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Fungal endophytes: The hidden helpers in sustainable agriculture

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ABSTRACT

Endophytes are becoming increasingly popular as a means of enhancing agricultural productivity, and they are seen as an important aspect in sustainable agriculture. These beneficial fungi form symbiotic relationships with plants, enhancing their growth, health, and resilience. Endophytes improve soil fertility by solubilizing minerals, fixing nitrogen, and producing plant growth-promoting substances. They also confer drought tolerance, disease resistance, and pest control, reducing the need for chemical inputs. Additionally, endophytes promote soil biodiversity, structure, and carbon sequestration, contributing to ecosystem services. Fungal endophytes residing symbiotically inside the plant tissues play an important role in the growth promotion and resistance to various biotic and abiotic stresses and diseases in plants. Endophytic fungi stimulate plant growth, lower oxidative stress, increase nutrient uptake, and alter levels of various phytohormones in plants grown in stressed conditions. Endophytic fungi are used as the most common microbial biological control agents (MBCAs) against various phytopathogens in the form of enhanced plant growth and induced systemic resistance, produce a variety of antifungal secondary metabolites (lipopeptides, antibiotics and enzymes) through colonization. By harnessing endophytes, we can develop innovative, eco-friendly solutions for sustainable food production, mitigating environmental impacts, and ensuring food security for future generations.

Contribution/Originality: This study provides significant insights into symbiotic relationship of fungi with plants. This mini review from existing literature highlights dynamic role of fungal endophytes in boosting agricultural productivity and promoting sustainable farming practices. Moreover, endophytes improve crop yields, soil fertility and environmental stress.

1. INTRODUCTION

The term 'endophyte' is derived from two Greek words: 'endo' = '*endon'* meaning within, and phyte' = '*phyton'* meaning plant and was first proposed by German scientist De Bary (1866) to denote all those microbes that residing inside healthy plant tissues without causing any harm to their host (Chhipa & Deshmukh, 2019; Kusari & Spiteller, 2012; Lata, Chowdhury, Gond, & White Jr, 2018). Sustainable agriculture demands multiple approaches for improving food production while decreasing health risks (Sarkar et al., 2020; Yadav, 2020). Plants are now suffering multiple pressures in the current scenario, resulting in enormous drops in agricultural production and food security (Raza et al., 2019). The use of endophytic fungi is the most sustainable technique, with plenty of advantages for both crops and the environment. Endophytes are important in sustainable agriculture because they improve plant health and defends against attack of phytopathogens (Akram et al., 2018). Fungal endophytes have been closely associated with practically every group of plant kingdom, starting with algae, lichens, bryophytes to lower cryptograms, i.e., pteridophytes, gymnosperms, and to the most advanced angiosperms flourishing in the wild and under cultivation (Ikram, Ali, Jan, Jan, & Khan, 2020; Kamat, Kumari, Taritla, & Jayabaskaran, 2020; Verma et al., 2017). This symbiotic interaction between plants and fungal endophytes results in the production of biologically active chemicals (antifungal, antibacterial, insecticides, plant growth regulators, and so on), which enhances the host crop tolerance to numerous biotic and abiotic challenges encountered in nature (Fadiji & Babalola, 2020; Ghasemnezhad, Khavazi, & Ghorbanpour, 2021). Endophytes have gained attention as biological fertilizers or phyto-remediation applications in agriculture (Ortega, Torres-Mendoza, & Cubilla-Rios, 2020). Endophytic fungi are known to secrete growth-promoting compounds such as phytohormones indole acetic acid (IAA), cytokinin (CKs), and gibberellins (GAs), which aid in fostering plant growth (Badawy et al., 2021; Muhammad Hamayun et al., 2017). Concurrently, several studies have revealed that these endophytic fungi release a variety of secondary metabolites responsible for strengthening plant defense, including phenols, flavonoids, and lignin (Yan et al., 2021).

