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Original Article

Endophytic fungi: an overview on biotechnological and agronomic potential

Fungos endofíticos: uma visão geral sobre o potencial biotecnológico e agronômico

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Abstract

Endophytic fungi colonize the inter- and/or intracellular regions of healthy plant tissues and have a close symbiotic relationship with their hosts. These microorganisms produce antibiotics, enzymes, and other bioactive compounds that enable them to survive in competitive habitats with other microorganisms. In addition, secondary metabolites confer protection to their host plant against other bacterial and fungal pathogens and/or can promote plant growth. Endophytic fungi are viewed as a promising source of bioactive natural products, which can be optimized through changes in growing conditions. The exploration of novel bioactive molecules produced by these microorganisms has been attracting attention from researchers. The chemical and functional diversity of natural products from endophytic fungi exhibits a broad spectrum of applications in medicine, agriculture, industry and the environment. Fungal endophytes can also enhance the photoprotective effects and photochemical efficiency in the host plants. Modern omic approaches have facilitated research investigating symbiotic plant-endophytic fungi interactions. Therefore, research on endophytic fungi can help discovery novel biomolecules for various biotechnological applications and develop a sustainable agriculture.

Keywords: endophytes, bioactive compounds, photoprotection, plant growth, omic tools.

Resumo

Fungos endofíticos colonizam as regiões inter e/ou intracelulares de tecidos vegetais saudáveis e possuem uma relação de simbiose com seus hospedeiros. Esses microrganismos produzem antibióticos, enzimas e outros compostos bioativos que os permitem sobreviver em habitats competitivos com outros microrganismos. Além disso, os metabólitos secundários conferem proteção à planta hospedeira contra outros patógenos bacterianos e fúngicos e/ou podem promover o crescimento vegetal. Os fungos endofíticos são considerados uma fonte promissora de produtos naturais bioativos, que podem ser otimizados por meio de mudanças nas condições de cultivo. A exploração de novas moléculas bioativas produzidas por esses microrganismos tem chamado a atenção dos pesquisadores. A diversidade química e funcional dos produtos naturais de fungos endofíticos exibe um amplo espectro de aplicações na medicina, agricultura, indústria e meio ambiente. Os fungos endofíticos também podem aumentar os efeitos fotoprotetores e a eficiência fotoquímica nas plantas hospedeiras. As abordagens ômicas modernas têm facilitado as pesquisas sobre as interações simbióticas entre plantas e fungos endofíticos. Portanto, a pesquisa sobre fungos endofíticos pode ajudar na descoberta de novas biomoléculas para diversas aplicações biotecnológicas e a desenvolver uma agricultura sustentável.

Palavras-chave: endófitos, compostos bioativos, fotoproteção, promoção de crescimento vegetal, ferramentas ômicas.

1. Introduction

The term endophyte was first defined by Bary (1866) as any organism that grows within plant tissues. Endophytes were defined as asymptomatic microorganisms living inside plants (Carroll, 1986) and microorganisms that inhabit internal plant tissues and organs at part of their life without causing apparent harm to the host plant (Petrini, 1991). Over the decades, the concept of endophytes has been revised (Hallmann et al., 1997; Hardoim et al., 2015).

There are numerous reports on the presence of endophytic fungi inhabiting a diverse group of plant species (Rajamanikyam et al., 2017; Souza and Santos, 2017; Toghueo and Boyom, 2019). These microorganisms can be isolated from surface-disinfected plant tissues or extracted from the inner parts of plants (Hallmann et al., 1997).

Endophytic fungi are a rich source of bioactive compounds such as antimicrobial agents, hormones

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(e.g., auxin, gibberellins), and hydrolytic enzymes (e.g., cellulases, proteases, chitinases) important for the survival and maintenance of endophytes in plants and for host plant health and tolerance to stressful environments (Eid et al., 2019). These metabolites have great potential for numerous biotechnological applications (Rana et al., 2019; Rustamova et al., 2020). In this review, we describe the benefits of endophytic fungi for their host plants, the potential of these microorganisms for the production of natural products with a broad spectrum of biological activities, and the importance of omic tools for better understanding symbiotic interactions to improve plant health.

