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SPECIALTY SECTION

This article was submitted to
Plant Abiotic Stress,
a section of the journal
Frontiers in Plant Science

RECEIVED 15 November 2022

ACCEPTED 16 December 2022

PUBLISHED 19 January 2023

CITATION

Samal I, Bhoi TK, Majhi PK, Murmu S,
Pradhan AK, Kumar D, Saini V,
Paschapur AU, Raj MN, Ankur, Manik S,
Behera PP, Mahanta DK, Komal J,
Alam P and Balawi TA (2023)
Combatting insects mediated biotic
stress through plant associated
endophytic entomopathogenic fungi
in horticultural crops.
Front. Plant Sci. 13:1098673.
doi: 10.3389/fpls.2022.1098673

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Combatting insects mediated biotic stress through plant associated endophytic entomopathogenic fungi in horticultural crops

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Horticultural production is a vital catalyst for economic growth, yet insect infestations reduce horticultural crop yield and quality. Pesticides and other pest control methods are used during planting to eliminate pests that cause direct and indirect losses. In such situations, endophytic entomo-pathogenic fungi (EPPF) can act as a potential tools for biological control. They protect plants by boosting growth, nutrition, morpho-physiology and salt or iron tolerance. Antixenosis, antibiosis and plant tolerance change insect performance and preferences. EPPF- plant colonisation slows herbivore development, food consumption, oviposition and larval survival. EPPF changes plant physio-chemical properties like volatile emission profile and secondary metabolite production to regulate insect pest defences. EPPF produces chitinases, laccases, amylases, and cellulases for plant defence. Recent studies focused on EPPF species' significance, isolation, identification and field application. Realizing their full potential is difficult due to insufficient

mass production, storage stability and formulation. Genetic-molecular and bioinformatics can help to build EEPF-based biological control systems. Metagenomics helps study microbial EEPF taxonomy and function. Multi-omics and system biology can decode EEPF interactions with host plants and microorganisms. NGS (Next Generation Sequencing), comparative genomics, proteomics, transcriptomics, metabolomics, metatranscriptomics and microarrays are used to evaluate plant-EEPF relationships. IPM requires understanding the abiotic and biotic elements that influence plant-EEPF interaction and the physiological mechanisms of EEPF colonisation. Due to restricted research, there are hundreds of unexplored EEPFs, providing an urgent need to uncover and analyse them.

KEYWORDS

horticultural crops, endophytic entomo-pathogenic fungi (EPPF), insects, biological control, EEPF- plant colonisation

1 Introduction

The current global population is estimated to be around 7.7 billion people, with a projected increase to 10 billion by 2050 (Etesami and Jeong, 2018). Population growth has a significant impact on the environment and climate change caused by human activities poses a serious threat to the food supply and people's livelihoods (Food and Agriculture Organization, 2008; United Nations, 2019). With limited resources, the agriculture sector is struggling to feed such a large population. Intensive agriculture, defined by increased pesticide and fertiliser use and a lack of crop diversification poses a serious threat to biodiversity and ecological processes (Flynn et al., 2009). Although the global food system is more reliant on a few staple cereals, which account for roughly 60% of plant-based human energy intake, there is enormous potential to include horticultural produce to diversify diets and improve human health (Tiwari and Charuvi, 2021). The worldwide horticulture market is anticipated to be valued at USD 20.77 billion in 2021, rising at a CAGR of 10.2% to USD 40.24 billion by 2026 (GME, 2022). A variety of abiotic and biotic variables, however, have a detrimental effect on horticultural crop yield. Drought, salt, heat, and cold are the main abiotic stressors affecting horticulture crops and they can cause losses of up to 50–70% (Tiwari et al., 2020), whereas biotic stresses, primarily insects and diseases, can cause losses of 40–60% (Oerke and Dehne, 2004). Amongst all biotic constraints, insect pests are one of the major concerns across the globe (Saha et al., 2020). Horticultural crop growers are most concerned with developing an eco-friendly management method that is compatible with the current pest control strategy, given the risks associated with overusing chemicals, such as pest resurgence, resistance, pesticide residue and biomagnification at higher trophic levels (Banjo et al., 2003). Entomopathogenic microorganisms are a non-chemical,

sustainable pest management solution (Fanning et al., 2018). Entomopathogenic fungi (EPF) have cost-effectiveness, increased output potential, no pesticide residues, and enhanced biodiversity (Litwin et al., 2020). However, only a few genera, including *Lecanicillium*, *Metarhizium*, *Hirsutella*, *Isaria* and *Beauveria* have been commercialized as entomopathogens. Thus far, 12 species of Oomycetes, 65 species of Chytridiomycota, 339 species of Microsporidia, 474 species of Entomophthoromycota, 238 species of Basidiomycota, and 476 species of Ascomycota have been reported (Litwin et al., 2020). To date, more than 700 species from approximately 90 different genera have been established as insect-pathogenic fungi (important EPFs have enlisted in Table 1) (Khachatourians and Qazi, 2008), while, only 170 strains have been formulated as mycopesticides and are available for commercial use (Bamisile et al., 2021). *Metarhizium*, *Beauveria*, *Paecilomyces*, *Isaria* and *Lecanicillium*-based biopesticides have all received widespread application (Chen et al., 2015). When it comes to controlling pests and fungal plant pathogens, *Beauveria bassiana* has the highest endophytic capacity among EPFs in roughly 25 plant species (Vega, 2018). While *I. fumosorosea* does not appear to have any major plant interactions. Although *Isaria* spp. are known to be susceptible to plant defence chemicals, *I. fumosorosea* isolates have been reported to be effective against root nematodes, *Meloidogyne javanica* despite very low infection rates (Inglis et al., 2001; Zimmermann, 2008). EPFs are highly host specific, UV instability and lesser ecological tolerance hinder their wider applicability. Keeping these in view, inhabiting/incorporating these fungi within plants could lead to noble ways to modify fungal entomopathogens' interactions with plants (Cory and Ericsson, 2010). In addition to direct insect pest control, numerous fungal entomopathogens were documented to have within plant development history (Schulz and Boyle, 2005) as

TABLE 1 List of Entomopathogenic Fungi (EPF).

SL. No.	Division of entomopathogenic fungi	Examples	References
1.	Ascomycota	<i>Metarhizium</i> (<i>M. anisopliae</i> , <i>M. robertsii</i> , <i>M. brunneum</i> , <i>M. lepidiotae</i> , <i>M. globosum</i> , <i>M. acridum</i> , <i>M. majus</i> , <i>M. flavoviride</i> , <i>M. rileyi</i> , <i>M. pingshaense</i> , <i>M. lepidiotae</i> and <i>M. guizhouense</i>)	Tkaczuk et al., 2015; Jaihan et al., 2016
		<i>Beauveria</i> (<i>B. bassiana</i> and <i>B. brongniartii</i>)	
		<i>Isaria</i> (<i>I. fumosorosea</i> -formerly <i>Paecilomyces fumosoroseus</i> , <i>I. farinosa</i> and <i>I. tenuipes</i>)	
		Ophiocordyceps (<i>O. sinensis</i> -formerly <i>Cordyceps sinensis</i> , <i>O. unilateralis</i>)	
		<i>Cordyceps</i> (<i>C. militaris</i>), <i>Torubiella</i> (<i>T. ratticaudata</i>)	
		<i>Pochonia</i> (<i>P. chlamydosporia</i>)	
		<i>Hirsutella</i> (<i>H. thompsonii</i> , <i>H. nodulosa</i> , <i>H. aphidis</i>)	
		<i>Lecanicillium</i> (<i>L. lecani</i> -formerly <i>Verticillium lecanii</i> , <i>L. longisporum</i>)	
2.	Entomophthoromycota	<i>Furia</i> , <i>Conidiobolus</i> , <i>Entomophaga</i> , or <i>Erynia</i>	Litwin et al., 2020

naturally existing endophytes and various successful attempts have been made to intentionally incorporate EPFs into plants (Vega, 2018). Various plant qualitative and quantitative characters were reported to be enhanced through the natural or artificial colonization of EPFs in plants (Klieber and Reineke, 2016). As a result, another possible strategy for combating horticultural crop pests could be to inoculate plants with highly virulent endophytic entomopathogenic fungi (EPPFs) (Arnold and Lewis, 2005). EPPFs colonise plants systemically, providing sustained resistance against insect pests and fungal entomopathogens. Due to a lack of research, many important EPPFs may remain operational but undetected. Some endophytes may become extinct due to pollution, habitat fragmentation, biodiversity loss, and deforestation (Kandalepas et al., 2015). These biological agent reservoirs should be researched for pest and disease management and to understand their variety and functionality in various agro-ecological zones. The current study focuses on the modus operandi of EPPF-plant association with insects, consequences and factors influencing the EPPF-tritrophic continuum, artificial inoculation of EPPFs in plant systems, and molecular approaches for unravelling the beneficial coordination, which can be used in plant protection measures.

