



## FUNGAL ENDOPHYTE-PLANT-INSECT INTERACTION: A TRIPARTITE ASSOCIATION NEEDING ATTENTION

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### ABSTRACT

**Fungal endophytes are microfungi which infect the aerial and underground living tissues of plants and live within them without causing any disease symptoms. Their association with plants confers several benefits to plants and enhances their innate ability to tolerate abiotic and biotic stresses. Despite their universal occurrence, their ability to improve plant performance and capacity to produce numerous novel bioactive compounds, information on the ecology of fungal endophytes is incomplete. The interaction of these fungi with plants, plant-associated organisms, cooccurring endophytes (other fungi and bacteria), and the environment is little understood. This article highlights one such interaction among plants-fungal endophytes-plant-feeding insects that needs attention.**

**Key words:** Entomopathogenic fungi, plant-feeding insects, plant microbiome, microfungi, plant performance, ecology, interactions

Fungi and insects are the most-speciose and most-widespread organisms. They not only interact among themselves but also with plants. Insect-fungus interactions cover the entire gamut of symbiosis from mutualism to antagonism. Different species of Hypocreales (Ascomycota), such as *Beauveria bassiana*, *Metarhizium robertsii*, and *Ophiocordyceps unilateralis*, are popular examples of pathogenic fungi that are associated with multiple taxa of arthropods and are presently exploited as biological-management agents to manage pestiferous-arthropod populations. When fungi and arthropods collectively interact with plants, such associations impact on the fitness of plants. Spores and mycelial fragments of plant-pathogenic fungi either sticking to insect bodies or ingested by insects are transported to healthy plant tissues (Willsey et al., 2017). An insect can also acquire a pathogenic fungus along with food, which then circulates within the insect body and reaches its mouthparts, and finally enters the plant when the insect feeds on the plant (Wielkopolan et al., 2021). Insect-fungus interactions can be categorized from 'symbiosis' (= mutualism) to 'antagonism'. The involvement of the plant as the third component in such associations, further confounds the interaction scene. Examples of such a tripartite interaction include the modification of flower nectar by different species of yeasts (e.g., *Metschnikowia gruessii*, *M. reukaufii* [Saccharomycetales: Metschnikowiaceae], *Aureobasidium pullulans* (Dothideales: Dothioraceae),

*Hanseniaspora uvarum* (Saccharomycetales: Saccharomycetaceae), and *Sporobolomyces roseus* [Sporidiobolales: *Incertae Cedis*) to make it more attractive nutritionally and by scent, for the pollinating *Apis mellifera* (Hymenoptera: Apidae) and parasitic *Aphidius ervi* (Hymenoptera: Braconidae) (Sobhy et al., 2018).

Generally, infection by a fungus alters the host plant's metabolism leading to either enhanced levels of defence compounds or diminished levels of nutrients (Raman and Suryanarayanan, 2017). Fungal-plant pathogens modify the phenotypes, nutritional profiles, and the chemistry of volatile-organic compounds (VOCs) of their host plants as a tactic to attract arthropod vectors enabling their dispersal. For example, the plant-pathogenic *Fusarium verticillioides* (Hypocreales: Nectriaceae) modifies the chemistry of its host-plant's mechanism of biosynthesis of volatile compounds making them attractive for the caterpillars of *Diatraea saccharalis* (Lepidoptera: Crambidae). Furthermore, this fungus influences both the host plant and insect's lifecycle to promote its infection and spread (Franco et al., 2021). Similarly, colonization of roots by 'mycorrhizae', the soil-inhabiting fungi that usually bear a symbiotic relationship with the roots of diverse flowering plants. Such mycorrhizal associations distinctly alter multiple morphological, physiological, and biochemical characteristics of the host plant, such that the overall performance of those insects that feed on the plant

is influenced either positively or negatively, which largely depends on the feeding mode and diet range of the insect taxon and associated mycorrhizal species (Koricheva et al., 2009). Plant-insect interactions have been studied in great detail because the plant-feeding arthropods affect production of crop plants in particular by feeding on the aerial and below-ground plant parts (Sharma et al., 2017). Moreover, the role of arthropods as vectors of plant pathogenic microbes is well known (Agrios, 1997).