2. Endophytic Fungi as a Source of Natural Bioactive Metabolites

Endophytic fungi are considered microbial biofactors for the production of new bioactive products with a high degree of biological and structural diversity (Gupta and Shukla, 2020). After the discovery of paclitaxel (or Taxol), a potent anticancer drug produced by *Taxomyces andreanae* associated with *Taxus brevifolia* (Stierle et al., 1993), many researchers reported on Taxol-producing endophytic fungi from different host plants (Naik, 2019a). Although endophytes can synthesize the same or similar plant-derived secondary metabolites, how and why these secondary metabolites occur is still not clear. Some studies suggest that molecular mechanisms could have arisen through the coevolution of endophytes with plant hosts during the establishment of symbiotic relationships (Tan and Zou, 2001; Naik et al., 2019).

The synthesis of bioactive compounds by endophytic fungi can be regulated according to environmental changes and specific needs during the developmental stages of fungal culture (Aly et al., 2010). Changes in culture parameters (e.g., medium composition, temperature, pH, light) can affect the metabolic profile of endophytic fungi (Morales-Sánchez et al., 2020). This strategy, called "One Strain Many Compounds" (OSMAC), has been considered efficient for the discovery of new natural substances from fungal endophytes (Supratman et al., 2021; Chen et al., 2020). Coculture has also been recognized as an efficient strategy to explore the chemical diversity of endophytic fungi (Ebrahim et al., 2016; Zhang et al., 2017) because it can simulate a competitive natural environment (e.g., space, nutrients) of two or even more microorganisms and activate the expression of silent gene clusters under standard laboratory growth conditions (Deepika et al., 2016).

In the face of growing microbial resistance worldwide, the discovery of novel antimicrobials is of great importance (Aslam et al., 2018). The *Diaporthe* genus has been described as an important source of antimicrobials. Antibacterial 3-hydroxypropionic acid (3-HPA) produced by the endophyte *Diaphorte phaseolorum* isolated from Brazilian mangroves showed in vitro activity against both *Staphylococcus aureus* and *Salmonella typhi* (Sebastianes et al., 2012). In another study, the crude extract obtained from *Diaphorte* sp. 94 (4) strain isolated from *Avicennia nitida* (Sebastianes et al., 2013) showed in vitro activity against the human pathogens *Escherichia coli* (ATCC 25922), *S. enteritidis* (ATCC 19196), *S. aureus* (ATCC 6538), and *Candida albicans* (ATCC 10231) (Moreira et al., 2020).

Nonantimicrobial therapeutic agents have also been obtained from endophytic fungi. Dhankhar et al. (2013) evaluated the activity of extracts obtained from mycelia of fungal endophytes associated with *Salvadora oleoides* Decne to investigate new antidiabetic drugs. Aqueous extract from unidentified fungi, methanolic extract from *Aspergillus* sp. JPY2 and JPY1 and acetone extract from *Phoma* sp. significantly reduced blood glucose levels. Aqueous extracts showed improvement in parameters such as body weight and lipid profile of alloxan-induced diabetic rats. Lethal effects on the animal were not observed up to doses of 1000 mg/kg b.w. Caicedo et al. (2019) used a 2,2-diphenyl-1-picrylhydrazyl *(*DPPH) free radical scavenging assay and verified the high antioxidant activity of exopolysaccharides present in crude extracts of the endophytic fungus *Fusarium oxysporum* isolated from the tropical medicinal plant *Otoba gracilipes.* Moreira et al. (2020) showed the antiparasitic activity of crude extracts obtained from the endophyte *Diaphorte* sp. 94(4) against the promastigote form of *Leishmania infantum chagasi* (MHOM/BR/1972/LD).

Bioactive compounds produced by endophytic fungi also have great importance in the improvement of crop productivity and quality of foods, contributing to sustainable agriculture (Lugtenberg et al., 2016). In this way, plant protection and growth can be achieved in different ways. For example, *Aspergillus niger* CSR3 was able to regulate endogenous rice seedlings by producing gibberellins and indoleacetic acid, promoting plant growth. The endophyte also solubilized phosphate and produced siderophores in culture, evidencing its potential as a biofertilizer and suppressor of plant diseases (Lubna et al., 2018). Cytochalasins H and J produced by the endophytes *Diaphorte miriciae* UFMGCB 7719 and 6350, associated with the tropical medicinal plants *Copaifera pubiflora* and *Melocactus ernestii*, exhibited activities against *Phomopsis obscurans* and *Phomopsis viticola*. These results demonstrated the potential of *Diaphorte* species for controlling fungal diseases in plants (Carvalho et al., 2018). Metabolomic analysis of organic extracts obtained from the liquid culture of *Talaromyces pinophilus* strain F36CF revealed the presence of the bioactive metabolite siderophore ferrirubin and antibiotic 3-O-methylfunicone. The first was involved in iron transportation and antibiotic activity, and the latter displayed insecticidal activity on aphids (Vinale et al., 2017).

