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Endophytes Potential Use in Crop Production

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Abstract

The endophytic microorganisms have the potential to improve the yield of agricultural crops. They can be used as biological control, plant growth promoter, or bioremediators. The action of endophytes in controlling phytopathogens, insects, and weeds that harm agriculture may be the result of microbial interactions with other organisms or the production of bioactive metabolites. Also, microorganisms can have the ability to favor plant growth and convert toxic compounds present in the soil. The presence of pollutants in the substrate reduces its quality for plant development, so bioremediation also impacts agricultural production. Therefore, prospecting endophytic microorganisms with agronomic potential may provide sustainable alternatives to increase crop yield.

Keywords: endophyte, agriculture, biological control, plant growth promoter, inoculant, bioremediator

1. Introduction

In order to apply sustainable solutions to problems related to food production, the biotechnological potential of endophytic microorganisms has been prospected in the agronomic area. The use of beneficial microorganisms in agricultural production aims for pest control, improvement of productivity and plant development, and/or recovery of ecological systems. Endophytes play a role in evolution of plant and in resistance of stresses through the production of bioactive metabolites, changes in enzyme metabolism, and gene expression related to resistance [1], and those beneficial effects of various endophytic genera may be the combined [2].

2. Biological control

Biological control of phytopathogens occurs when living microorganisms repress the development of the etiological agent in the plant [3]. Endophytes can act inducing resistance, promoting antibiosis and/or competition in consequence of the mutualistic relation with the plant [4]. These processes can occur independently, but the overlap of mechanisms may also happen [5], like is observed in the association of *Beauveria bassiana* and *Metarhizium brunneum* against the complex of *Fusarium*, the control occurs by competition and antibiosis [6].

The physiological definition of resistance is the delay or impediment of entry and/or subsequent activity of the pathogen in the plant [7]. Plants have numerous and efficient defense mechanisms naturally triggered when exposed to elicitors [8] that can be stimulated by the endophytes presence. The plant defense mechanisms are induced after the recognition of molecular patterns associated with pathogens/microbes (PAMPs/MAMPs), or plants' molecular patterns associated with damage (DAMPs) and effectors, by proteins or by nucleotide-binding leucine-rich repeat (NB-LRR) [9]. Endophyte induces systemic resistance on plants providing an alert state, the priming [10, 11]. Priming plants exhibits faster and stronger responses against pathogen attacks because transcription factors and signaling proteins have already accumulated in cells. This defense induction is a consequence of molecular signaling during the establishment of plant-endophyte symbiosis [10]. An example of the host-induced resistance by endophytes is the frequent isolation of *Curtobacterium flaccumfaciens* in plants without symptoms of citrus variegated chlorosis, suggesting that this endophyte has a role in the resistance of the citrus plant [12].

A reprogrammed genetic transcription occurs in plants associated with endophytes. The *Epichloë festucae* symbiosis with ryegrass (*Lolium perenne* var. *Lolii*) enhances gene expression of jasmonic acid (JA) precursors [13], and the expression of the systemic defense genes HvPr17b and HvHsp70 in barley is associated with the presence of the endophyte *Piriformospora indica* [14]. Further, presence of endophytes may alter pathogenesis-related proteins (PR-proteins) concentration, as chitinase, peroxidase, glucanase and cellulase in cucumber inoculated with *Trichoderma harzianum* [15], lignin and cellulose in *Theobroma cacao* in symbiosis with *Colletotrichum tropicale* [16], and PR2, PR6, PR15, and PR16 in rice with *Bacillus subtilis* [17]. The resistance response induced by symbiosis of plant-endophyte is systemic. Studies have shown that gene expression or protein production related to host defense was evidenced in plant portions distant from those inoculated with *Klebsiella pneumoniae* [18], *Rhizobium etli* [19], and *Pseudomonas fluorescens* [20].

The resistance induction is also related with the activity of defense enzymes, such as phenylalanine ammonia lyase, polyphenol oxidase, superoxide dismutase, peroxidase, ascorbate peroxidase, and guaiacol peroxidase. *Pseudomonas fluorescens* induces resistance related to the activity of lipoxygenase, catalase, aminocyclopropane carboxylate oxidase, and phenylalanine ammonia lyase [20]. *Pseudomonas fluorescens* is also capable to induce systemic resistance in plants by producing 2,4-diacetylphloroglucinol [21].