2 Fungal entomopathogens as endophytes

Endophytes are widespread in the plant kingdom, forming connections with a variety of organisms and providing secondary protection against pests (Hartley and Gange, 2009). Endophytic fungi are plant-associated microorganisms that colonise and live within a plant viz., roots, stems or leaves (Suryanarayanan, 2013) without adversely affecting it (Puri et al., 2016) and they can be either mutually beneficial root

endophytes or plant-related endophytes (Vega, 2008). The relationship of endophytic fungi with higher vascular plants (Arnold and Lewis, 2005) is referred to be symbiotic because the former assists their hosts return for nutrients from the hosts and in return it provides indirect protection against herbivores (Quesada-Moraga et al., 2009). By infecting sucking pest complexes, lepidopteran larvae, and other cosmopolitan insects, fungal endophytes have the potential to function as bio-agents that cause disease in insects. It has been established that they can infect specific hosts while posing a risk that is negligible or nonexistent to other species, including those that are beneficial (Akutse et al., 2014). For example, *Beauveria bassiana*, has been identified as an endophyte in tomato (Ownley et al., 2004), cocoa (Evans et al., 2003), potato (Jones, 1994), date palm (Gómez-Vidal et al. 2009), bananas (Posada et al., 2007) and opium poppy (Quesada-Moraga et al., 2006). Successful inoculation of cocoa and coffee seedlings with *B. bassiana* has been achieved by applying a spore suspension to the radicle immediately after germination. In addition, inoculation of the the fungi *Metarhizium brunneum* in *Capsicum annum* (sweet pepper) (Jaber and Araj, 2018) and *Paecilomyces* sp. in *Musa acuminata* were also reported to be successful (Cao et al., 2002).

3 Mechanism of successful colonization through EPPF offense vs. plant defense

The EPPF infection process begins with conidia, the fruiting body, which transforms into a germ tube after penetrating the host plant and becoming hypha (Dash et al., 2018). In both plants and insects, the infection process continues after entry into the host tissue (via natural openings of epidermal cells/mechanical

pressure). The plant and the EEPF must first overcome a variety of environmental stresses that are critical for plant growth and development (Manoussopoulos et al., 2019). For EEPF-insect interactions, the genera *Beauveria* and *Metarhizium* have been reported to serve as general models (Moonjely et al., 2016), and these EEPFs follow similar modus operandi to enter and establish inside their plant and insect hosts, with similar genetic involvement, which could have resulted from gene duplication or horizontal gene transfer (Zhang et al., 2019), indicating co-evolved processes (Moonjely et al., 2016). Invading insects search for suitable plant hosts, recognise hosts through associated molecular patterns, accept and suitability mediated by asexual spore attachment to host surfaces and invade and multiply inside plant tissue, where the EEPF establishes itself after evading the insect's immune system (Vega et al., 2012). Through its colonisation of plant tissues and infection of insects, EEPF forms a tripartite interaction in which it, the plant and the insect share nutrients (Figure 1). Most of what is known about these connections come from the fungus *Metarhizium robertsii*, whose mycelium colonises root cells and soil-dwelling larvae (Behie et al., 2012). The results of sophisticated radioactive isotope studies suggested that *M. robertsii* absorb carbon from

their host plant and transfer nitrogen from insects to their root systems (Behie et al., 2017). These studies monitored ¹⁵N and ¹³C in *M. robertsii* and plants and discovered that the fungus takes carbon from the plants and uses it to make chitin and trehalose, two types of fungal carbohydrates. As a result, we can hypothesise that EEPF, plants and insects engage in intricate tritrophic interactions. Different adhesion molecules, including MAD1 in *M. robertsii*, and hydrophobins in *Beauveria*, were reported to be required for spore adhesion to the insect cuticle (Zhang et al., 2011). Furthermore, certain surface proteins recognised insect cuticular proteins and initiated cuticular degradation. Following successful adherence, the conidia form hyphae, which then differentiate into blastospores in the insect haemocoel, which produces beauvericin and destruxins, which are insecticidal metabolites that cause insect mortality (Barelli et al., 2016). In addition, EEPFs produce antimicrobial compounds in the dead cadaver to reduce microbial competition and ensure adequate nutrient allocation (Fan et al., 2017). In contrast to the establishment of EEPFs in insects, the EEPF-plant adhesion process is dependent on the adhesin MAD2, which is similar to MAD1 in insect adhesion (Behie et al., 2015). *Metarhizium* adhesion to plant epidermis was impaired by genetic deletion of

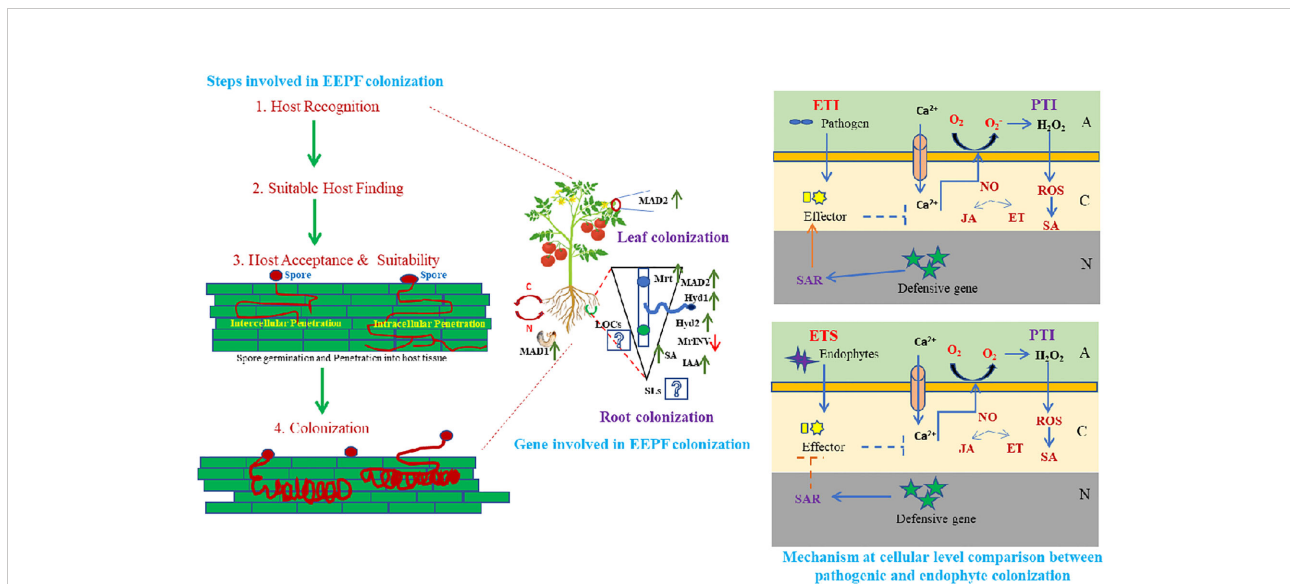


FIGURE 1

Host identification and establishment by entomopathogenic fungal endophytes involves diverse steps i.e. host recognition, suitable host finding, host acceptance and suitability followed by spore germination and penetration into host tissue leading to fungal colonization. This colonization can occur in any of the plant parts preferably roots and leaves either intra or intercellularly, leading to diverse local and/or systemic biochemical and molecular genetic up-regulation. Various adhesion molecules, MAD1 in insects and MAD2 in *Metarrhizium anisopliae* and hydrophobins (Hyd1, Hyd2) in *Beauveria bassiana*, Mrt (*Metarrhizium* raffinose transporter), MrlNV (extracellular invertase in *Metarrhizium*), certain fungal derived plant hormone like IAA (Indole acetic acid) and SA (Salicylic acid) are considered to be essential for spore adhesion. While, certain LCOs (Lipo-chitoooligosaccharides) and SLs (Strigolactones) promote EEPF- plant colonisation as signalling molecules, that initiates a chain of systemic reaction in plants, leading to EEPFs establishment in plants. Plant cell wall acts as the first line of defense, overcoming which EEPFs gain access to the innate immune system of plants after the MAMP (Microbe associated molecular pattern) or PAMP (Pathogen associated molecular pattern) is recognised by the plants, leading to activation of MTI (MAMP- triggered immunity) or PTI (Pattern triggered immunity). Further, plants secrete certain effector molecules, that leads to downstream synthesis of SA (Salicylic acid), JA (Jasmonic acid), NO (Nitric oxide) and generation of ROS (Reactive oxygen species), which enables the EPF (Entomopathogenic fungi) to overcome the ETI (Effector triggered immunity) (essential for pathogenesis) and making the plant susceptible for EEPF colonisation through ETS (Effector triggered susceptibility) (essential for endophytism). (A, Apoplast; C, Cytoplasm; N, Nucleus).