3. Endophytic Fungi as Sources of Hydrolytic Enzymes

Endophytic fungi produce lytic enzymes such as cellulases, pectinases, amylases, phosphatases, lipases and proteases (Mishra et al., 2019), which help endophytes establish symbiotic associations with host plants (Hallmann et al., 1997) and suppress plant pathogen activities (Gao et al., 2010). These associations have encouraged us to investigate and select endophytic fungi to explore their potential enzymatic activity for applications in agriculture. Recently, Rajini et al. (2020) established cellulase production as one of the traits of endophytes *Trichoderma asperellum*, *Epicoccum nigrum* and *Alternaria longipes* involved in *Sorghum bicolor* colonization and in vitro inhibition growth of *Fusarium thapsinum*, *Epicoccum sorghinum*, *Alternaria alternata* and *Curvularia lunata* by hydrolysis of the cell wall. Moreira et al. (2020) studied the endophyte *Diaphorte* sp. FS-94(4) and attributed the production of celullase in this strain as one of the traits related to in vitro inhibition growth of phytopathogens *Colletotrichum* sp., *Fusarium oxysporum*, *Phythophthora sojae* and *Rhizopus microspores*.

Lytic enzymes produced by fungal endophytes are frequently more stable than enzymes produced by traditional chemical catalysts and often function under moderate pH, temperature, and pressure conditions (Tiwari, 2015). These factors also make these enzymes promising for numerous industrial processes, including food processing, detergent manufacturing, paper recycling, treatment of plant fibers for textile application, and energy and biofuel production (Rana et al., 2019; Naik, 2019c). Sunitha et al. (2012) evaluated the ability of endophytic fungi from the medicinal plant *Alpinia calcarata* (Haw.) Roscoe to produce amylase and standardized the maximum enzyme production conditions. The fungus *Cylindrocephalum* sp. (Ac-7) showed the highest amylolytic activity in growth media containing maltose at 1.5% and sodium nitrate at 0.3% as carbon and nitrogen sources, respectively, at 30°C and pH 7.0. The optimization of fungal amylase production can be useful for starch processing for the food, detergent and textile industries (Souza and Magalhães, 2010). Zaferanloo et al. (2014) optimized protease production by the endophyte *Alternaria alternata* (El-17) isolated from *Eremophilia longifolia*. Overall, the optimum conditions for fermentation were 30°C and pH 7.0, with soybeans as the carbon source and tryptophan or yeast extract as the nitrogen source. The authors suggested the potential use of *A. alternata* as a source of proteases for application in the dairy industry.

No less important is the potential of enzymes secreted by fungal endophytes as an alternative in treating wastes and degrading pollutants (Mishra and Sarma, 2017), contributing to more eco-friendly and sustainable environments. Extracelullar ligninolytic activities in endophytic *Ceratobasidum stevensii* isolated from *Bischofia polycarpa* were demonstrated by Dai et al. (2010). The data showed that manganese peroxidase was the predominant ligninolytic enzyme in polycyclic aromatic hydrocarbon degradation. Russell et al. (2011) demonstrated the ability of two endophytic *Pestalotiopsis microrspora* isolates from woody plants to produce serine hydrolases and degrade the polymer polyester polyurethane. In another study, Xie and Dai (2015) demonstrated the potential of endophytic *Phomopsis liquidambari* for the degradation of methoxyphenolic and ferulic acid pollutants through the production of ferulic acid descarboxilase, laccase and protocatechuate 3,4-dioxygenase.

4. Endophytic Fungi and Weed Control

Agrochemicals are widely used to eradicate plant diseases and control specific plants or animals, which consequently promotes an improvement in crop yield, quality, and shelf life (Omomowo and Babalola, 2019). However, such agents have drawn considerable attention concerning issues related to sustainability as well as negative repercussions on the environment and human health (Cullen et al., 2019), and changes in environmental conditions induced by the application of these products are reported to affect the microbial community (Suryanarayanan, 2019).

Competition for nutrition between the crop and weeds might cause severe losses in agricultural systems, representing an economic problem (Harding and Raizada, 2015). However, modern agriculture is entirely dependent on the widespread use of herbicides, which leads to the emergence of multiple resistance to these agents (Peterson et al., 2018). However, bioherbicides are ecofriendly compounds naturally produced by living organisms or their natural metabolites that are used to control weed populations (Radhakrishnan et al., 2018). These phytotoxins are secondary metabolites that play an important role in the induction of disease symptoms in agrarian and forest plants and weeds (Cimmino et al., 2015).

