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Endophytic Mycorrhiza-mediated Pathogen resistance in plants

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ABSTRACT

Objective: Mycorrhizal fungi are a group of microorganisms that live insithusants, thus, maintaining perceptible associations with their host plants in certain parts of their life cycle. They can be characterized by their capacity to synthesize secondary metabolites and to promote growth and induce plant-disease resistance, therefore, gaining greater biotechnological importance in pest and diseases management for crops of agricultural relevance. The study of these microorganisms has been a widely researched area subject for more than half a century.

Design/methodology/approach: Their biology and molecular relationships in plant-microorganism interactions, on the other hand, have only recently begun to gain relevance for understanding the colonization process in recent decades. There has been observed a complexity in the generation of formulations that can guarantee the permanence of fungi outside the host plant.

Findings/conclusions: This review article will address topics related to their biology, ecological role, possible negative effects on commercially important animals, and successful cases in Mexico regarding biotechnological products based on these microorganisms.

Keywords: Plant-endophyte interaction, mycorrhizae, biological control.

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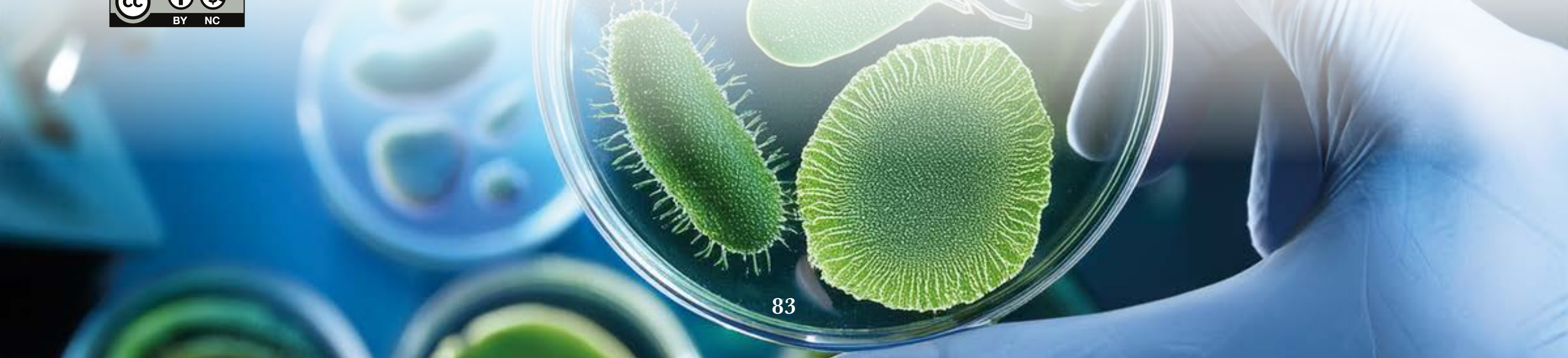
INTRODUCTION

At the end of the 20th century, the Mycology Committee of the American Phytopathological Society (APS) held one of the first discussions on the presence of endophytic fungi in woody plants and grasses. This event marked the beginning of a series of publications aimed at highlighting the phenomenon of endophytism in these species to the scientific community (Backman & Sikora, 2008). In 1996, a book on the ecology and evolution of endophytes was published, mostly focused on clavicipitaceous fungi, which were frequently associated with the reduction in grass consumption due to insects and some mammals (Redlin & Carris, 1996).



Endophytes are microorganisms that reside wholly or partially within the tissues of living plants without causing negative symptoms in their hosts; their internal presence can be demonstrated. Unlike mycorrhizae, endophytic fungi lack external structures such as hyphae or mycelia and can utilize various nutrient sources (Ownley *et al.*, 2010).

The objective of this work was to conduct a literature review on the role of endomycorrhizae in promoting resistance to different phytopathogens when they are in a plant-microorganism association.