MAD2 (Wang and Leger, 2007). Proteins such as Hyd1 (Hydrophobin1), Hyd2 (Hydrophobin2), Mrt (*Metarhizium* raffinose transporter), MrINV (extracellular invertase in *Metarhizium*), fungal-derived plant hormone (IAA), and plant hormone (SA). Furthermore, different EEPF LCOs (lipochitooligosaccharides) and plant SLs (strigolactones) act as signalling metabolites in plants - EEPF colonisation (Hu and Bidochka, 2021). After overcoming the first line of defence, the recognition of microbe or pathogen-associated molecular patterns (MAMPs or PAMPs) like conserved molecules and activating MAMP-triggered immunity (MTI) and/or pattern triggered immunity (PTI) is carried out by pattern recognition receptors (PRRs) present in plant cells (Newman et al., 2013); while plants secrete certain effector molecules, which induce effector triggered immunity (ETI) against the potential pathogen (Mendoza-Mendoza et al., 2018). A growing body of research suggests that beneficial microbes may evade ETI or short-circuit plant defence responses at the effector-triggered susceptibility state to allow successful colonisation of host roots or by evading recognition by removing or mutating recognised effectors (Zamioudis and Pieterse, 2012). Another notable example of PTI is the EEPF chitosan molecules, which have been shown to induce host defence (Sánchez-Vallet et al., 2015). LysM is a carbohydrate-binding module found in many extracellular proteins and receptors that recognise polysaccharides containing N-acetylglucosamine residues (in EEPF chitosan). Chitin and chitin polymers, as well as their modified form, chitosan, have been shown to induce host defence responses in a variety of horticultural crops. In the context of fungal endophytes, plant chitin-specific receptors (PR-3) recognise chitin oligomers produced on the fungal cell wall, which accelerates subsequent defensive reactions (Sánchez-Vallet et al., 2015). In response to plant defensive behaviour, EEPFs have been shown to elicit counteractive features such as molecule secretion for non-recognition of chitin, defensive enzymes and production of salicylate hydrolase to inhibit salicylic acid defence and a raffinose transporter and an extracellular invertase for sucrose hydrolysis in plant roots. EEPFs, on the other hand, devise mechanisms to protect themselves from plant defence mechanisms. Chitin deacetylases, for example, deacetylate chitosan oligomers, rendering them unrecognisable by plant receptors (Cord-Landwehr et al., 2016). In addition, certain defensive enzymes such as catalases (CAT), superoxide dismutases (SOD), alkyl hydroperoxide reductases (AhpC), peroxidases (POD) and glutathione-S-transferases (GSTs) are activated in response to oxidative burst (Zeidler et al., 2004). Although the details on all of the genes involved in EEPF-plant establishment are unknown, research on *M. robertsii* has highlighted the plant colonisation and endophytism mechanisms. The salicylic acid (SA) cascade is started by the plant's immune system and is dependent on the rate at which spores adhere to and penetrate the plant (Martínez-Medina et al., 2017). Low spore adherence can lead to decreased root tissue

penetration, which may allow *B. bassiana* to generate stronger endophytes. An examination of the activation of the immune system in plants in response to *B. bassiana* colonisation shows that it can overcome SA-dependent systemic acquired resistance by producing a (fungal) salicylate hydrolase enzyme. The fungus can grow endophytically without affecting the plant's immune system. According to a study, *M. robertsii*'s establishment in plants depends on a raffinose transporter and a sucrose-hydrolyzing extracellular invertase (Fan et al., 2017). Root exudates contain raffinose and sucrose, which are required for *M. robertsii* rhizosphere proliferation and root competence. Plant offence and EEPF defence boost colonisation by making raffinose and sucrose available for EEPF growth and colonisation. EEPFs could provide multimodal protection for plants against phytophagous insects, either directly (e.g., poisonous chemical production) or indirectly [volatile organic compounds (VOCs)] to attract natural enemies. Understanding the tritrophic interaction involving EEPF- colonised plants is thus required, as described below.

4 Consequences of multitrophic interactions of EEPF in the trophic chain

Plant-associated microorganisms help plants, herbivores, and natural enemies interact. Endophytes can change host resistance to herbivores and natural enemies (Hatcher, 1995). Systemic or transitory endophytic colonisation provides multimodal protection to plants by affecting multitrophic relationships between pest species and plants, as well as between insect pests and their predators, parasitoids, and natural enemies (Quesada Moraga, 2020). Endophytes impact and modulate plant metabolic processes because they live in and interact with plants. In some cases, the benefitting plant and endophyte share a pathway to produce new compounds (Poling et al., 2008). Both partners can modify metabolite backbones to create new metabolites (Pimentel et al., 2011). The effects and consequences of EEPF colonisation at various trophic levels, as well as their interaction, are described below with appropriate examples.

4.1 Trophic level one: EEPF and plant

With the gradual exposure to a wide range of positive effects imparted by endophytic fungi on their hosts, the close interaction between plants and endophytes has gotten a lot of attention. Fungal endophytes help to boost plant robustness (Khan et al., 2012), plant growth, nutrient intake capacity, photosynthesis, and plant hormone levels (Li et al., 2018). Recent studies have demonstrated that EEPFs have additive effects on host plant growth and development by enhancing plant height, plant weight and growth rate (Greenfield et al.,

2016; Jaber and Araj, 2018). The insect derived nitrogen is transferred from endophytic *Metarhizium* spp. to the host plant and in turn it receives carbon from the host plant (Behie and Bidochka, 2014; Behie et al., 2017). Furthermore, the fresh weight of roots, shoots and the height of broad bean, *Vicia faba* were reported to increase after foliar treatment with EPF, *B. bassiana*, *B. brongniartii*, and *M. brunneum* (Jaber and Enkerli, 2017). Similarly, tomato plants treated with *M. anisopliae* were reported to boost plant height, root length, shoot as well as root dry weight (Elena et al., 2011). Furthermore, soil drenching with fungal conidial suspension resulted in enhanced growth of sweet pepper (*Capsicum annum*) (Jaber and Araj, 2018). Numerous abiotic and biotic factors such as plant and microbe genotypes, climatic circumstances, the dynamics of interaction within the plant and soil biomes and the inoculation method were reported to influence the extent of endophytism (Raya-Diaz et al., 2017). Furthermore, plants are able to withstand biotic stresses (underground herbivory by nematodes, root-feeding insects) and abiotic stresses (salt, drought, heat stress) because EEPFs have been shown to release toxins that impede the development and proliferation of other competitors, including pathogenic organisms (Clark et al., 1989; Khan et al., 2012; Cosme et al., 2016).