The vast majority of endophytes are biotrophic [22]. Therefore, it is important to consider that when colonization of the plant by biotrophic endophytes begins, the salicylic acid (SA) route activates defenses, so endophytes need to be able to suppress this defense by specific effectors. The expression of the Ca^{2+} /calmodulin kinase enzyme is capable to suppress the pathway of SA [23]. In addition, the possibility of recruiting gibberellic acid (GA) reduces the proportion of DELLA proteins, altering the salicylic acid and jasmonic acid (JA) signaling [24]. The suppression of the SA stimulates JA route precursors and genes, which increases resistance to chewing insects and necrotrophic fungi and promotes susceptibility to biotrophics [10, 22]. To ensure plant protection against biotrophic fungi and sucking insects, endophytes have the ability to biosynthesize compounds responsible for antibiosis; besides they can also control these organisms through mycoparasitism and competition.

The endophytes are able to biosynthesize secondary metabolites, which are important for plant colonization processes [2] and are toxic to insects, pathogens [10], and algae [25]. These compounds are classified as alkaloids (amines and amides; indole derivatives), steroids, terpenoids (sesquiterpenes, diterpenes,

monoterpenes), isocoumarin derivatives, quinones, flavonoids, phenylpropanoids and lignans, peptides, phenol and phenolic acids, aliphatic compounds, and chlorinated metabolites [25]. The antagonistic activity of endophytes associated with antibiosis is described for different cultures, like potato [26, 27] and turmeric rhizome [28].

Alkaloids are an important group of metabolites produced by endophytes; some characterized classes are ergot alkaloids, diterpene indole, pyrrolizidines, and peramine. These compounds have important biological activity (antitumor, antimicrobial), including the reduction of insect performance [10, 13]. The resistance of chickpeas (*Cicer arietinum*) colonized by endophytic *Streptomyces* spp. against *Sclerotium rolfii* is attributed to the production of phenols and flavonoids by the endophyte [29]. Nematicide compounds such as 4-vinylphenol, methionine, piperine, and palmitic acid were evidenced to have high concentrations in soybean colonized by *Bacillus simplex* [30].

The need for nutritional factors, like carbon, nitrogen, and iron, may also promote biological control. Direct parasitism is a fungus-fungus antagonism, in which one directly attacks another and utilizes its nutrients [31]. This kind of control, independent of a systemic defense response, was observed with the colonization of previously endophyte-free leaves of *Theobroma cacao* that significantly decreases necrosis in the local of inoculation when challenged with *Phytophthora* sp. [32]. Endophyte colonization can directly control a phytopathogen even without inducing defense mechanisms such as PR-proteins, like evidenced by the control of *Trichoderma stromaticum* over *Moniliophthora perniciosa* [33]. A scanning electron microscope showed that the *Trichoderma* endophytes cause deformities in the mycelia of *Pythium aphanidermatum* and *Rhizoctonia solani*, such as hyphal fragmentation, perforation, lysis, and mycelial degeneration [28]. A strain of *Trichoderma harzianum* showed in vitro growth contact points that suggest mycoparasitic activity against *Fusarium solani* [34]. Endophytic and epiphytic fungi isolated from fruits of organic *Olea europaea* were able to inhibit mycelial growth, germination, and sporulation and cause pathogenic hyphae abnormalities of *Colletotrichum acutatum*, particularly at mycelial contact [35]. In addition, endophytic fungi from *Pachystachys lutea*, mainly *Diaporthe* sp. perform antagonistic activity against *Colletotrichum* spp. and *Fusarium oxysporum*, in which contact interactions of the endophyte with the pathogen predominated [36].

Competition and direct parasitism require endophyte-pathogen contact, but those microorganisms have very little to no direct contact with the plant. Because of this, contact mechanisms are not the most important biological control pathway [4].

3. Plant growth promoters

Endophytic bacteria promote plant growth directly or indirectly: directly, producing phytohormones or enzymes [37, 38] and indirectly, contributing to plant nutrient uptake through nitrogen fixation, phosphate solubilization, or iron transformation [39, 40]. For this, the inoculant competes with an adapted indigenous microbiota; therefore, for the colonization of plant, some bacterial characteristics are important, such as motility and polysaccharide production [41–44].