MATERIALS AND METHODS

The development of this work was based on a search and review of articles dealing with the associations between mycorrhizal fungi published with the most up-to-date information. The information from studies conducted in Mexico is presented from these articles, providing insights into important concepts of mycorrhizal symbiosis and the mechanisms involved in the interaction between these endomycorrhizae and the host species. The search included experimental and review studies from databases such as SCOPUS, Web of Science, Forest Science, PubMed, and Scielo. The searches were conducted using Spanish keywords: “micorrizas” and “México”.

RESULTS AND DISCUSSION

As a result of this review, the information is structured into the following sections: 1) Biology of endomycorrhizae; 2) Endomycorrhizae and their ecological role; 3) Endomycorrhizae and their classification; 4) Mechanisms of action; 5) Adverse effects of some mycorrhizae; 6) Dual effect of endomycorrhizae; 7) Endomycorrhizae in Mexico and success study-cases.

Biology of Endomycorrhizae

Fungi are among the most important and abundant microorganisms on Earth. Their origin dates back more than 400 million years, when interactions between these microorganisms and aquatic plants began the colonization of soils, resulting in our current knowledge. They are present in almost all groups of terrestrial plants (Simon, 1996). The interactions between fungi and plants have changed the Earth’s ecology (Berbee *et al.*, 2017). Fungi are characterized by their great diversity, including microscopic fungi, unicellular and macroscopic multicellular fungi (Schoch *et al.*, 2014). Fungi are generally saprophytic, maintaining ecosystem functions and forming a key part of food chains. These qualities make them important for biotechnological applications such as fertilizers, natural pigments, cosmetics, and in the food industry (Muzzarelli *et al.*, 2012).

Currently, there are several types of mycorrhizal fungi, based on the characteristics of their infection and the organisms with which they establish mutualistic relationships. However, for practical purposes, they are distinguished as ectomycorrhiza, endomycorrhiza, and a third intermediate group between these two former groups (Franco-Navarro, 2002).

The term endophyte refers to fungal internal association with plant tissues without causing harmful damage (Petrini, 1991). Endophytic fungi penetrate the cells of the root cortex. They are a group of fungi often grouped according to their physiological condition, method of infection, secondary metabolism, stages of development and evolution, colonization patterns, and the taxonomic relationship of the symbiosis. This symbiosis is continuous and balanced between the fungus and the host, ranging from mutualism, parasitism, and commensalism (Aly *et al.*, 2011). Their interactions involve a balance of antagonisms independent of the plant organs they infect and encompass almost all taxonomic classifications of plants, especially those of agricultural interest, such as wheat, salvia, thyme, among others (Schulz & Boyle, 2005).

Endomycorrhizae and Their Ecological Role

Endomycorrhizae are involved in the mechanisms of acquired resistance to different types of stress. Stress is defined as external factors that negatively influence the plant and can be biotic, such as pathogens and heavy metals, or abiotic, such as water, salt, thermal, light excess, anoxia, and oxidative stress (Rodriguez & Redman, 2008). Additionally, mycorrhizae improve nutrient uptake, produce phytohormones, and participate in the synthesis of compounds with biological activity, such as antibiotics and secondary metabolites like antioxidants, anticancer, antidiabetic, and immunosuppressive compounds (Aly *et al.*, 2011; Chamkhi *et al.*, 2018; Tanabe *et al.*, 2004). Therefore, it is said that endomycorrhizae have profound effects on the environments where they are found, in addition to evolving alongside the plant species they colonize.

Mycorrhizae have the ability to absorb carbohydrates from the plant roots, and in this absorption process, they exchange minerals with the plant's vascular system. In the absorption of phosphorus, these microorganisms play a decisive role. It has been shown that inoculation with fungal isolates provides protection to plants in soils with lead and zinc toxicity due to phosphorus solubilization (Díaz *et al.*, 2016).

Endomycorrhizae and Their Classification

The current classification of endomycorrhizae is divided into Clavicipitaceous, which are mutualistic organisms that, together with their host, promote defense against herbivorous insect attacks and also colonize grasses (Clay & Schardl, 2002), and non-Clavicipitaceous, which are characterized by colonizing non-vascular plants such as conifers, ferns, and angiosperms (Rodriguez & Redman, 2008).