Endophytic fungi sustain crop plant growth under various types of abiotic stresses, including salinity, temperature, drought, heavy metals (HMs), and ultraviolet radiation (UV) as demonstrated by a number of previous studies (Bouzouina, Kouadria, & Lotmani, 2021; El-Sayed, Ismaiel, Ahmed, Hassan, & El-Din, 2019; Guler, Pehlivan, Karaoglu, Guzel, & Bozdeveci, 2016; Husna et al., 2021). Interestingly, fungal endophytes have also been isolated from plant parts growing in extreme conditions and this enormous diversity of these fungal endophytes in different conditions may be correlated with their massive positive role in the ecosystem and its processes (Sangamesh et al., 2018). Endophytic fungi are isolated from plant parts using both culture dependent and culture independent approaches (Dissanayake et al., 2018). The culture dependent method is widely used to identify fungal endophytes (Hyde & Soytong, 2008; Sun & Guo, 2012) and to estimate the diversity of endophytic species (Koukol, Kolařík, Kolářová, & Baldrian, 2012). The standard classification manuals (i.e., "Manual for fungi") are most frequently used for the isolation and identification of fungi (Dugan, 2006).

2. ROLE OF FUNGAL ENDOPHYTES IN SUSTAINABLE AGRICULTURE

Endophytes are gaining recognition for their potential to boost agricultural productivity and promoting sustainable farming practices (Akram et al., 2018). The excessive use of chemical pesticides has sparked concerns over environmental pollution, toxic residual effects, resistance development in plant pathogens and the non-target effect on beneficial microbes prompting researchers to explore eco-friendly alternatives like fungal endophytes to meet growing agricultural demands sustainably (Ahmed et al., 2020; Akram et al., 2018; Singh, Trivedi, Egidi, Macdonald, & Delgado-Baquerizo, 2020). Endophytes are widely known for their mutualistic relationship with plants as they impart several beneficial effects without causing any deterrent harm (Khare, Mishra, & Arora, 2018; Saikkonen, Faeth, Helander, & Sullivan, 1998).

Moreover, they improve plant growth and yield and additionally improving the health of plants by means of biotic and abiotic stress tolerance (Barka, Nowak, & Glick, 2002; Vega, Posada, Aime, & Pava-Ripoll, 2008). It is also reported that crops with an accurate endophyte proportion have stronger resistance and faster growth than crops without potential endophytes (Rai et al., 2014). This is likely due to their production of defensive compounds, including alkaloids, flavonoids, terpenoids, quinones, chlorinated metabolites and phenolics (Kaur, 2020; Wei et al., 2021).

Furthermore, endophytes induce systemic resistance and directly combat plant pathogens through production of compounds like salicylic acid, HCN, siderophores, cell wall disintegrating enzymes and antifungal chemicals (Jacob, Krishnan, Thankappan, & Amma, 2020; Yuan et al., 2019). Endophytes are also reported to produce hormones that promote plant growth, such as gibberellin, indole acetic acid, and cytokinin, and also enhance phosphate solubilization in various crops (Hassan, 2017; Sandhya, Shrivastava, Ali, & Sai Shiva Krishna Prasad, 2017).

3. FUNGAL ENDOPHYTES AS BIOLOGICAL CONTROL AGENTS AGAINST PATHOGENIC FUNGUS

Plant pathogens pose a major threat to food security and ecosystem stability (Savary et al., 2019). It is estimated that pathogen attacks will reduce about 30–50% of global crop production, leading to an increase in poverty and malnutrition (Pimentel, 2009). Among the phytopathogens, fungi are considered as one of the most destructive pathogens in agriculture (Almeida, Rodrigues, & Coelho, 2019). The research on the biological control of phytopathogens is a relatively emerging field, however, several studies have supported the role of endophytes in pathogen inhibition. Fungal endophytes play an important role in plant–pathogen interactions. Endophytic microorganisms improve the adaptability of plants by employing different mechanisms of action. Endophytic fungi commonly adopt mechanisms including pathogen inhibition directly through competition, antibiosis and mycoparasitism while indirectly through the induction of resistance, thereby activating the defense system of plant to resist the disease (Ahmed et al., 2020). Also, some produce antimicrobial compounds that inhibit pathogen growth, while others compete for niche and nutrients (Fadiji & Babalola, 2020). The endophytic biocontrol strains of *Trichoderma* and *Sebacinales* spp. have been known to control many root, foliar, and fruit pathogens, alleviate various abiotic stresses, physiological stresses (seed age) as well as enhance nutrient absorption. These endophytic strains also increase the photosynthesis and respiratory activities of plants. These functions are associated with their ability to reprogram plant gene expression, possibly by activating some of the universal plant pathways (Shoresh, Harman, & Mastouri, 2010). Sustainability in agriculture in an eco-friendly way can be achieved by management strategies involving endophytic symbiosis that reduce excessive fungicide use.