Presently, we know too well that flowering plants harbour different species of bacteria and fungi, which do not manifest any disease symptoms. Such nonpathogenic fungi and bacteria are termed the 'endophytic fungi' and 'endophytic bacteria', respectively. Species of *Colletotrichum* (Glomerellales: Glomerellaceae), *Phomopsis* (Diaporthales: Valsaceae), *Phyllosticta* (Botryosphaerales: Botryosphaeriaceae), and *Xylaria* (Xylariales: Xylariaceae) are common endophytic fungi and *Pseudomonas* (Pseudomonadales: Pseudomonadaceae), *Burkholderia* (Burkholderiales: Burkholderiaceae), and *Bacillus* (Bacillales: Bacillaceae) are common endophytic bacteria, which colonize the leaves of almost all terrestrial plants. Few algae (Chlorophyta) such as *Cephaleuros* (Trentepohliales: Trentepohliaceae) also occur as endophytes in some plants. Endophytic lifestyle is so common among fungi such that plant-fungal endophyte relationship could be ancestral in nature. Ancestors of fungi possibly were endophytes such that they infected plants and switched their lifestyle to either saprobes or pathogens. This hypothesis is supported by fossil evidence and the lifestyle shifts, common among fungal endophytes (Bhunjun et al., 2023). It is estimated that 1-3 million fungal-endophyte species exist, although presently only c. 150,000 species have been determined and named (Bhunjun et al., 2023).

Based on the types of symbiosis they manifest, the fungal endophytes are presently classified into four types (Rodriguez et al., 2009): 1. Species of the Clavicipitaceae cause systemic intercellular infections in the shoots of some cool-season grasses and are transmitted vertically through seeds. Here, the endophyte fungal mycelium grows systemically within the host plant and enters its seeds; when such endophyte infected seeds germinate, the endophyte mycelium within the seed grows systemically within the seedling and continues to grow as the plant matures only to infect its seeds again. All the other three classes of endophytes are non-Clavicipitaceous fungi. The

type 2 endophytes colonize the roots, stems, and leaves and are transmitted through seed coats and rhizomes. The type 3 endophytes infect the above-ground tissues of vascular and non-vascular plants. They are hyperdiverse, ubiquitous and their spores are transmitted to new plant hosts through air or insect vectors (horizontal transmission). The type 4 endophytes colonize the roots and have dark septa in their mycelium. In this opinion article, I will refer to the type 3 fungal endophytes to underscore the need to study the tripartite interaction between the plant, endophyte and insect.

### Fungal endophyte-plant interaction

A leaf is usually and entirely colonized by 10-15 species of fungal endophytes. These could be either symbiotic or latent pathogens (Hyde et al., 2019). The ecological functions of fungal endophytes and their interaction with plants and simultaneously with other associated endo-microbes are not clear (Suryanarayanan, 2020). A few studies have shown that infection by a fungal endophyte protects the host plant from other pathogens (Arnold et al., 2003) by upregulating many defense genes of the host plant, thus making it more resistant to pathogens (Mejía et al., 2014). Furthermore, fungal endophytes are a novel source of bioactive secondary metabolites exhibiting interesting bioactivities including anticancer, anti-fungal and anti-diabetic, as proved by their ability to produce such molecules in aseptically cultured in the absence of their plant hosts (Schulz et al., 2002; Suryanarayanan et al., 2009; Aly et al., 2010). Apart from producing novel metabolites without the association with their host plants, a few fungal endophytes are capable of producing the secondary metabolites of their host plants; these include the anticancer metabolites such as paclitaxel (Stierle et al., 1993) and camptothecin (Kusari et al., 2009; Kusari and Spiteller, 2012).