Class I Clavicipitaceous are related to a few phylogenetically related species with host selectivity (Rodriguez & Redman, 2008). These promote the development of plant biomass, confer resistance to water stress, and produce insecticidal compounds for herbivorous animals. They are divided into three types:

- Type I: The life cycle involves symptomatic and pathogenic species. Their propagation is through ascospores, they are heterothallic and require the transfer of spermatia for successful reproduction.
- Type II: The reproduction of fungi in this classification in already colonized plants involves the formation of fungal fruiting bodies and plant inflorescences as a mechanism of mixed interaction. They are the so-called pleiotropic symbionts transmitted vertically by seeds and horizontally by sporulation.

- Type III: They remain within the plant tissue throughout their life, including the flowering of the host. They have an asymptomatic life cycle and do not produce sexual spores, so there is no genetic recombination for these fungi (Clay & Schardl, 2002).

Non-Clavicipitaceous endomycorrhizae include:

- Class II: (Ascomycota and Basidiomycota) which enhance the morphogenesis of their host, root biomass, synthesis of hormones, growth-regulating enzymes, and provide protection to their host (Campanile *et al.*, 2007).
- Class III: Which grow in fruiting bodies above ground with horizontal transmission in plant organs such as flowers, fruits, and stems (Tejesvi *et al.*, 2007).
- Type IV: Distinguished as fungi with dark melanized septa, mainly ascomycetes that produce conidia forming intercellular and intracellular hyphae in plant roots.

Mechanisms of Action

Salicylic Acid-Mediated Signaling

Secondary plant metabolites serve to prevent or mitigate different sources of stress in plants (Glazebrook, 2005). In this section, we analyze those produced by known attackers, such as secondary metabolites produced by biotrophic agents, which are known for salicylic acid signaling. Necrotrophs, on the other hand, induce programmed cell death (Thomma *et al.*, 1998).

Salicylic acid acts as a "signaling molecule" that triggers the initiation of the acquired resistance mechanism in healthy tissues, in addition to the genetic expression of coding messengers related to pathogenesis (Pieterse *et al.*, 2009). Various experiments in mutant and transgenic plants in these genes are unable to develop the acquired resistance mechanism, as the activation of PR genes is not observed when an infection by a pathogenic organism is present (Durrant & Dong, 2004). This allows us to conclude the fundamental role of salicylic acid as an intermediary in the signaling pathway, with the NPR1 protein being an important transducer of the salicylic acid signaling pathway (Dong, 2004).

Jasmonic Acid and Ethylene-Mediated Signaling

The mechanism of action of salicylic acid represents the interaction of plants with pathogenic organisms (Pieterse *et al.*, 2009). In beneficial interactions, the recognition patterns present different molecular patterns, activating the immune system response at a systemic level. In this response, there is a signal that travels long distances through the plant's vascular system, activating the immune system. This is commonly regulated by jasmonic acid and ethylene-dependent pathways and does not activate the PR genes of systemic acquired resistance. The activation of this signaling is mediated by beneficial soil microorganisms, rhizobacteria, and mycorrhizae, which promote plant growth (Pozo & Azcón-Aguilar, 2007; van Loon *et al.*, 1998).

Tolerance to biotic stress

The main characteristic of these beneficial endophytic organisms is the production of secondary metabolites, such as antibiotics with antifungal, antibacterial, and insecticidal properties (Gunatilaka, 2006), which inhibit the development of phytopathogens. These properties promote the search and prospecting of endophytic organisms, derived from their activity as phytopathogen controllers and their contribution to biomass production.

Some endophytic fungi, such as *Piriformospora indica*, isolated from sandy soil in the Indian desert from the shrubs *Prosopis juliflora* and *Ziziphus nummularia* (Verma *et al.*, 1998), induce resistance to saline stress in barley (*Hordeum vulgare*) plants and resistance to pathogens like *Fusarium culmorum* and *Cochliobolus sativas* (Kumar *et al.*, 2002). In addition to these examples of resistance to these types of stress, it also stimulated biomass production. At the root level, the roots showed greater antioxidant capacity, increasing the concentrations of ascorbic acid and dehydroascorbate reductase, reducing cell death (Waller *et al.*, 2005).