4.2 Trophic level two: EEPF and herbivore

Numerous studies have demonstrated that endophytic entomopathogenic fungi can inhibit insect pests that feed on microbe-colonized plants (Sánchez-Rodríguez et al., 2018). Endophytic fungi reduce insect herbivore damage by inhibiting insect development (Akutse et al., 2013), providing a feeding deterrent (Vega, 2008), retarding insect development and restricting insect survival and oviposition (Martinuz et al., 2012). According to Leckie (2002), the incidence of *Helicoverpa zea* was reported to be reduced in *B. bassiana* treated tomato plants. Klieber and Reineke (2016) observed 50% mortality and reduced longevity in the larvae of *Tuta absoluta* (Meyrick) on *B. bassiana*-treated tomato leaves. Moreover, Qayyum et al. (2015) found a reduction in *H. armigera* damage in tomato plants in response to *B. bassiana* colonisation. Similar results were also obtained by Posada et al. (2007) when the coffee berry borer (*Hypothenemus hampei*) was fed on *B. bassiana*-treated coffee plants. Furthermore, Akello et al. (2008) showed a comparable decline in the larval survival and overall population of the banana weevil, *Cosmopolites sordidus* (Coleoptera: Curculionidae). The bulk of these studies link insect pest damage reduction due to mycotoxin accumulation in plant tissues (Gurulingappa et al., 2011). Lozano-Soria et al. (2020) revealed that volatile compounds produced by two EEPFs, *B. bassiana* (Bb1TS11) and *M. robertsii* (Mr4TS04), can deter the banana Rhizome weevil, *C.*

sordidus. Gas chromatography/mass spectrometry-solid-phase micro extraction (GC/MS-SPME) studies revealed the identification of 97 diverse VOCs, out of which seven VOCs (styrene, benzothiazole, camphor, borneol, 1,3-dimethoxybenzene, 1-octen-3-ol and 3-cyclohepten-1-one) were found to have insect repellent activity (Lozano-Soria et al., 2020). *B. bassiana* has also been shown to have insect repellent properties against the palm weevil, *Rhynchophorus ferrugineus*. Whitefly, *Bemisia tabaci* does not prefer *B. bassiana* inoculated tomato seedlings, according to Wei et al. (2020), because of the formation of bioactive chemicals chitin and glucans. Destruxin A was discovered to be effective against whiteflies 48-72 hours after *Metarhizium brunneum* colonisation in diverse tissues of potato plants and melon leaves (Garrido-Jurado et al., 2017). However, not all fungi can colonise plants due to their inability to adapt to the plant's nutrients (Mercado-Blanco and Lugtenberg, 2014). Transient fungal/plant interactions may remain for several days after spraying due to the broad distribution of leaves (Mantzoukas and Lagogiannis, 2019). According to recent studies, EPF's temporary endophytic colonisation of plant tissues kills chewing and sucking insects that feed exophytically on plants (Resquín-Romero et al., 2016).

4.3 Trophic level three: EEPF and natural enemy

The complete understanding of herbivores and EEPF colonized host plants require integration of the third trophic level (Price et al., 1980). The slow growth-high mortality hypothesis (SG-HM) revealed that the altered nutritional chemistry of the EEPF associated host plants prolonged the larval development that ultimately enhances the qualitative and quantitative foraging efficiency of predators and parasites (Clancy and Price, 1987). The multitrophic relationships among *M. brunneum* colonized host plants - pest *Spodoptera littoralis* (Boisduval) (Lepidoptera: Noctuidae)- natural enemy *Hyposoter didymator* indicated 33% higher parasitisation and reduced reproductive potential of the parasitoid on *Spodoptera littoralis* fed on *M. brunneum* inoculated host plants than on non-inoculated ones (Miranda-Fuentes et al., 2020). Moreover, the rate and time of *Aphis gossypii* (prey) consumption by *Chrysoperla carnea* and rate of mummification by *Aphidius colemani* was not significantly differed in response to endophytic colonisation by *B. bassiana* (González-Mas et al., 2019a). However, predator behaviour on aphids infesting *B. bassiana* endophytically colonised plants concluded the potential use of EEPFs in IPM programmes in combination with other biocontrol agents that would provide additive pest suppression (Gonzalez-Más et al., 2019b). EEPFs are safe and compatible with other biocontrol agents, but this less explored area requires a better understanding of potential changes in the chemical ecology of the plant post-colonization, multitrophic

relationships between insects and plants, and insects and their entomophagous natural enemies. Endophytic colonisation of plants can modify volatile content, resulting in differential biotic and/or abiotic tolerance/resistance. When parasitoids and predators work with EEPFs, insect herbivores and plant damage are minimised. Jaber and Araj (2018) suppressed the green peach aphid (*Myzus persicae* Sulzer) with EEPF *B. bassiana*, *M. brunneum* and *Aphidius colemani* Viereck. Prior research suggests that EEPFs negatively influence natural enemies' development, reproduction, and adult survival (Omacini et al., 2001; Kunkel et al., 2004). Mycotoxins travel from colonised plants to insects and ultimately to their parasites. Kunkel et al. (2004) claimed that endophyte-produced poisons could cause indirect harm to natural adversaries (Omacini et al., 2001). Insect herbivores that consume EEPF-colonized plants may be smaller and have less nourishment (Richmond et al., 2004).

4.4 Effect of EEPF colonised plants on insect-natural enemy interaction through production of secondary metabolites

Aside from directly influencing tritrophic interactions, certain volatile organic compounds (VOCs) and secondary metabolites produced by EEPF-colonized plants have significant effects. Sphaeropsidin A (SphA) is a pimarane diterpene that has been shown to have larvicidal and phagodeterrent effects on lepidopteran insects such as *Spodoptera littoralis* (Andolfi et al., 2014). SphA was discovered to have contact and oral toxicity against the chewing lepidopteran *S. littoralis*, depending on its ability to perform SphA biosynthesis *in vivo* (Di Lelio et al., 2022). An *in vitro* study reveals the sub-lethal effect of a partially-purified protein derived from the EEPF, *Lecanicillium lecanii* (Zimmerman), associated with solanaceous crops such as tomato, on the green peach aphid *Myzus persicae* (Sulzer). Furthermore, RT-qPCR expression analyses of key genes associated with the salicylic acid (SA) and jasmonic acid (JA) pathways were found to be upregulated and thus revealed significant negative effects on *M. persicae* survival and fecundity. The *L. lecanii*-derived protein was found to strongly enhance the SA associated genes PR1, BGL2, AOS, PAL, LOX and AOC, indicating the enhancement of systemic resistance in plants, implying that it should be purified and characterised as a novel biomolecule against aphids and other phloem-feeding insect pests (Hanan et al., 2020). *Trichoderma harzianum* Tr6 is also a potent inducer of induced systemic resistance (ISR) and can stimulate the immune system in plants and also adversely affect the host preference and egg production of *Trialeurodes vaporariorum* (Aldaghi et al., 2021). Furthermore, the systemic effects of EEPFs (*Trichoderma asperellum*, *Gibberella moniliformis*, *B. bassiana*, *M. anisoplaie*, and *Hypocrea lixi*)

application on *Vicia faba* via seed treatment were observed and the aphid growth rate, offspring performance and fecundity were found to be retarded. Endophyte treatment was reported to reduce the number of *Aphis fabae* and *Aphis pisum* nymphs by 1.6-14.6 and 3.7-11.0 times, respectively, while endophyte seed treatment increased seedling survival by 20-100% compared to none in the control treatment at 20 days post infestation (Akello and Sikora, 2012). Individual or combined inoculation of *Rhizophagus intraradices*, an arbuscular mycorrhizal fungus and *B. bassiana*, an EEPF, resulted in increased levels of monoterpenes and sesquiterpenes in beet armyworm (*Spodoptera exigua* Hübner) - infected tomato plants, indicating a stronger terpenoid mediated defence response in host plants (Shrivastava et al., 2015). Four *Trichoderma* isolates, including two trichodiene (TD) (a non-phytotoxic VOC) producers (T34-5.27, E20-5.7) and their parental strains (T34, E20) were evaluated, and differential host preference (higher repellancy with the E20 strain) and altered emergence (reduced emergence with the E20 and T34 strains) of *Acanthoscelides obtectus* were observed in wild and cultivated common beans colonized by *Trichoderma* isolates (Rodríguez-González et al., 2019).