Fungal endophytes also are a source of novel enzymes of industrial importance such as inhibitor-resistant biomass-degrading enzymes (Sengupta et al., 2017; Suryanarayanan et al., 2012) and anticancer enzymes (Nagarajan et al., 2014). A few recent studies reveal that fungal endophytes increase the fitness of their host plants by increasing their tolerance to abiotic stressors (Suryanarayanan and Uma Shaanker, 2021). For instance, a fungal endophyte isolated from the salt-tolerant *Oryza sativa* var. *Pokkali* (Poaceae) water-logged coastal parts of Alappuzha, Thrissur, and Ernakulam districts of Kerala, when inoculated in a salt-sensitive variety of *O. sativa* enables it to tolerate salt stress and to grow in salt water (Sampangi-Ramaiah et

al., 2020). Similarly, fungal endophytes from plants of geothermal habitats when transferred to heat-sensitive plants confers heat tolerance to them (Rodriguez et al., 2008).

### Insect partners in the complex association

Despite being a consistent endosymbiotic component of plants, the association and interactions of plants-fungal endophytes-plant-feeding insects has received little attention. This could be due to that some patterns are apparent while considering interactions between plants and fungi; however, when the plant-feeding insects are considered in the equation, no discernible pattern is obvious probably due to the increased level of complexity involving three components (Raman and Suryanarayanan 2017). Considering the extensive width of taxonomic variability, the endophytic fungi and their ability to infect nearly all of the species of the Plantae, numerous patterns of interactions involving plants, fungi, and insects become evident (Suryanarayanan, 2013). For instance, it is highly likely that a direct relationship exists between insects and fungal endophytes on a flowering plant. One indirect evidence for this comes from the study of endophyte status of *Bt* (*Bacillus thuringiensis*) gene-incorporated varieties of *Gossypium hirsutum* (Malvaceae) (Suryanarayanan, 2013). When compared with the wild type, different tissues *Bt*-incorporated *G. hirsutum* had strikingly lesser density of fungal endophytes. This suggests that insects visiting *G. hirsutum*, for either pollinating or feeding possibly transmit the inoculum of the endophyte fungus (Suryanarayanan et al., 2011).

Moreover, injuries inflicted by insects on plants possibly act as portals for the fungal endophyte infection. Plant-feeding insects visiting and damaging plants are possibly influenced by the metabolites produced by the fungal endophyte–plant association. It is known that the fungal pathogen *F. verticillioides* enters the host plant through the injuries caused by the feeding activity of *Diatraea saccharalis* (Lepidoptera: Crambidae). Once established in the host plant, the fungus emits volatile compounds to attract the immatures; when the caterpillars become adults, the fungus is vertically transmitted through their offspring, which continues the cycle by inoculating the fungus into healthy plants (Franco et al., 2021). Extending this example, studies are needed to know if fungal endophytes similarly alter plant metabolism and physical properties to either attract or deter insect visits to host plants (Li et al., 2014). Supporting of certain

species of fungal endophytes deters plant-feeding insects from attacking the host thus enhancing plant performance. For example, the foraging behaviour of *Atta colombica* (Hymenoptera: Formicidae) in Panama isthmus is influenced by the endophytes harboured in the leaves of *Merremia umbellata* (Convolvulaceae). The presence of endophytes negatively affected the foraging preferences of populations of *A. colombica*, although the reasons for avoidance of endophyte-rich host leaves by *A. colombica* are not clear as yet (Van Bael et al., 2009). These results suggest that interactions among fungi in the leaf endobiome and between the leaf tissue and fungal endophytes could alter the chemical environment, thus rendering it less attractive for *A. colombica*.