Cytochalasins are a large and chemically diverse group of fungus-derived natural products (polyketide synthase-nonribosomal peptide synthetases) that exhibit a broad spectrum of biological activities (Cimmino et al., 2015; Han et al., 2019). Such compounds are considered potential mycotoxins. Nevertheless, a *Xylaria* strain endophytically isolated from *Toona sinensis* is described as a producer of cytochalasin E, which demonstrated high growth inhibition on lettuce *Lactuca sativa* and radish *Raphanus sativus* seedlings (Zhang et al., 2014). Later, Han et al. (2019) used OSMAC approach on *Xylaria* sp. XC-16 for the isolation of epoxyrosellichalasin, hydroxyldecandrin G, and cytochalasin K, which strongly inhibited *Triticum aestivum* shoot elongation, whereas cytochalasin E is a potent inhibitor of root elongation of *Raphanus sativus*.

Endophytic fungus *Phomopsis* sp. HCCB03520 (*Diaporthe*) is also reported as a phytotoxin producer such as cytochalasins (H, N, and epoxycytochalasin H), herbaria (I and II), and a nonenolide compound that was isolated from solid cultures, which exhibited phytotoxic effects on the germination and radicle growth of *Medicago sativa* L., *Trifolium hybridum* L., and *Buchloe dactyloides* (Yang et al., 2012).

Chloroplasts are organelles originating from endosymbiotics in plants that are responsible for the production of several metabolites and photosynthesis (Zhang et al., 2020). The phytotoxic effect on the photosynthesis machinery of spinach chloroplasts has been observed by natural and semisynthetic compounds produced by the endophytic *Xylaria feejeensis* isolated from the tropical medicinal tree *Sapium macrocarpum*. A semisynthetic derivative of coriloxine showed a significant enhancement in the phosphorylating electron transport rates and Mg^{2+}-ATPase activity, whereas the semisynthetic quinone inhibited the Hill reaction at electron transport on the water-splitting enzyme (Macías-Rubalcava et al., 2017).

5. Fungal Endophytes Might Influence the Photosynthetic Apparatus

Photosynthesis is considered the basis of plant growth. Such a photochemical process is performed by a variety of organisms, ranging from plants to bacteria, which are capable of capturing and converting energy from sunlight into biochemical energy (Evans, 2013).

Green-colored plant pigment chlorophyll may be found in plants, bacteria, and algae and is a porphyrin-based molecule that plays a critical role in the photosynthetic pathway. Its molecular structure exhibits a tetrapyrrole ring that is capable of absorbing blue light and red light of solar radiation at 430 nm and 660 nm, respectively, as well as UV-B (280–320 nm), but it reflects the green and yellow spectrum (Arof and Ping, 2017; Pareek et al., 2018).

Absorption of UV-B by chlorophyll, despite a minor component of sunlight, is reported to be harmful to biomolecules. Molecular oxygen atoms in the ground state ($3O_2$) are converted into singlet oxygen ($1O_2$), which is highly reactive and can react with various biological molecules, including lipids, proteins, and nucleic acids, causing the death of cells (Figure 1) (Quinn et al., 2014; Barrera et al., 2020).

Photoprotective effects promoted by fungal endophytes were reported by Barrera et al. (2020). The endophytic fungi *Alternaria* sp., *Eupenicillium osmophilum, Penicillium brevicompactum*, *P. chrysogenum*, and *Phaeosphaeria* sp. were identified as the most abundant in association with the Antarctic plant *Colobanthus quitensis*. In addition, the endophytically colonized plants exhibited the accumulation of key flavonoids that are known to regulate oxidative stress and photoprotective effects, as well as the expression of genes associated with UV-B photoreception, lower lipid peroxidation, and an improvement in photosynthesis efficiency in comparison with noncolonized plants.

However, members of the *Epichloë* genus possess numerous features beneficial to their host plants (Song et al., 2016). As mentioned, photosynthesis plays an important role in plant growth, and under stress conditions, photosynthetic capability might suffer losses (Harman et al., 2021). Rozpądek et al. (2015) described the improvement of photosynthetic activity of photosystem II, carbon assimilation, and biomass increase of *Dactylis glomerata* promoted by the symbiotic fungus *E. typhina*.