4.5 Impact of climate change on EEPF and its interaction with tropic levels

Climate change affects many biological processes and may impact bottom-up and top-down agroecosystem characteristics through tritrophic interactions (Chidawanyika et al., 2019). Global warming can alter interspecies relationships and community structure (Boukal et al., 2019) and thus influence the variety, distribution and function of plant associated microorganisms (Cavicchioli et al., 2019). Plants interact selectively with their microbiota to upregulate abiotic, biotic stress tolerance and growth enhancement (Rodríguez and Durán, 2020). Temperature impacts plants' physiology, chemistry, life cycle stages, development and growth, which affects microorganism-plant interactions (Pieterse and Dicke, 2007). Sui et al., 2020 explored temperature - EEPF interactions and temperature-induced physiological changes (2020) in *Zea mays* and *Beauveria bassiana*. In the ambient temperature range, maize's photosynthesis and respiration were reported to be increased (Bokhorst et al., 2010); PAL (Phenyl Alanine Ammonia Lyase) and PPO (Polyphenol Oxidase) are overexpressed in stress-adapted cells. Although *B. bassiana* develops at 20^o to 30^oC, EEPFs develop normally at an elevation of 2^o C (Rangel et al., 2010). Under elevated air temperature, maize had positive effects on *B. bassiana* (conidia yield, germination rate of conidia and virulence), while *B. bassiana*'s growth and biological characteristics remained unchanged. This suggests that elevated air temperature could shift the interactions between plants and EEPFs, possibly from

mutualism to commensalism. Moreover, EEPFs' rapid adaptation and ability to 'transfer' resistance to their hosts may speed plants' climate change adaptation, which can be regarded as positive feedback and better exploited for breeding varieties with higher colonisation potential of EEPFs to tolerate, adapt and mitigate climatic stresses. EEPFs may accelerate climate change responses in crops and wild plant communities and require efforts to improve EEPF-facilitated plant health. Such information could help develop better climate change mitigation methods for plant communities (Suryanarayanan and Shaanker, 2021).

5 Constraints associated with EEPF colonization in plants and their artificial inoculation

Weather patterns and soil conditions strongly influence the biology and ecology of fungi. Only one-tenth of the 1.5 million fungal species in soil have been examined. The natural relationship of EEPFs with plants is influenced by climate, vegetation, soil, location, and human and other biotic activities (Bing and Lewis, 1991) (Behie et al., 2014). However, other elements have been observed to play a role, such as an inoculum density, growing medium, plant age and species and

fungal species (Parsa et al., 2013). Success in the endophyte colonisation of a host plant also depends on the isolate or isolates of EEPFs utilised, the intended crop species, and the growth environment (Qayyum et al., 2015) (Figure 2). However, a different study indicated that the growth media employed had a bigger impact on the plant's endophytic colonisation than the inoculation strategy (Parsa et al., 2013). Thus, plants can be artificially inoculated with EEPFs using a variety of methods, such as foliar spraying, stomatal penetration, adhesion to the plant, seed dressing, soil inoculation, and even stem injections with varying results that could surpass the constraints associated with non-associated EEPFs in plants and thus affect the effectiveness of the fungal treatment and the degree of systemic colonisation (Vega et al., 2012). Colonisation can occur intracellularly, intercellularly, locally or systemically (Vega, 2018) or even vertically (Landa et al., 2013). Table 2 contains a list of successful cases of artificial plant inoculation with endophytic EPF in horticultural crops. Because it is restricted and protected from both abiotic and biotic influences within the plant, endophytic EPF requires less inoculum than inundative applications to soil or substrate (Akello et al., 2008). Therefore EEPF's isolation, identification, colonization, recovery, mass multiplication and commercialisation is of utmost concern in the present day. The potential roadmap for the commercialization of EEPF is detailed in flowchart form in Figure 3.

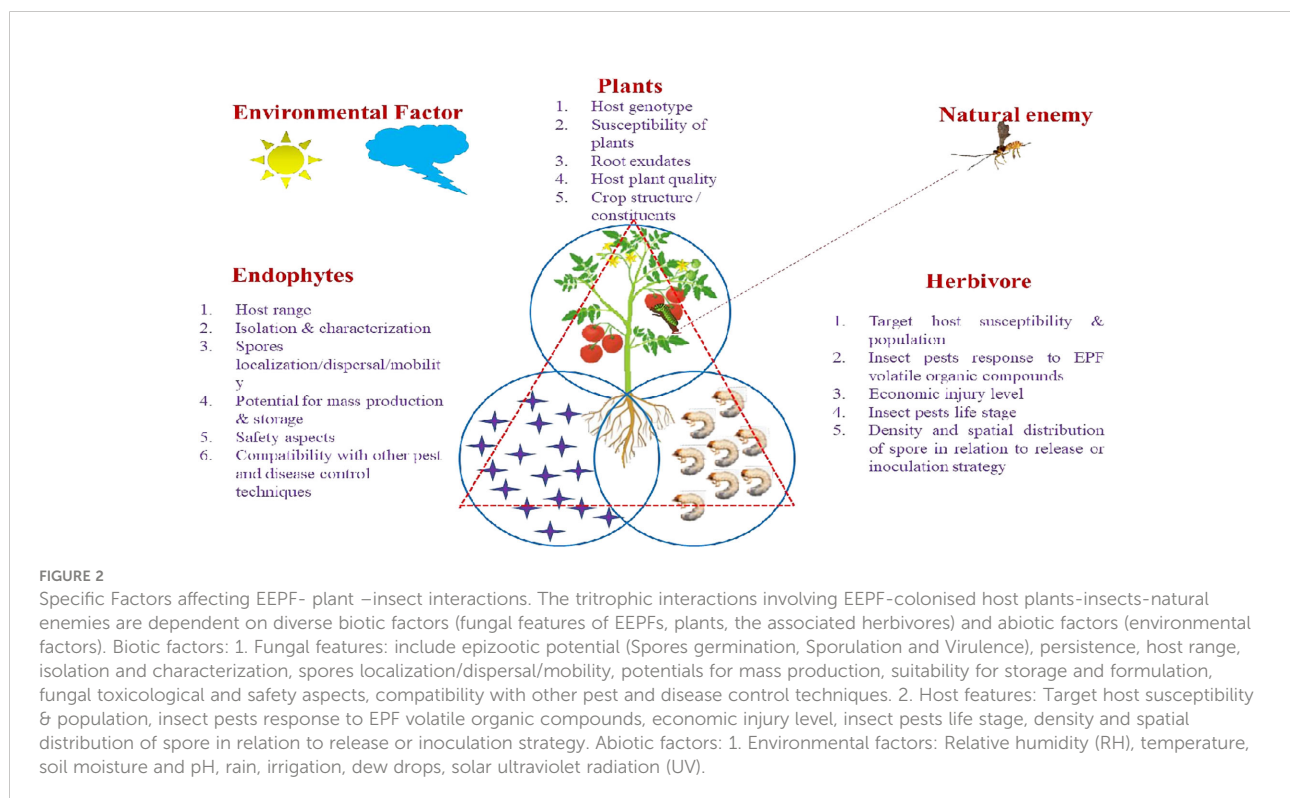
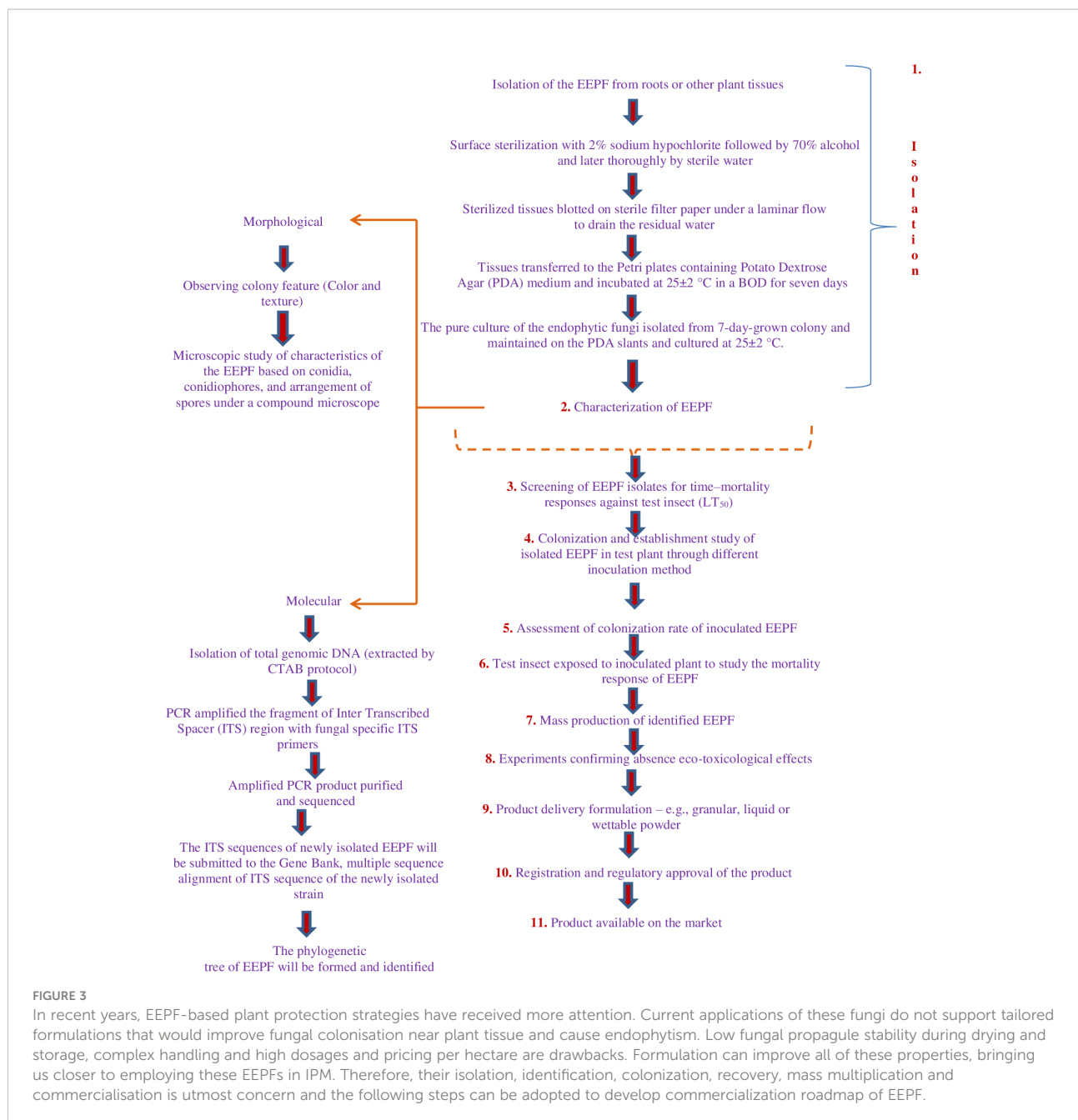