Figure 1 Illustrates the potential role of endophytes in agriculture.

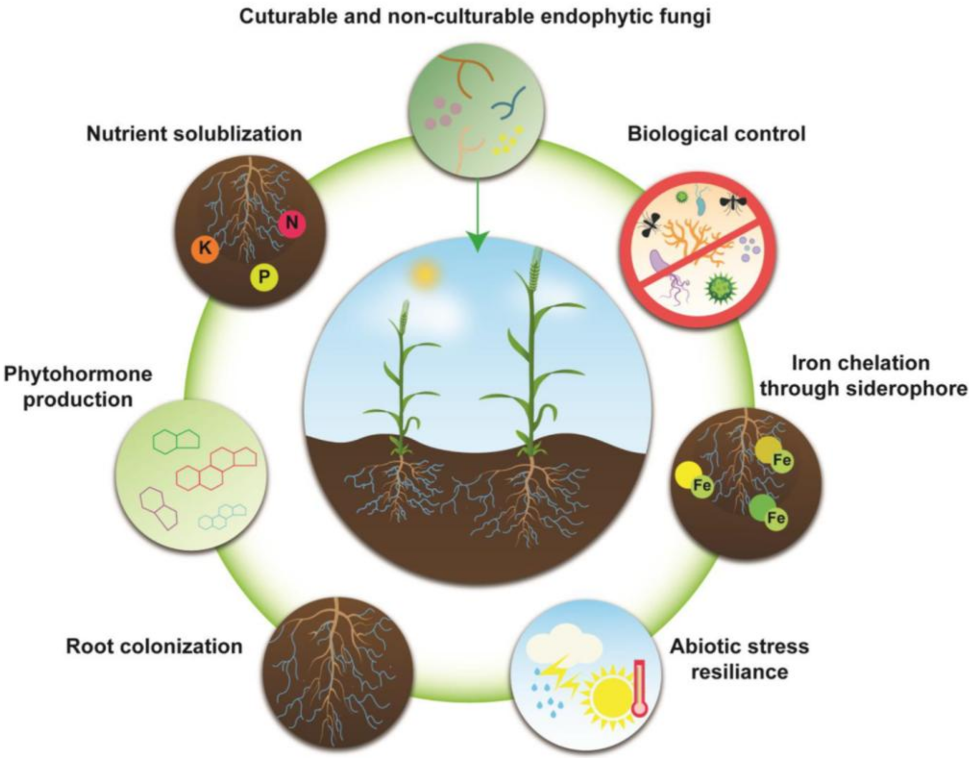

Figure 1. Potential roles of endophytes in agriculture.

Source: Akram et al. (2018).

Table 1. Fungal endophytes as biological control agents against pathogenic fungus.

S.no.	Endophytic fungi	Pathogenic fungi	Target disease	Reference
1.	*Verticillium lecanii* (Chrysanthemum host)	*Puccini horiana*	White rust	Whipps (1993)
2.	*Trichoderma viride, Epico cumnigrum, Fusarium tricinctum, Alternaria alternata, Sclerotinia sclerotiorum, Cytospora*	*Diplodia corticola*	Cankers, vascular necrosis, and dieback	Rubini et al. (2005)
3.	*Beauveria bassiana* strains (Sugar cane)	*Colletotrichum falcatum*	Red rot of sugar cane	Sanivada and Challa (2014)
4.	*Beauveria bassiana* (Cotton seed)	*Rhizoctonia solani, Pythium myriotylum, and Thielaviopsisbasicol*	Seedling diseases	Griffin (2007)
5.	*B. bassiana* (Cotton and tomato seed)	*Rhizoctonia solani, Pythium myriotylum, and Xanthomonas axonopodis* pv. *malvacearum*	Damping off seedlings and root rot (Bacterial blight).	Veselý and Koubova (1994)
6.	*B. bassiana Vuillem* in (Tomato seedling)	*Pythium myriotylum*	Pythium damping-off	Clark (2006)
7.	*Colletotrichum gloeosporioides, Clonostachys rosea* and *Botryosphaeria ribis*	*Monilio roreri, Phytophthora* spp.	Black pod rot	Mejía et al. (2008)
8.	*Aspergillus flavus, A. niger, A. terreus. Aspergillus* spp., *Penicillium sublateritium, Penicillium* spp. from FCV tobacco	Pathogenic fungi	Black mold in fruits and vegetables	Subhashini (2018)