In another study, a non-pathogenic strain Fo47 of *Fusarium oxysporum* reduced the symptoms of the strain *Fusarium oxysporum* f. sp. *radicis lycopersici* in tomato cultivation (Bolwerk *et al.*, 2005). These symptoms were root and stem collar production. For this, a concentration 50 times higher of biocontrol spores is needed. The control mediated by this strain is due to the occupation and reduction of fixation sites, resulting in fewer symptomatic lesions. The interaction of the strain used as biocontrol had a direct effect on the acquired resistance mechanism, as it increased the levels of PR-1, β-1-3-glucanase, and β-1-4-glucanase (Duijff *et al.*, 1998; Fuchs *et al.*, 1997), indicating that this beneficial fungus acts similarly to the acquired resistance system, *i.e.*, it conserves the patterns that, like pathogenic organisms, trigger the plant's defense systems with a positive symbiosis.

The most studied entomopathogenic fungi are *Lecanicillium* spp., *Metarhizium* spp., *Hirsutella* spp., *Isaria* spp., *Nomuraea* spp., *Sporothrix* spp., *Aschersonia* spp., *Paecilomyces* spp., *Tolypocladium* spp., and *B. bassiana*. These fungi have been shown to produce secondary metabolites with antagonistic activities against mammals, microorganisms, insects, and even plant cells (Vidal & Jaber, 2015). Studies on *Metarhizium* spp. have shown that it causes susceptibility in *Drosophila* spp. to infection by other bacterial entomopathogens (Vega *et al.*, 2009).

Beauveria bassiana is one of the fungi considered as an entomopathogen and is the most used in the control of insect pest populations. Synergistic applications of *M. brunneum* on alfalfa, tomato, and melon plants lead to endophytic colonization, causing an increase in mortality rates of *Spodoptera littoralis* larvae when they feed directly on the inoculated plants. Particularly in melon, a whitefly mortality rate of 53% was observed (Garrido-Jurado *et al.*, 2017; Jaber & Ownley, 2018).

Adverse effect of some endomycorrhizae

The function of secondary metabolites produced by endophytic fungi can be either positive, such as providing protection to plants against herbivore attacks, or negative, such as the emission of certain alkaloids. Their production has diversified due to the increased number and diversity of herbivores, which affects even the natural enemies of plants, leaving them unprotected from other more complex organisms (Tanaka *et al.*, 2005).

The main function of volatile organic compounds is the communication of the plant with its environment and therefore, they affect other organisms in various ways. When a plant is invaded by an endophytic microorganism, this situation can disrupt such communication, depending on the species and colonizing strain.

Dual effect of endomycorrhizae

There are reported cases of fungi that exhibit this type of functionality. The fungus *Phomopsis oblonga* produces alkaloids and mycotoxins, which in turn can control the population of the insect *Physocnemum brevilinenu*, considered a non-pest. However, the interaction of this fungus with trees like the Dutch elm also decreases the spread of the pathogenic fungus *Ceratocytis ulmi*, as the insect targeted by biotechnological products based on this fungus is controlled (Dutta *et al.*, 2014; Webber, 1981).

The fungus *B. bassiana* produces active metabolites that exhibit mycotoxin activity against phytopathogenic fungi under laboratory conditions, unlike in soil assays where its activity is directed against soil pathogens such as *Pythium*, *Rhizoctonia*, and *Fusarium* species. The fungus *Lecanicillium* spp. induces systemic resistance and acts as a mycoparasite against powdery mildew (Ownley *et al.*, 2010).

Endomycorrhizae in Mexico

Mexico ranks fifth globally in terms of biodiversity and endemism, hosting 10% of the world's diversity, the geographical location, topography, altitude, and climate types create an environmental diversity that promotes habitat variety (Aguirre-Acosta *et al.*, 2014; Comisión Nacional para el Conocimiento y Uso de la Biodiversidad, 1998).

In the cultivation of fava beans, 758 endophytic fungi have been identified, classified into 129 families and 66 genera. The most representative genera include *Alternaria*, *Colletotrichum*, *Curvularia*, *Fusarium*, and *Phomosis* (López-González *et al.*, 2017).