Additionally, the leaf could be less attractive due to chemicals produced by the fungal endophytes that are capable of producing several novel secondary metabolites (Sumarah and Miller, 2009). The foliar-fungal endophyte *Phialocephala scopiformis* (Helotiales: Mollisiaceae) produces the anti-insect compound ‘rugulosin’, when residing in some species of Pinaceae, thus negatively affecting the growth and development of *Choristoneura fumiferana* (Lepidoptera: Tortricidae) (Sumarah and Miller, 2009). Fungi generally known to live as either heterotrophs (e.g., species of *Alternaria*, Pleosporales: Pleosporaceae) or latent pathogens (several species of the Botryosphaeriaceae) or entomopathogenic (*B. bassiana*) exist as endophytes in leaves of plants. Established entomopathogenic fungi such as species of *Beauveria*, *Isaria* (Hypocreales: Cordycipitaceae), and *Metarhizium* (Hypocreales: Clavicipitaceae) survive as endophytes in tissues of both non-crop and crop plants (Vega, 2008). Vega et al. (2008) demonstrated that the two entomopathogenic fungi, viz., *B. bassiana* and *Clonostachys rosea* (Hypocreales: Bionectriaceae) living as endophytes in laboratory-maintained *Coffea arabica* (Rubiaceae) are potentially capable of regulating populations of *Hypothenemus hampei* (Coleoptera: Curculionidae). The ability of such entomopathogenic fungi to colonize and survive in plants as endophytes and to protect their host plants against insects has enhanced the hope of using endophytes for biological management of pestiferous arthropods and heterotrophic fungi such as *Botrytis cinerea* (Helotiales: Sclerotiniaceae) (Bamisile et al., 2018; Mantzoukas and Eliopoulos, 2020).

However, more studies are necessary to understand several aspects including the host preference and density of colonization of different crop plants by

entomopathogenous endophytes, and their interaction with other endophytes (Jaber and Ownley, 2018) before employing them as useful biological-management agents. It is further important to note that the ambient environment, soil nutrients, agricultural practices, and soil-microbial structure influence the establishment of the endosymbiotic community of a plant (Mighell et al., 2019). For instance, Suryanarayanan et al. (2018) showed that entomopathogenic fungal genera rarely colonize leaves of forest trees as foliar endophytes. It is also essential to screen non-entomogenous endophytes for their potential to ward of plant pests. *Trichoderma harzianum* (Hypocreales: Hypocreaceae) endophytic in *Sargassum wightii* (Phaeophyceae: Fucales: Sargassaceae) produced metabolites, which reduced the feeding on the leaves by the caterpillars of *Helicoverpa armigera* (Lepidoptera: Noctuidae); plants inoculated with *T. harzianum* had significantly fewer eggs of *H. armigera* (Suryanarayanan et al., 2018). *Trichoderma harzianum*, however, could not survive as an endophyte when sprayed as spores in crop plants for more than three weeks indicating that colonization of a plant by an alien endophyte may be viable only for 2–3 weeks (Suryanarayanan et al., 2018). Thus, even if an endophyte species with insect deterring properties is identified, methods to prolong its presence in a non-host crop have to be addressed for increasing its efficiency as a biological-management agent. Notwithstanding the inhibitory effects of fungal endophytes, plant-feeding insects could aid in the dispersal of endophytic fungal inoculum in the plant community. *Poeciloceris pictus* (Orthoptera: Pyrgomorphidae) when fed with the leaves of *Calotropis gigantea* (Apocynaceae) leaves, the leaf endophytes pass through their guts without being digested, retain their viability, could grow and sporulate on fecal pellets (Devarajan and Suryanarayanan 2006). This suggests that phytophagous insects could function as agents for the dispersal of fungal endophytes in plant communities such as tropical forests.

### CONCLUSION

Understating more comprehensively the interactions among three participants belonging to three different kingdoms *viz.* fungal endophytes, plants and insects, constituting one complex, intricately intertwined system would strengthen efforts to managing plant loss by pestiferous insects with lesser damage to the environment.

### ACKNOWLEDGEMENTS

I thank Swami Shukadevananda, Secretary,

Ramakrishna Mission Vidyapith, Chennai 600 004 for facilities and support.

### AUTHOR CONTRIBUTION STATEMENT

All authors equally contributed.

### CONFLICT OF INTEREST

No conflict of interest.

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(Manuscript Received: March, 2023; Revised: March, 2023;

Accepted: March, 2023; Online Published: April, 2023)

Online First in [www.entosocindia.org](http://www.entosocindia.org) and [indianentomology.org](http://indianentomology.org) Ref. No. e23262