Table 1 presents role of fungal endophytes as biological control agents against pathogenic fungus.

4. ENDOPHYTIC FUNGI AND ABIOTIC STRESS ALLEVIATION IN PLANTS

4.1. Salinity

Salinity is the primary limiting factor and serious risks to agricultural food production, particularly in semi-arid or dry conditions (Munns & Tester, 2008).

Most agricultural land in the globe has been seriously harmed, and some assumptions suggest that by 2050, almost 50% of arable lands would be under major salinity danger (Chandrasekaran & Muthukumar, 2014; Rubin & Stedinger, 2017). Soil exposure to Na+ ions impair normal physiological functioning as well as crop yield (Gupta et al., 2021) and soil salinity disrupts ion distribution and metabolism in the cell. Plants are vulnerable to ion toxicity, osmotic stress, nutritional (N, K, P, Ca, Fe, Zn) deficiencies, and oxidative stress, all of which impede water uptake (Bano & Fatima, 2009; Talaat & Shawky, 2013).

Different salt-tolerant fungi have been studied to increase crop growth under salinity stress (Table 2). Bouzouina et al. (2021) found that applying endophytic fungi (*Chaetomium coarctatum* and Alternaria chlamydospore) to wheat plants enhanced plant growth rate, relative water content (RWC), ion balance (Na+ and K+), and sugar and proline levels under salt stress. The up-regulation of vacuolar NHX1 Na+/H+ antiporters aids in the storage of Na+ in vacuoles and modulates the concentration of Na+/K+ ions, resulting in salt stress tolerance in tomato and lettuce (Molina-Montenegro, Acuña-Rodríguez, Torres-Díaz, Gundel, & Dreyer, 2020). Table 2 outlines the numerous studies that have found that endophytic fungus can help minimize salt stress in important crops.

Table 2. A list of recent studies illustrating the influence of endophytic fungi in alleviating salt stress in important crop plants.

S. no.	Endophytic fungi	Host plant	Effects on host plant	References
1.	*Piriformospora indica* (PiHOG1)	*Oryza sativa*	• Enhanced photosynthetic rate, pigment and proline contents • Increased shoot and root lengths, biomass • Delayed phosphorylation	Jogawat, Singh, and Singh (2016)
2.	*Trichoderma longibrachiatum*	*Triticum aestivum*	• Higher chlorophyll content and shoot proline content • Increased water content in leaves and roots	Zhang, Gan, and Xu (2016)
3.	*Porostereum spadiceum* AGH786	*Glycine max*	• High GAs and low ABA • Enhanced endogenous level of two isoflavones including daidzin and genistein	Muhammad Hamayun et al. (2017)
4.	*Trichoderma harzianum*	*Brassica juncea*	• Restricted Na^+ uptake • Modulation of osmolytes and antioxidants • Improved uptake of essential elements	Ahmad et al. (2015)
5.	*Epichloë* sp.	*Hordeum vulgare*	• Lower Na^+ and higher N, P, and K^+ contents • Increased biomass • Lower ratios of C:N, C:P, Na^+: K^+ and higher ratio of N:P	Song et al. (2015)
6.	*Piriformospora indica*	*Zea mays*	• Decreased levels of Na^+ and K^+ in roots	Yun et al. (2018)

