vulgaris* (Mutune *et al.* 2016). Endophytic establishment of *M. anisopliae* has been reported to effect *Aphis fabae*, *Acyrtosiphon pisum* (Hemiptera: Aphididae) in faba bean, *Vicia faba* (Leguminosae) (Akello & Sikora 2012) and *Sesamia nonagrioides* Lefebvre (Lepidoptera: Noctuidae) in sweet sorghum (Mantzoukas *et al.* 2015).

Negative effects were also recorded for other entomopathogenic fungal endophytes including the cotton aphid, *Aphis gossypii* Glover (Hemiptera: Aphididae) in cotton (Gurulingappa *et al.* 2010); the pea leafminer, *Liriomyza huidobrensis* Blanchard (Diptera: Agromyzidae) with *Fusarium oxysporum*, *Hypocrea lixii* and *Gibberella moniliformis* in broad bean (Akutse *et al.* 2013) and onion thrips, *Thrips tabaci* Lindeman (Thysanoptera: Thripidae) with *Clonostachys rosea*.

The mechanism underlying the detrimental effects of EIPF on insect herbivores has not yet fully unraveled (Vidal & Jaber 2015; Vega 2018). While systemic plant resistance has been described against plant disease antagonism, presumably similar systemic resistance is also elicited by EIPF against insect herbivores (Jaber & Ownley 2018). So far, a very little number of studies had reported mycosis of insect cadavers when herbivore was encountered endophyte colonized plants. Interestingly, a small number of studies reported mycosis, especially when *B. bassiana* colonized endophytically in the host plant (Powell *et al.* 2007; Akello *et al.* 2008a; Akello *et al.* 2008b; Powell *et al.* 2009; Vidal & Jaber 2015; Klieber & Reineke 2016); although the mechanism leading to mycosis has not been elucidated. In one of those studies, (Powell *et al.* 2009) assumed that the insect might have consumed an intact and sufficient amount of hypha to cause the mycosis.

Feeding deterrence or antibiosis due to the production of secondary metabolites by fungal endophytes in the colonized plant has been commonly suggested as the mechanism of negative effects on insect herbivores in host plant-endophyte-insect interactions (e.g. (Akello & Sikora 2012; Akutse *et al.* 2013; Golo *et al.* 2014; Muvea *et al.* 2014; Mantzoukas *et al.* 2015; Lefort *et al.* 2016; Dash *et al.* 2018; Jaber & Ownley 2018). For example, *B. bassiana* is known to produce numerous secondary metabolites including beauvericin, bassianolides, bassianolone, oosporein, etc. which have been found to have antifungal, antibacterial and insecticidal properties (Ownley *et al.* 2010; Gibson *et al.* 2014). Similarly, *Metarhizium* spp. also produce a variety of secondary metabolites, including destruxins, serinocyclins, cytochalasins etc. (Krasnoff *et al.* 2007).

6. Endophytic entomopathogenic fungi as biocontrol agents

There is now substantial evidence that entomopathogenic fungi can colonize plants following various inoculation techniques (Bamisile *et al.* 2018) and successful colonization of them provides host plant multiple benefits (Vega *et al.* 2009; Vega 2018) even they can promote plant growth as well as dual biological control of insect pests and plant pathogenic bacteria, fungi and nematodes (Kabaluk & Ericsson 2007; Goettel *et al.* 2008; Kim *et al.* 2008; Ownley *et al.* 2010; García *et al.* 2011; Sasan & Bidochka 2012; Liao *et al.* 2014; Bogner *et al.* 2016; Zhou *et al.* 2016). Previous studies have reported that in planta presence of endophytic fungi *B. bassiana* can provide longer protection in plants; for example, three months in jute (Biswas *et al.* 2012) and even upto nine months in radiata pine following endohytic colonization (Brownbridge *et al.* 2012). Use of endophytic fungal entomopathogen can overcome several inherent problems reported while using EPF as inundative approach (Vega 2018). For example, seed treatment with fungal endophyte have been found to systemically colonize the host plant as they have been recovered from root, stem and even leaves indicating their potential as protecting the whole plant upon a single application as seed treatment (Jaber & Enkerli 2016; Dash *et al.* 2018). This suggests that endophyte can offer protection against soil dwelling as well as cryptic pests (e.g. internal borers) which would otherwise be difficult to control by traditional control approaches (Jaronski 2010).