Ethylene and indole-3-acetic acid (IAA) are phytohormones that are involved in almost all aspects of plant growth and development, from seed germination to shoot growth, and they control the response of the plant to stress [45, 46]. Plant growth is promoted by reducing ethylene levels and increasing IAA. Biotic and abiotic stresses result in increased ethylene production in plants, leading to

inhibition of root elongation, lateral root development, and root hair formation. Plant-associated microorganisms can increase root growth and budding of plants by reducing ethylene levels [47]. The endophytic bacteria can produce an enzyme called 1-aminocyclopropane-1-carboxylate (ACC) deaminase, which hydrolyzes ACC, an ethylene immediate precursor, relieving stress and improving the growth of plants under disturbed conditions [42, 48, 49]. An inoculum from *Burkholderia phytofirmans* with the gene responsible for producing mutated ACC deaminase was unable to promote root growth of canola. The reintroduction of the ACC deaminase gene restored the microorganism's ability to promote plant growth, highlighting the importance of the enzyme in promoting host plant growth [48]. On the other hand, the IAA is an auxin, a growth hormone that promotes differential cell elongation and functions as the plant growth regulator. Besides being produced by plants, IAA may also be produced by root-associated bacteria, such as *Enterobacter* spp., *Pseudomonas* spp., and *Azospirillum* spp. [50].

Endophytic bacteria can benefit the host by producing cytokines and gibberellins. Corn endophytic bacteria, *Azospirillum lipoferum*, produce gibberellin, which is important in relieving plant stress [51]. Similarly, extracts of two endophytic bacteria from *Gynura procumbens*, *Pseudomonas resinovorans*, and *Paenibacillus polymyxa* presented cytokines [52].

Nitrogen is the most important nutrient for plant growth and productivity. Although abundant in the atmosphere, it is not available to plants. For this, it requires to be transformed by a biological nitrogen fixation (BNF) process in which N_2 is converted to NH_3 by bacteria expressing nitrogenase, such as *Burkholderia* spp., *Azoarcus* sp., *Gluconacetobacter diazotrophicus*, *Herbaspirillum* sp., *Azospirillum brasilense*, and *Paenibacillus* sp. [53–55]. Nitrogen-fixing endophytes outperform rhizosphere microorganisms in this process allowing plants to thrive even in nitrogen-limited soil environments, promoting plant health and growth [56]. Endophytic nitrogen-fixing bacteria can also increase the buildup and the nitrogen fixation rate in plants residing in soils with nitrogen limitation.

Phosphorus is an important micronutrient for the enzymatic reactions of plant physiological processes [57]. Although present in large quantities, most of the soil phosphorus is insoluble and therefore unavailable to the plant. In addition, almost 75% of phosphorus applied as fertilizer forms complexes in the soil, which prevents its absorption by the vegetable [58]. The endophytic bacteria can increase soil phosphorus availability to plants by solubilizing precipitated phosphates through mechanisms of acidification, chelation, ion exchange, and the production of organic acids [59]. They can also increase the availability of phosphorus in the soil by secreting acid phosphatase, which can mineralize organic phosphorus [60]. Furthermore, endophytic bacteria can prevent phosphate adsorption and fixation under phosphate-limiting conditions and assimilate solubilized phosphorus [61]. Studies show that endophytic populations of cactus, strawberry, sunflower, soybean, and other legumes have the ability to solubilize phosphate [62–64]. A study examined the role of phosphate-solubilizing endophytic bacteria in cactus cultivation and observed that inoculated plants grew well without added nutrients and that their growth was comparable to fertilized plants. This indicates that endophytic bacteria provide the limiting nutrient to seedlings [65].

Iron is a component of proteins that control physiological processes such as respiration and transpiration [66]. Generally, it occurs in the ferric insoluble form, unavailable to the plants. The endophytic bacteria produce iron chelators called siderophores that may bind to insoluble ferric ions allowing this nutrient uptake by plants [66–68]. The action of bacterial-produced siderophores has already been correlated with the growth of cultivars such as corn, including shoot and root biomass [69], and on tomato development in hydroponic crops [70].

The ability to promote plant growth by endophytic bacteria may be influenced by host genotype [71]. However, many endophytic bacteria can have a wide range of hosts, such as *B. phytofirmans*, which promote growth of *Arabidopsis thaliana*, grapes, corn, potatoes, grass, tomatoes, and wheat [72–74]. Similarly, the bacterial genotype also influences the capacity and potential of stimulatory effects over host plants. For example, the individual ability of different *B. phytofirmans* strains to promote growth of a single potato cultivar [75] and the plant colonization by different *Salmonella enterica* isolates were observed [76]. Therefore, colonization and growth promotion of plants by endophytic bacteria are active processes controlled by genetic factors of both partners.