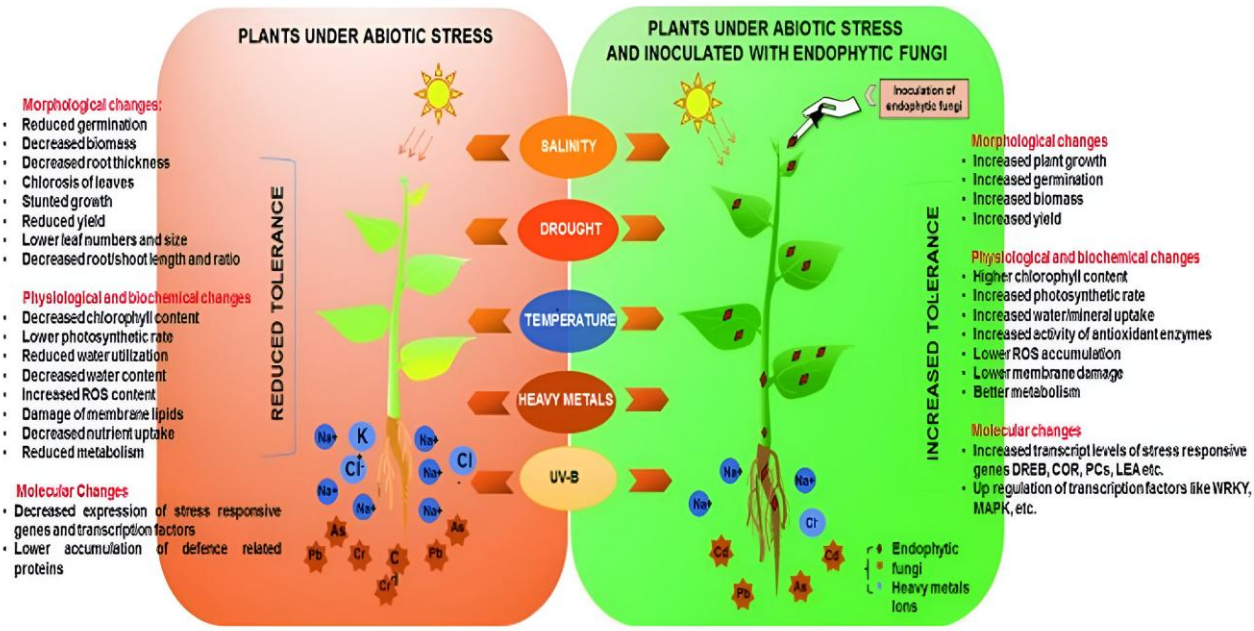

Figure 2. Endophytic fungi mediated abiotic stress amelioration mechanisms in plants.

Source: Toppo and Mathur (2022).

Figure 2 Illustrates role of Endophytic fungi in abiotic stress mitigation mechanisms in plants.

4.2. Drought

Drought is a recurrent, more severe, and unpredictable meteorological state that has a global impact on crop production, particularly in dry and semi-arid regions (Attafi, Darvishi Boloorani, Fadhil Al-Quraishi, & Amiraslani, 2021; Kogan, Guo, & Yang, 2019). Plants adapt to drought stress by altering their physiological and biochemical functions (Basu, Ramegowda, Kumar, & Pereira, 2016).

The symbiotic interaction of endophytic fungi such as *Penicillium minioluteum* with *Chenopodium quinoa* improves crop production during extreme drought, with inoculated plants showing a 40% increase in root development (González-Teuber, Urzúa, Plaza, & Bascuñán-Godoy, 2018). Endophytic fungus protects drought-stressed plants against ultrastructural damage (including mitochondria), alter root morphology, and modulate endogenous hormonal equilibrium (IAA, ABA) (Liu & Wei, 2021).

Guler et al. (2016) investigated the effect of *Trichoderma atroviride* ID20G on drought-stressed maize seedlings and found that increasing fresh and dry root weight, boosted chlorophyll and carotenoid content while preventing membrane damage. A study found that five endophytic fungi improved drought tolerance in barley plants (*Hordeum murinum* subsp. *murinum*), resulting in more tillers, higher grain production, and higher shoot biomass (Murphy, Martin Nieto, Doohan, & Hodkinson, 2015).

Table 3 presents potential role of endophytic fungi in the alleviation of drought stress in different host plants.

Table 3. A list of recent studies depicting the effect of endophytic fungi in the alleviation of drought stress in different host plants.