TABLE 2 Successful cases of artificial plant inoculation with endophytic EPF in horticultural crops against herbivore.

Sl. No.	Horticultural crop	EEPF	Inoculation method	Target pest	Country	Reference
1	Potato, <i>Solanum tuberosum</i>	<i>Beauveria bassiana</i>	Foliar application	European corn borer, <i>Ostrinia nubilalis</i>	North Carolina	Jones, 1994
2	sweet pepper, <i>Capsicum annuum</i>	<i>Metarhizium brunneum</i>	Soil drenching	Green peach aphid, <i>Myzus persicae</i>	Jordan	Jaber and Araj, 2018
3	Grapevine, <i>Vitis vinifera</i>	<i>Beauveria bassiana</i>	Foliar application	Vine mealybug, <i>Planococcus ficus</i>	Germany	Rondot and Reineke, 2018
4	Banana, <i>Musa</i> spp.	<i>Beauveria bassiana</i>	Root and rhizome dip	Banana weevil, <i>Cosmopolites sordidus</i>	Uganda	Akelo et al., 2008
5	Tomato, <i>Solanum lycopersicum</i>	<i>Beauveria bassiana</i>	Seed treatment	Corn earworm, <i>Helicoverpa zea</i>	USA	Powell et al., 2009
6	Tomato, <i>Solanum lycopersicum</i>	<i>Beauveria bassiana</i>	Root dip, injection, solid substrate and direct foliar application	Tomato shoot and fruit borer, <i>Helicoverpa armigera</i>	Pakistan	Qayyum et al., 2015
7	Cauliflower, <i>Brassica oleracea</i>	<i>Beauveria bassiana</i> , <i>Metarhizium brunneum</i>	Foliar application	Sweetpotato whitefly, <i>Bemisia tabaci</i>	Jordan	Jaber et al., 2018
8	Strawberry, <i>Fragaria</i> × <i>ananassa</i>	<i>Beauveria bassiana</i> , <i>Isaria fumosorosea</i> and <i>Metarhizium anisopliae</i> var. <i>robertsii</i>	Rhizome treatment	Green peach aphid, <i>Myzus persicae</i>	Greece	Manoussopoulos et al., 2019
9	Pepper, <i>Capsicum annuum</i>	<i>Beauveria bassiana</i> , <i>Metarhizium anisopliae</i> and <i>Isaria fumosorosea</i>	Foliar application	Green peach aphid, <i>Myzus persicae</i>	Greece	Mantzoukas and Lagogiannis, 2019
10	Common bean, <i>Phaseolus vulgaris</i> , Faba bean, <i>Vicia faba</i>	<i>Beauveria bassiana</i> , <i>Hypochoeris lixii</i>	Seed soaking	Leaf minor, <i>Liriomyza</i> spp.	Kenya	Akutse et al., 2013
11	Onion, <i>Allium cepa</i>	<i>Clonostachys rosea</i> , <i>Fusarium</i> sp., <i>Hypocera lixi</i> , <i>Trichoderma harzianum</i>	Sedd treatment	Onion thrips, <i>Thrips tabaci</i>	Kenya	Muvea et al., 2014
12	Tomato, <i>Solanum lycopersicum</i>	<i>Acremonium strictum</i>	Soil drenching	American bollworm, <i>Helicoverpa armigera</i>	Germany	Jallow et al., 2008
13	Pumpkin, <i>Cucurbita maxima</i>	<i>Beauveria bassiana</i> , <i>Lecanicillium lecanii</i> , <i>Aspergillus parasiticus</i>	Foliar spray	Melonor cotton aphid, <i>Aphis gossypii</i> , Australian plague locust, <i>Chortoicetes terminifera</i>	Australia	Gurulingappa et al., 2010
14	Cauliflower, <i>Brassica oleracea</i>	<i>Beauveria bassiana</i>	Foliar spray	Diamondback moth, <i>Plutella xylostella</i>	India	Gautam et al., 2016
15	Cucumber, <i>Cucumis sativus</i>	<i>Lecanicillium longisporum</i>	Foliar spray	Cotton or melon aphid, <i>Aphis gossypii</i>	Canada	Kim et al., 2010
16	Date palm, <i>Phoenix dactylifera</i>	<i>Beauveria bassiana</i>	Stem injection	Red palm weevil, <i>Rhynchophorus ferrugineus</i>	Egypt	Arab and El-Deeb, 2012
17	Melon, <i>Cucumis melo</i>	<i>Beauveria bassiana</i> and <i>Metarhizium brunneum</i>	Foliar spray	Sweet potato whitefly, <i>Bemisia tabaci</i>	Spain	Garrido-Jurado et al., 2017
18	Melon, <i>Cucumis melo</i>	<i>Metarhizium brunneum</i>	Foliar spray	Leaf worm, <i>Spodoptera littoralis</i>	Spain	Miranda-Fuentes et al., 2021
19	Tomato, <i>Solanum lycopersicum</i>	<i>Beauveria bassiana</i>	Seed soaking, Leaf spraying, Root dipping	Tomato leafminer, <i>Tuta absoluta</i>	Argentina	Allegrucci et al., 2017
20	Faba bean, <i>Vicia faba</i>	<i>Beauveria bassiana</i>	Seed or leaf inoculation	Aphid, <i>Aphis fabae</i>	Denmark	Jensen et al., 2019



6 Integrated omics approaches to understand EFPF-host plant- insect interaction

The primary emphasis of these beneficial microbial associations was multitrophic interaction involving EFPF colonised plants-insects-natural enemies. However, the underlying physiological elements of endophyte-host interactions remain unknown. Identifying, isolating, and characterising the genes implicated in such beneficial

connections is therefore crucial for efficiently regulating their interplay (Harith-Fadzilah et al., 2021). Plant-microbe interactions, particularly plant-EFPF interactions can be studied using multi-omics approaches. This thorough investigation of endophytic multi-omics data, from the genome to the metabolome, will aid in understanding their potential to biosynthesize secondary metabolites and lay the groundwork for the future development of this lucrative resource (Crandall et al., 2020). We explored the importance of several omics technologies in understanding the role of EFPFs and their interactions with related hosts in the following sections.

6.1 Genomics approaches

Owing to advancements in genome sequencing technology, identifying the fungus isolated from plants is now a cheap and quick process. One of the most popular programmes for sequence alignment, Basic Local Alignment Search Tool (BLAST), is utilised in the in-silico identification procedure to determine the degree of similarity between the sequences (Altschul et al., 1990). First, the coffee (*Coffea arabica*) fungal endophytes were identified using the BLAST approach and it was found that there were 15 different species in the area, two of which, *B. bassiana* and *Cladosporium rosea*, demonstrated pathogenicity against the coffee stem borer (Vega, 2008). The sequencing revolution and computer techniques for assembling and annotating genome sequences made fungal genome reconstruction conceivable. Many specialised metabolites are generated by pathways encoded by physically nearby genes on fungal endophyte genomes. These microbial secondary metabolites are a major untapped resource of natural products (NPs) with agrochemical and medicinal applications. Quantity and composition vary on host plant type, plant development phases, environmental stress, and other factors affecting plant growth, such as insect-pest attacks (Baudoin et al., 2003; Gunatilaka, 2006).