4. Bioremediators

The prompt development of agriculture has made it possible to increase the food supply all over the world. However, the intensification of agricultural activities brought serious environmental impacts, which not only affect food security but also have impacts on socioeconomic aspects. These impacts comprise contribution to air pollution, impacts on land, waste of water, loss of biological and ecological diversity, and perturbation of global biogeochemical cycles. The pollutants generated by agricultural activities can affect the global or local scale. An example of global-scale agro-environmental problem is the increase in atmospheric concentrations of the greenhouse gasses (GHG) and carbon dioxide (CO₂) through deforestation and nitrous oxide (N₂O) arising from crop production. Agriculture is the largest water consumer and the main source of nitrate, ammonia, and phosphate pollution. These pollutants affect the local scale; some examples are the salinization of irrigated lands and the buildup of nitrate fertilizer residues in groundwater and surface water [77–81].

Most of the negative environmental impacts generated by the intensification of agricultural activities can be reduced or prevented [77]. The use of new technological approaches, physicochemical- or biological-based, could remove pollutants from nature. Biological-based methods are preferred due to the low cost and because they are less harmful to the environment. Atlas and Pramer [82] defined the term bioremediation as “the use of biological agents to reclaim soils and waters polluted by substances hazardous to human health and/or the environment.” In other words, bioremediation is a biological-based method involving the use of living organisms, such as plants or microorganisms (bacteria, fungi, and algae), to remove pollutants from the environment [83].

Degradation of pollutants by a microorganism demands favorable conditions of nutrients, temperature, pH, and oxygen. Bacteria and fungi are commonly used in bioremediation strategies, because they are ubiquitous and capable in withstanding different environmental conditions, so they can be used for a broader range of application. There are two main mechanisms of bioremediation: biosorption and bioaccumulation. Biosorption involves sequestration of pollutants through binding onto surfaces, such as the cell wall. Bioaccumulation involves transport and accumulation of pollutants in the cells and, in some cases, the transformation of pollutants into less harmful compounds [78, 83]. The degradation of target pollutants can also be achieved by employing nonliving subcellular entities of biological origin as bioremediators [84]. To overcome the instability due to the rapid decline in the inoculated cell amount during its competition with indigenous microorganisms, some authors have proposed solutions. For example, a new strategy for the efficient removal of phenylurea herbicides from contaminated soil uses transgenic plants. Transgenic *Arabidopsis thaliana* plants expressing a bacterial N-demethylase

(PdmAB) that demethylated isoproturon were constructed. The synergistic relationship between the transgenic plant and *Sphingobium* sp., which is capable of mineralizing the intermediate of isoproturon excreted from the transgenic plant in the rhizosphere, is an innovative strategy of treatment [85].

Endophytes can remove pollutants by employing either the biosorption or the bioaccumulation mechanisms [83, 86–90]. They have the ability of decreasing and/or removing contaminants from soil, water, sediments, and air. Endophytic fungi have a great potential to manage toxic pollutants; many studies report those fungi to clean up environmental pollutants, such as white rot fungi like *Phanerochaete chrysosporium* that can degrade pesticides, dyes, and xenobiotics [91, 92]. There are several examples of endophytic microorganisms with promising applications in bioremediation [93]. As an example, symbiotic fungal endophytes from agricultural, coastal, and geothermal native grasses colonized tomato plants and conferred disease, salt, and heat tolerance, respectively. Coastal plant endophyte colonized rice and conferred salt tolerance. In addition, coastal and geothermal plant endophytes conferred drought tolerance to monocot and eudicot hosts [88]. In leguminous plants including soybean, salinity is correlated with poor yield and reduction in plant growth [94]. Basidiomycetous endophytic fungus *Porostereum spadiceum* was reported to produce six types of gibberellins that reduce the effects of salinity in soybean by modulating endogenous phytohormones of the seedlings [95].

Heavy metals are one example of pollutants generated by agricultural activity that bioremediators can remove. The use of some pesticides and fertilizers can introduce into the environment copper (Cu), and some insecticide and herbicides can contain lead (Pb). Fungi have emerged as potential biocatalysts to access heavy metals and transform them into less toxic compounds [92, 96]. Endophytic fungi isolated of *Portulaca oleracea* growing in metal-contaminated soils increased the biomass *Brassica napus*. The results indicated that the endophytic fungus strain had the potential to remove heavy metals from contaminated water and soils [97]. Bioremediation of Pb-contaminated soil occurs by cultivation of *Solanum nigrum* combined with *Mucor circinelloides* [22]. Endophyte isolates from *Phragmites* also showed potential to metal tolerance and absorption of Cu, Pb, and chromium (Cr) [98].