Trichoderma spp. are described as endophytes but might be found in several environments. These species have been reported to have protective effects against phytopathogenic fungi (Tseng et al., 2020). Interestingly, *Trichoderma* spp. is capable of enhancing photosynthesis by inducing the upregulation of genes and pigments and activating biochemical pathways that reduce the harm caused by reactive oxygen species (ROS) (Harman et al., 2021).

6. Omics Approaches to Explore Endophytic Fungi-Plant Interactions in Agriculture

Endophytic fungi exhibit complex interactions with host plants, which involve biotic, abiotic, and genetic factors (Hardoim et al., 2015). A better understanding of this relationship becomes of great importance to improve the ways in which these microorganisms can be applied in agriculture to increase plant growth and crop yields, control pests, suppress virulence in pathogens, and/or help plants survive in environmental stress, including extreme temperatures and pH levels, drought, heavy metal toxicity, and nutrient limitation (Naik, 2019b ; Lugtenberg et al., 2016).

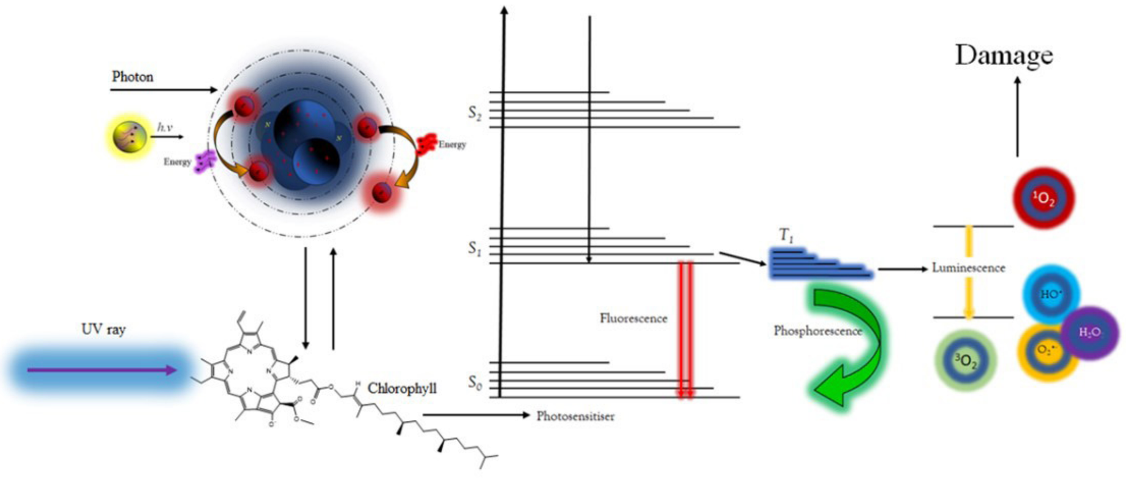

Figure 1. Photodynamic reaction induced by UV-B. Initially, chlorophyll absorbs a photon that excites the chlorophyll to the short-lived singlet state and may decay by nonradioactive relaxation with heat emission or fluorescence emission to the long-lived triplet state. In this triplet state, chlorophyll can interact with molecular oxygen in two ways, type 1 and type 2, leading to the formation of oxygen radicals and singlet oxygen.

Keeping in mind the benefits of endophytic fungi on plant health and for sustainable and eco-friendly agricultural productivity (Kaur, 2020), many studies in recent decades have focused on exploring the aspects of this symbiotic relationship.

Recent advances in technologies and bioinformatic tools to generate and process extensive omic data are revolutionizing research on endophyte-plant relationships. In this context, genomic studies based on next-generation sequencing (NGS) platforms provide valuable information about the structural and functional aspects of genes, taxonomy, and phylogeny of endophytes (Bosamia et al., 2020), which can integrate other data from omics approaches to unravel the effects on plant gene expression during interaction with fungal endophytes (Table 1).

Thus, genomics provides an overview of the full genetic complement of an organism; transcriptomics, proteomics and metabolomics determine the total set of transcribed RNAs, proteins and metabolites, respectively, in a cell, tissue or organism under a given set of conditions (Kaul et al., 2016; Bosamia et al., 2020)

The plant defense system comprises many factors, and endophytic fungi can have substantial influence on the plant metabolic process, inducing systemic resistance and leading to tolerance to pathogens (Gao et al., 2010). Employing quantitative transcriptomic analysis, Ambrose and Belanger (2012) evaluated the differential expression of genes associated with *Festuca rubra* colonization or not with the endophyte *Epichloë festucae.* Data revealed that over 200 plant genes involved in various physiological processes were differentially expressed between the two samples. The transcript abundance and the nature of one secreted protein suggested that protein may be involved in disease resistance in endophyte-infected *F. rubra.* Correlation of transcriptomic data with genomic data was essential to understand that the uniqueness of this gene in *E. festucae* can confer resistance to the host.