Therefore, utilizing gene clustering in EEPFs that are organized into operon structures under a single promoter, several computational methods have been developed to identify metabolic gene clusters and pursue the discovery of specialized metabolites. Co-inheritance, co-transcriptional regulation, and coordinated post-transcriptional processes, such as protein synthesis export, are benefits of gene clustering. Genome sequencing and annotation for *M. acridum* and *M. robertsii* (Gao et al., 2011), *B. bassiana* (Xiao et al., 2012), and *M. anisopliae* (Pattimore et al., 2014) give information on secondary metabolite encoding. With so much genetic data, secondary metabolite gene clusters are abundant. The present objective is to tie biosynthetic gene clusters (BGCs) to as many known molecules as feasible and forecast the molecules that encode the most promising compounds. NP.searcher (Chavali and Rhee, 2018), ClustScan (Starcevic et al., 2008), CLUSEAN (Weber et al., 2009), antiSMASH (Medema et al., 2011), SMURF (Khaldi et al., 2010), MIDDAS-M (Umemura et al., 2013) and ClusterFinder (Cimermancic et al., 2014) like computational approaches have helped researchers uncover genes producing secondary metabolites like Non-ribosomal Peptide Synthases (NRPSs), NRPS-like enzymes, and polyketide synthases (PKSs). Most core enzymes were distributed into 75 BGCs (Wang et al., 2015). To comprehend and manipulate EEPFs, and clarify endophytes' metabolic potential and beneficial qualities (Dinsdale et al., 2008), metagenomics allows the discovery of new genes, proteins or even full genomes of uncultivable organisms in less time and with more precision than conventional microbiological and molecular approaches,

providing information beyond individual taxon genomics. Amplicon sequencing and whole genome shotgun sequencing are used to study the microbiome. Internal Transcribed Spacers (ITS) of nuclear ribosomal DNA (rDNA) serve as a marker to distinguish most fungal species since it is extremely repetitive and variable portions are flanked by more conserved DNA sequences (Hillis and Dixon, 1991; Schoch et al., 2012). Over 100,000 fungal ITS sequences generated by Sanger sequencing are stored in the International Nucleotide Sequence Database (INSD) and/or other databases, providing extensive reference material for identifying endophytic fungal species (Nilsson et al., 2009). PCR was used to identify endophytic fungi from diverse tomato plant parts. Using ITS1 and ITS4 primers, *B. bassiana* was validated based on sequence homology (Leckie, 2002). In another study, fungal-specific ITS1-F and ITS4 primers were used in coffee seedlings and a drop in *B. bassiana* colonisation was detected. This may be due to competition with other endophytes in coffee plants, such as *Alternaria* sp. and *Chaetomium* sp (Posada et al., 2007). Potent endophyte isolates of *Aspergillus nidulans* were reported with larvicidal activity against *Spodoptera littoralis* larvae on the sequencing of the flanking ITS regions (El-Sayed et al., 2020). A similar molecular approach was employed to identify 15 native EEPF species isolated from two insect hosts viz., *Hypera postica* and *Gasteracantha fornicata* to study their pathogenicity against the apple blossom beetle (ABB). In addition to molecular characterization, ITS region based phylogenetic analysis of the obtained isolates was also performed using MEGA (Kumar et al., 2008) for the identification of the isolates. The results showed that all the isolates of *B. bassiana* have significant effective activity against ABB adults (Uçar et al., 2022). The ITS (ITS4 and ITS5) sequence analysis of the entomopathogenic fungal isolates from cocoa seedling tissues were carried out and three naturally occurring fungal endophytes viz., *Fusarium redolens*, *Trichoderma asperellum*, *F. solani*, *B. bassiana*, *Metarhizium* sp. and *Hypocrea* sp were identified using molecular techniques. The latter three were reported to show high virulence against termites (*Odontotermes* sp.) (Ambele et al., 2020). 18S rDNA region of ribosomal RNA is another molecular marker broadly applied in molecular fingerprinting studies of fungi. *B. bassiana* isolated from *Atractylodes lancea* was identified based on the conserved sequences in the 18S rDNA (Lv et al., 2014).

6.2 Transcriptomics approaches

Transcriptome analysis that is useful for identifying gene function (Iyer et al., 1999) (Yuan et al., 2019) include microarrays that represent almost exclusively mRNAs, i.e. genes translated into proteins. Microarray approach has now been replaced by RNA-Seq, a high-throughput RNA sequencing method (Wang et al., 2009). Transcriptome study of EEPF can help discover its secondary metabolites in two ways. Firstly,

these methods can highlight co-regulated gene clusters which comprise such clusters that are separately involved in the synthesis of various secondary metabolites, but whose expression is linked. Secondly, transcriptome techniques can be applied to understand the relationships between genes and secondary metabolites or between genes and active traits (Mao et al., 2015; Cheng et al., 2020). Transcriptome analyses have also revealed the shifting of endophytes lifestyle from biotrophic to necrotrophic during adverse conditions such as reduced carbohydrate levels in bud (Ribeiro et al., 2020). The effects of two *B. bassiana* strains (BG11, FRh2) on *Arabidopsis thaliana* growth and resistance to two herbivore species (aphid, *Myzus persicae* and diamond back moth, *Plutella xylostella*) were studied (Raad et al., 2019) using transcriptomic and metabolomics approaches through microarrays, and upregulation and downregulation of defense-related phytohormones and glucosinolates (GLSs). Root injection with *B. bassiana* BG11 increased plant growth, while FRh2 did not. Both *Beauveria* strains showed no significant effect on *Myzus persicae* population increase or *Plutella xylostella* growth. Metabolomics microarray investigations of leaves from endophyte-inoculated *A. thaliana* showed transcriptional reprogramming of plant defence pathways, with strain-specific changes in the expression of genes linked to pathogenesis, phytoalexin, jasmonic (JA), and salicylic acid (SA) signalling pathways. *B. bassiana* colonisation did not increase JA, SA, or leaf GLSs profiles, which Brassicas use for defence. Thus, EEPF-plant associations can increase biomass and sesquiterpenoids accumulation in *A. lancea* by increasing photosynthesis efficiency, sink expansion (glycolysis and tricarboxylic acid cycle), and metabolic flux (sesquiterpenoids biosynthesis pathway). This study will help clarify plant-EEPF interactions (Yuan et al., 2018).

6.3 Proteomics approaches

Besides the aforementioned technologies, the fungal secondary metabolome can also be studied from a proteomics perspective. Recent proteomic analyzes have paved the way for identifying important biomarkers and are able to explain post-transcriptional modifications that can occur during the synthesis of secondary fungal metabolites. Proteomics can also be used to study the fungal secondary metabolome. Recent proteomic analyses have helped discover significant biomarkers and explain post-transcriptional alterations during secondary fungal metabolite production. NRPS, PKS, DMATS, and 2D polyacrylamide gel electrophoresis (PAGE)-LC-MS/MS can be utilised to understand the secondary metabolome and protein alterations. Proteomics can be an effective technique for understanding plant-microbe interactions, despite the complexity of biological materials. Gómez-Vidal et al. (2009) studied the proteomic response of date palm to the endophytic

colonization by various EEPF which included *B. bassiana*, *L. dimorphum*, and *L. psalliotae* isolated from infected *Thaumatococcus panyocampa*, *Saissetia oleae* and *P. marlatti*. Peptides were identified from MS/MS data used to search the nr-NCBI database using the MASCOT software (<http://www.matrixscience.com>). They identified proteins encoding R genes, proteins associated with stress responses, and smHSPs, to be differentially expressed in infected date palm plants as compared to healthy leaves. These proteins could play a role in plant defence against both biotic and abiotic stress. The study suggested that endophytic colonization of date palm tissue by EEPFs induces a plant defense response, possibly by alerting the plant's innate immune system (Gómez-Vidal et al., 2009). Further molecular analysis studies conducted on plants infected with EEPFs revealed that endophytes induce important changes in plant metabolism, even if the plants do not show symptoms of endophytic infection. To study low abundance proteins, isobaric tags for relative and absolute quantification (iTRAQ) like strategies have been developed (Wiese et al., 2007; Taylor et al., 2008) which can help decipher the post-transcriptional modifications and proteomics experiments. However, recent advances in metabolomics have provided a facile method to directly detect secondary metabolites and also account for post-transcriptional as well as post-translational modifications. Gómez-Vidal et al. (2009) studied the molecular interactions between three EEPFs viz., *B. bassiana*, *Lecanicillium dimorphum*, *Lecanicillium psalliotae* and the date palm (*Phoenix dactylifera*) using proteomics techniques.