Phytoremediation is the process that uses plants associated with microorganisms to remediate contaminants from soil, sludge, sediments, wastewater, and groundwater [92, 96]. Plants naturally harbor endophytes that may have natural tolerance and adaptation toward the pollutants. Studies explored the potential of using endophytes associated with plants for removal of pollutants in this process of phytoremediation [86, 88, 96, 99]. Plants growing in metal-contaminated soils accumulate the pollutant consumed directly or indirectly by humans and animals [100, 101]. Besides the human risk, polluted soil slows plant growth and reduces the biomass accumulation, compromising some crop productivity [102, 103]. Endophytic fungi resistant to different metals, including cadmium, lead, zinc (Zn), chromium, manganese (Mn), and cobalt (Co), are associated with plant species present in contaminated sites, indicating that these microorganisms have metal bioremediation potential [83, 97–99, 104, 105]. Chromium toxicity influences a number of processes that can lead to low yield. The accumulation of Cr from industrial activities in soil is a serious threat to some crops [106–108]. To minimize the Cr effects from contaminated soils, it is possible to use plants that harbor endophytic fungi that act as bioremediators. In experiments, strains of *Aspergillus fumigatus*, *Rhizopus* sp., *Penicillium radicum*, and *Fusarium proliferatum* isolated from healthy plants were able to remove Cr from soil and culture media as well as biotransform it from highly toxic hexavalent to least toxic trivalent form, instead of simply storing it. Roots of *Lactuca sativa* colonized by those endophytes restored its normal growth into Cr-contaminated soil, making them potential candidates as biofertilizer

in Cr-contaminated soil. Likewise, *Rhizopus* sp. and *F. proliferatum* reduced the translocation of Cr to the leaves, making it safer for human consumption [102]. Other biofertilizer candidates to be used in fields affected with heavy metals are the endophytic *Mucor* sp. MHR-7 that presented tolerance to chromium, manganese, cobalt, copper, and zinc by biotransformation and/or accumulation of those metals in its hyphae. Co-cultivation of MHR-7 reduced in 90% the Cr absorption and promoted growth in mustard cultivation [103].

Studies reported the use of *Mucor* sp. in another remediation strategy called phytoextraction. Phytoextraction refers to the removal of heavy metal from the soil through their uptake by a metal-accumulating plant. One limitation is the long growth cycle of those plants. One strategy is to combine plants with endophytes that promote stress tolerance to toxicity and high biomass accumulation, increasing metal accumulation in plant tissues. Oilseed rape plants combined with *Mucor* sp. strains promoted stress tolerance to Cd and Pb, increasing biomass of plants and reducing the concentrations of those metals in the soil [109]. Similar results were found using the fungal endophyte *Peyronellaea* associated with maize under heavy metal stress [110], and the *Microsphaeropsis* sp. strain isolated from *Solanum nigrum* has also been studied for their biosorption capacity of cadmium [111]. Mercury volatilization and bioaccumulation of this metal in plant tissues mediated by endophytic fungi were demonstrated with *Aspergillus* sp. A31, *Curvularia geniculata* P1, *Lindgomycetaceae* P87, and *Westerdykella* sp. P71 on maize and *Aeschynomene fluminensis* [112].

Similar to metal pollutants, triphenylmethane (TPM) dyes are water-soluble organic compounds extensively used in industrial processes and have adverse effects on living organisms. TPM is phytotoxic for several cultivated plants, such as *Sorghum bicolor*, *Triticum aestivum*, *Vigna radiata*, *Lemna minor*, and *Zea mays* [83]. A *Diaporthe* sp. endophyte presented biosorption and biodegradation potential on TPM dyes. The microorganism removed TPM dyes through biodegradation and biosorption [113]. Other endophytes, *Pleurotus ostreatus*, *Polyporus picipes*, and *Gloeophyllum odoratum*, also demonstrate potential to remove TPM dye [114, 115].

5. Conclusion

Endophytic microorganisms are inestimable natural resources for solving problems in different areas such as human health, veterinary, industrial and ecological systems, and agronomy. In contrast to current agricultural practices that degrade systems and produce food with high concentrations of various contaminants, endophytes are a sustainable alternative to increase crop productivity. For this, they can be exploited by the ability to control pests, to promote plant growth, and by the bioremediation potential. This is possible because these microorganisms are able to induce resistance mechanisms in the host, release compounds with biological activity, compete for space and nutrients with pathogens, provide nutritional elements present in the soil, stimulate the production of phytohormones and cytokines, and neutralize the presence of pollutants in the system. Ultimately, bioprospecting and the use of endophytes in agriculture are a viable alternative to the need of increased food production with quality and sustainably.

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