Plant growth promotion effects by fungal endophytes are also well documented (Bilal et al., 2018; Khalil et al., 2021). Using comparative transcriptomics and proteomics, Yuan et al. (2019) verified the impact of the endophyte *Gilmaniella* sp. AL12 in the regulation of metabolism of the medicinal herb *Atractylodes lancea*. This study showed

Table 1. Benefits of endophytic fungi to host plants revealed by omics-based approaches.

Host Plant	Endophyte	Benefits	Omics Approaches	Reference
Zea mays	*Exophiala pisciphila*	Heavy metal tolerance by the remodeled host cell walls	Transcriptomic	Shen et al. (2020)
Eucalyptus globulus	*Chaetomium cupreum*	Heavy metal tolerance; plant growth promotion by a complex regulation of auxin biosynthesis and metabolism	Transcriptomic	Ortiz et al. (2019)
Brassica napus	*Piriformospora indica*	Stress/defense responses; energy production; nutrient acquisition; biosynthesis of essential metabolites; root's architectural modification; cell remodeling; cellular homeostasis	Proteomic	Shrivastava et al. (2018)
Lolium arundinaceum	*Epichloë coenophiala*	Disease resistance; abiotic stress responses	Transcriptomic	Dinkins et al. (2017)
Hordeum vulgare	*Piriformospora indica*	Salt stress tolerance	Metabolomic Transcriptomic Ionomic	Ghaffari et al. (2016)
Lolium perene L. cv Samson	*Epichloë festucae*	Changes in host development, particularly trichome formation and cell wall biogenesis; resistance to drought and infection by fungal pathogens	TranscriptomicMetabolomic	Dupont et al. (2015)
Theobroma cacao	*Colletotrichum tropicale*	Changes in host physiology, metabolism and anatomy; resistance to pathogens and herbivores	Transcriptomic	Mejía et al. (2014)
Hordeum vulgare	*Piriformospora indica*	Drought stress tolerance through photosynthesis stimulation, energy releasing and enhanced antioxidative defense system	Proteomic	Ghabooli et al. (2013)
Zea mays	*Fusarium verticillioides*	Reduction of harmful effects of phytopathogen	TranscriptomicMetabolomic	Jonkers et al. (2012)
Hordeum vulgare	*Piriformospora indica*	Induction of systemic disease resistance	Transcriptomic Metabolomic	Molitor et al. (2011)

that endophytes weakened the plant immune response, suggesting that this regulation may contribute to beneficial plant-endophyte interactions. In addition, the presence of *Gilmaniella* sp. AL12 upregulated plant genes involved in the production of proteins related to carbon fixation and carbohydrate and energy metabolism, leading to an increase in biomass and sesquiterpenoid content in the shoots of *A. lancea*.

Abiotic stresses can restrict plant growth and development and impact crop productivity (Kumar, 2014). Saline stress is considered one of the main factors that leads to morphological and physiological changes in plants (Fougère et al., 1991). Alikhani et al. (2013) used a proteomic approach to evaluate the influence of the endophyte *Piriformospora indica* on the tolerance of *Hordeum vulgare* L. to salt stress. Mass spectrometric analysis led to the identification of 51 proteins related to different functions, including photosynthesis, cell antioxidant defense and energy production. These results indicated that endophytic fungi induced a systemic response to salt stress by altering the physiological and proteome responses of the plant host, opening perspectives to improve plant adaptability to environmental stresses.

In this way, omics-based technologies have been fundamental to provide clearer insights into metabolism, physiology, gene expression, and other aspects of endophytic-plant interactions (Chetia et al., 2019), contributing to a better understanding of the beneficial effects of endophytic fungi in improving plant health.

7. Conclusion

This review has indicated that endophytic fungi can produce bioactive compounds that originate from their host plants, encouraging us to investigate and select these microorganisms for biotechnological exploration. Fungal endophytes appear to have the potential to produce a range of metabolites with significant biological activity for applications in pharmaceuticals, medicine, industry, crop protection and improvement, and environmental recovery. Omic technologies have been incorporated into studies of plant-endophytic fungi interactions, providing us with directions to solve problems of plant disease and improve the productivity and quality of crops, bringing important environmental and economic implications for agriculture.

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