6.4 Metabolomics approaches

Mass spectrometry is used in metabolomics to discover secondary metabolites in microbial cultures and de-duplicate molecules (MS). No separation or purification of fungal cultures is required before analysis therefore, enormous data sets are accessible. To organise MS/MS data by spectrum similarity, comparable sequences are grouped and representative sequences are identified. MS-based molecular cross-linking de-duplicates complex chemical samples like natural products. GNPS (Global Natural Products Social Molecular Networking) archives and makes available processed MS/MS spectrum data (Wang et al., 2016). Together, molecular bridging and GNPS can aid in the identification of certain chemical classes and substances, allowing researchers to better prioritise samples for follow-up analysis. The effects of *B. bassiana* inoculation on lettuce plant development, tissue nutrient content, and proximate composition were investigated, and it was observed that the *B. bassiana* strain induced a mean insect death of 78% at the maximum dose (1×10^8 conidia mL⁻¹). Up to 76% of plants were endophytically colonised by *B. bassiana* when exposed to 1×10^8 conidia mL⁻¹. Endophytic colonisation had a substantial effect on the plant's tissue carbon content, which was also

connected with the lettuce plants' antioxidant capacity. Plants treated with *B. bassiana* had higher FRAP (Ferric ion reducing antioxidant power) and TEAC (Trolox equivalent antioxidant capacity) (antioxidants) than those not treated. Further, phytochemical and proximate investigations may shed light on the plant tissue's macronutrient, micronutrient, and antioxidant composition. The connection between carbon concentration and antioxidant ability may be further understood through metabolomics research in the future (Macuphe et al., 2021).

7 Conclusion and future perspectives

EEPFs protect plants from insects, parasitic nematodes and disease pathogens; they promote nutrient uptake, and improve abiotic stress tolerance. Understanding how EEPFs promote nitrogen uptake in host plants might help organic and inorganic fertiliser users save money. EEPFs' ability to improve plant tolerance to abiotic stresses like heat, salt, and drought can add a new dimension to their interaction with host plants and could be explored or used in agriculture not only to mitigate pests and/or diseases under climate change conditions, but also as an alternative to EPF auto-distribution in inundating applications. Because EPFs applied as inundative sprays for short-term pest control are susceptible to environmental factors, EEPFs residing within plant tissues can help overcome this limitation. When successfully established as endophytes in plants, EPFs can provide long-term, sustainable protection against pests and diseases in horticultural crops. Multi-omics data, including downstream signalling processes, can reveal their nutri-metabolic role as a sustainable pest control tool. The review focuses on the EEPF-plant beneficial relationship on tritrophic interaction, mode of colonisation in diverse horticultural crops, and molecular and biochemical interactions involved in EEPF-mediated insect and natural enemy performance. The current review suggests the following conclusions and future developments.

7.1 Qualitative and quantitative alteration of host plant nutrients

It has been reported that EEPF infested plants impact herbivory and the feeding and survival of natural enemies. Through altered VOCs produced by EEPF-colonised plants, EEPF-plant colonisation considerably affects and modulates the insects' preference, performance, as well as natural enemies' functional and numerical host finding efficiency. Endophytic fungus-inoculated plants have a distinct profile of volatile organic chemicals than endophyte-free plants, which attracts more insect herbivores. The ecological effect of EEPF in the host plant-insect-natural enemy interaction must be described.

7.2 Enhancing nutritional quality of plants

Certain growth and development promoting factors that are caused by EEPF colonisation include nutritional enrichment of plants, morpho-physiological development and tolerance and/or sustenance of varied biotic and/or abiotic challenges and increasing leaf chlorophyll contents.

7.3 Increasing constitutive and induced plant defense

Although plants have morpho-chemical constitutive and induced defence mechanisms against various sucking and chewing pests, EEPF association has been shown to increase the protective layers of the plants, promoting both intrinsic and extrinsic resistance.

7.4 Constraints in wider application

Though EEPF colonisation has been recorded intracellularly, intercellularly, locally, systemically, and even vertically, research on the artificial establishment of EPF in plants for endophytic colonisation is still in its infancy for pest management. Furthermore, when compared to inundative biological control, EEPFs require a lower inoculum dose, which can be beneficial to farmers in the long run. Pest management in today's world requires plant protection options that are both economical and environmentally sustainable; EPF can certainly assist. The inclusion of EPF in plants as endophytes seems like a highly fascinating and promising strategy in horticulture crops, but its wider use has been hampered by certain climatically unfavourable situations. Commercially, supplying pre-colonized tomato plants through seedling inoculation may be a good alternative (Silva et al., 2020). EEPF inoculation in horticultural crops may be preferable to chemical applications because of its potential for long-term economic and ecological benefits. When comparing the cost-benefit ratio of different biocontrol methods, such as introduction (classical biological control), augmentation, and conservation, the cost-benefit ratio for classical biological control is extremely favourable (1:250), while the cost-benefit ratio for augmentative control is comparable to that of insecticides (1:2-1:5), with much lower development costs (Bale et al., 2008). EEPFs that establish in the host plants frequently yield larger economic returns than a pesticide application, although the initial stages of identification, isolation and characterization and inoculation methods might be more expensive than for pesticides. In contrast to what has been reported in the past, the danger of resistance and undesirable side effects is higher in chemical control, while the profit per unit of money invested

and specificity are higher for biocontrol agents (van Lenteren, 1997; Bale et al., 2008). Although this has not yet been investigated, it is possible to compare the pros and downsides of using pesticides against inoculation EEPFs on horticultural crops.

7.5 Lesser explored areas

Despite extensive research on EEPFs, only a few species have been investigated. Because of the scarcity of research in this field, it is often assumed that there are thousands more unknown EEPFs. As a result, there is an urgent need to identify and assess these unknown EEPF strains. Molecular methods and bioinformatics tools may be useful in uncovering this hidden treasure. Studies in the future may concentrate on isolating, identifying, and characterising EEPFs, as well as providing qualitative and quantitative estimates, elucidating structures, and screening the structure-activity link of biologically active molecules.

7.6 EEPF study beyond omics

Many bioactive agrochemicals are derived from secondary metabolites produced by endophytes. The current reliance on plants as a source of bioactive compounds can be reduced by the discovery of drugs based on natural products through the EEPF. Fungal endophytes may represent a substantial untapped resource of bioactive natural products/biotic insecticides, as their genomes can be sequenced to reveal previously unknown specialised metabolites and their production methods. In most cases, evidence of endophyte-host mutualism studies were only confined to *Beauveria sp* and *Metarrhizium sp*. There are still many uncovered areas and undiscovered genera of EEPFs, that could potentially serve to understand the intricate yet complicated relationships among host plants- EEPF colonisation on insect-natural enemy interaction. Further studies on the involvement of different receptors, patterns as well as effector molecules that lead to diverse physiological mechanisms in endophytes colonisation, intra and interplant movement of fungal

inoculum, EEPF- plant association on insect abundance, survival, preference and response of natural enemies are limited. Additionally, an in-depth knowledge of the abiotic and biotic variables that influence the insecticidal action of EPF and their endophytic behaviour is required for the actual introduction of EEPFs into the IPM programmes.

Though EEPFs have been the subject of a great deal of research, only a small fraction of species have been examined thus far. Due to a lack of investigation, it is widely assumed that there are still thousands of endophytes that have yet to be discovered. Consequently, identifying and assessing these unidentified endophytic strains of EEPFs is of utmost importance.

Author contributions

IS, TB, PM, SnM, AP, SuM, AP, PA: Conceptualization, writing, original draft preparation, preparation of tables and supervision; A, VS, DM, JK, NM, PB, DK, TaB: Preparation of figures, supervision, review and editing. All authors contributed to the article and approved the submitted version.

Conflict of interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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