Recently, endophytic strains of entomopathogenic fungi have been reported to be compatible with other biocontrol agents such as predators (Canassa *et al.* 2019) and parasitoids (Akutse *et al.* 2014; Gathage *et al.* 2016; Jaber & Araj 2018). For example, (Akutse *et al.* 2014) did not find significant differences in parasitism rate of two parasitoids of the pea leafminer *Diglyphus isaea* Walker (Hymenoptera: Eulophidae) and *Phaenotoma scabriventris* Nixon (Hymenoptera: Braconidae) when parasitized on 2nd and 3rd instar larvae of the pea leaf miner *Liriomyza huidobrensis* Blanchard (Diptera: Agromyzidae) on broad bean plants colonized by several fungal isolates of *B. bassiana* and *H. lixii*. In another study, (Jaber & Araj 2018) also observed no difference in the development time and adult longevity of *Aphidius colemani*, a parasitoid of green peach aphid, *Myzus persicae* in sweet pepper plants colonized by *B. bassiana* and *M. brunneum*.

In a recent study, (Canassa *et al.* 2019) inoculated two isolates of *Metarhizium robertsii* (ESALQ 1622) and *Beauveria bassiana* (ESALQ 3375) in strawberry through seed treatment to study the effect of endophytism against spider mite, *Tetranychus urticae* and behavioral responses and predation rates of the predatory mite *Phytoseiulus persimilis*. The authors reported significant reduction in the populations of *Tetranychus urticae* whereas the predatory mite *P. persimilis* showed no difference in predation rate when *T. urticae* were provided from endophyte colonized or endophyte free strawberry plants (Canassa *et al.* 2019). The same author in their recent field study with same isolates demonstrated that no negative effect was reported on numbers of naturally occurring predatory mites in strawberry field when plant root was inoculated with endophytic entomopathogenic fungi (Canassa *et al.* 2020). All these findings therefore indicate that entomopathogenic fungi as endophyte can be successfully used in IPM program as biocontrol agent.

7. Conclusions and future perspectives

Due to increased environmental concerns about the consequences of synthetic chemical pesticides, efforts are being concentrated on developing eco-friendly pest management techniques and biological control is considered as sustainable pest management option in IPM. Recent discovery of endophytic properties of EPF provides great opportunities to overcome many limitations faced during their inundative use and offer long term protection of host plant from biotic and abiotic stresses.

To date, most of the endophyte research have been conducted in the laboratory or greenhouses, very few have been examined in field condition (but see (Cherry *et al.* 2004; Quesada-Moraga *et al.* 2009; Castillo Lopez *et al.* 2014; Mantzoukas *et al.* 2015; Gathage *et al.* 2016; Canassa *et al.* 2020). For example, Parsa *et al.* (2018) demonstrated that endophytic colonization of fungal isolates were significantly reduced when natural field soil was used instead of sterile soil with the same isolate. This study indicates that the effectiveness of the promising technology needs to be proven in the field condition before it can be recommended for commercial use for economic benefits to the growers.

Although there are numerous studies on endophytic entomopathogenic fungi, very few species (*Beauveria*, *Metarhizium*, *Lecanicillium*) have been studied to date. Therefore research should be extended for other unexplored potential insect pathogenic fungi for their ability to interact with plants as endophyte. A deeper understanding about the association and persistence of entomopathogenic fungi in the host plant is necessary before they can be recommended for incorporating into IPM program. A better understanding on the cost to host fitness while establishing EPF is also required.

A deeper understanding of host-endophyte relationships at the molecular level can help to explore the mechanism of endophytism by EPF. The evaluation of various inoculation methods for extended colonization is also necessary for effective management strategy. Moreover, it is clear that fungi produce several secondary metabolites during their endophytic presence in the host plant; possibility of producing toxic metabolite and their inclusion in the human food chain also need to be carefully examined.

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