In the medicinal species *Dendropanax arboreus*, 45 endophytic fungi have been isolated from various plant organs such as leaves, bark, and roots. The predominant genera include *Fusarium*, *Alternaria*, *Colletotrichum*, as well as *Corynespora*, *Endomelanconiopsis*, and *Thozetella*, which show potential for generating antimicrobial compounds (Ramos-Garza *et al.*, 2016).

Successful commercial products based on endophytic fungi

The development of a biotechnological product generally begins with the identification of the microorganism and its properties, large-scale production, product development, efficacy testing, and finally, registration and commercialization. Below are descriptions of three filamentous fungal products with endophytic characteristics, two with insecticidal activity and one as a mycotoxin.

Strains 5 and F52 of the fungus *M. brunneum*, isolated from codling moth or apple moth, are the active ingredients in a wettable powder. They have a broad spectrum of insect targets including thrips, whitefly, aphids, beetles, weevils, mosquitoes, and mites (Ríos-Moreno *et al.*, 2016; Singh *et al.*, 2011). This biocontrol agent causes insect death through physical obstruction, nutrient depletion, organ invasion, or paralysis, and it produces 15 toxins known as destruxins (A-E, Ed and Ed1, A2, B and B2, D2, E2, CL, DesmA, and DH-A), with destruxin A being the most abundant, mainly produced by the genus *Metarhizium* (Ríos-Moreno *et al.*, 2016).

The biopesticide process is as follows: conidia germinate on the host surface and form appressoria that penetrate the exoskeleton. The infective hypha then penetrates through the host's cuticle, eventually emerging as a homothallic, where the fungus produces cells and toxins. Upon the insect's death, and under humid conditions (25-30 °C), the mycelium penetrates the insect's cuticle and produces infectious conidia outside the cadaver. Under minimal humidity conditions, the fungus survives in the mycelial phase but does not produce conidia outside the insect's body (Authority, 2012).

Application of this formulation on insects *Strophosoma melanogrammum* and *Strophosoma capitatum* under laboratory conditions showed 100% pathogenicity at 21 days, with average survival rates of 13.5% and 96.5% at 32 days, respectively, and a mean survival time of 22.6 days. In field conditions, with two applications at a 15-day interval to the soil of pine and red fir crops, a prevalence of 90% and 78% was achieved in both species after 3 years. This study demonstrated suppression of *Strophosoma* spp. populations and potential cumulative effects preventing population increases in the next generation (Nielsen *et al.*, 2006).

Naturalis-L is a bioinsecticide from strain ATCC 74040 of *B. bassiana* oil-based. It was primarily sourced from the cotton boll weevil *Anthonomus grandis* in Texas, USA (Mayoral *et al.*, 2006). This pesticide is recommended for controlling larvae of the *Aleyrodidae* family, including greenhouse whiteflies *Trialeurodes vaporariorum* and *Bemisia* spp. These organisms are highly reproductive, significant in crops, and have a wide range of hosts, including weeds, and they also act as vectors for plant viruses. This biopesticide, applied at different doses (125, 250, and 300 mL L^{-1}) weekly during the fruit ripening stage of tomato crops, reduced greenhouse whitefly infestations by reducing live nymphs with 72% and 82% efficacy compared to the control (Mayoral *et al.*, 2006).

Lastly, the product "Tricovab," *Trichoderma stromaticum*, affects cocoa tree witches' broom disease (WBD) caused by *M. perniciosa*, a disease of great importance in Latin America. The basidiospores of the fungus infect plant growth tissues, causing a variety of symptoms depending on the infected organ, particularly in apical meristems (De Souza *et al.*, 2008).

CONCLUSIONS

The biological potential and alternative use of endomycorrhizal fungi for plant disease control are huge. The biological description of these microorganisms, their ecological role, action mechanisms, and potential dual or adverse effects are aspects that biotechnological production and technology should address in the upcoming years of research. Additionally, integrating social aspects, such as the transition from traditional products to these alternatives, should be included in all biotechnological research focused on such applications.

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