S. No.	Endophytic fungi	Host plant	Effects on host plant	References
1.	*Neocamarosporium chichastianum N. goegapense Periconia macrospinosa*	*Cucumis sativus Solanum lycopersicum*	• Increased proline and antioxidants levels	Moghaddam, Safaie, Soltani, and Hagh-Doust (2021)
2.	*Cladosporium* sp.	*Nicotiana benthamiana*	• Differential accumulation of metabolic compounds like cytosine, diethylene glycol, etc. • Increased root dry mass and relative water content	Dastogeer et al. (2017)
3.	*Penicillium minioluteum*	*Chenopodium quinoa*	• Enhanced plant growth and root formation	González-Teuber et al. (2018)

4.3. Temperature

Fungal endophytes play a crucial role in the alleviation of temperature stress in crop plants as demonstrated by previous investigations (Shaffique et al., 2022). High temperatures impede crop productivity and microbial colonization, causing significant cellular damage such as protein breakdown and aggregation (Hussain, 2019). Endophytic fungi have been found to be associated with plants growing in adverse conditions and to support their growth. Endophytic fungi, *Gliocladium cibotii*, isolated from *Verbena officinalis*, have been shown in studies to improve plant growth and increase ROS degrading enzymes (such as ascorbic acid oxidase, CAT, glutathione reductase (GR, POD, and SOD) content in *Glycine max* and *Helianthus annuus* exposed to heat stress (Hamayun et al., 2021). Sangamesh et al. (2018) described some thermotolerant endophytic fungus found in plants growing in Rajasthan's Thar Desert. Some of the main endophytic fungi that were isolated were ACJ-2, ACJ-5 (*Aspergillus flavus*), SAP-3 (*Aspergillus* sp.), SAP-6, LAS-4 (*Aspergillus* sp.), and LAS-6 (*Chaetomium* sp.). A study of barley seed produced under low-temperature stress found that the presence of root endophytic fungus *Chaetomium globosum*, *Epicoccum nigrum*, and *Piriformospora indica* resulted in significantly higher survival rates. The results showed that seeds inoculated with endophyte *P. indica* had increased nutritional input, earlier flowering, and higher grain dry weight (Murphy, Doohan, & Hodkinson, 2014). Table 4 lists some of the studies that found endophytic fungus to be effective in alleviating temperature stress in different plants.

Table 4. A list of recent studies depicting the effect of endophytic fungi in the alleviation of temperature stress in different host plants.

S. no.	Host plant	Endophytic fungi	Effects on host plant	References
1.	507 endophytic fungal Dominating fungi were *Aspergillus flavus* (ACJ-2, ACJ-5), *Aspergillus* sp., (SAP-3, SAP-6, LAS-4) *Chaetomium* sp. (LAS-6)	*Oryza sativa*	• Higher shoot and root growth	Sangamesh et al. (2018)
2.	*Aspergillus japonicas* (EuR-26)	*Helianthus annuus Glycine max Oryza sativa*	• Higher content of flavonoids, phenolics, soluble sugars, proteins and lipids • Increased ABA levels • Increased activity of catalase and ascorbic acid oxidase	Muhammad Hamayun, Hussain, Iqbal, Khan, and Lee (2018)
3.	*Thermomyces* sp.	*Cucumis sativus*	• Increased antioxidant enzyme activities and metabolite pool • Enhanced photosynthesis and water use efficiency	Ali, Abdelrahman, Radwan, El-Zayat, and El-Sayed (2018)
4.	*Paecilomyces formosus* LHL10 *Penicillium funiculosum* LHL06	*Glycine max*	• Higher photosynthetic activity • Increased plant growth • Decreased lipid peroxidation • Enhanced micronutrient uptake	Bilal et al. (2020)

5. CONCLUSION

To summaries, fungal endophytes are a game changer in sustainable agriculture, providing a viable option for environmentally friendly food production. Endophytes improve crop yields, soil fertility, and environmental stress reduction by creating symbiotic interactions with plants. As the world's population is projected to reach 9.7 billion by 2050, the importance of sustainable agriculture cannot be overstated. Future prospects include the development of endophyte-based biofertilizers, biopesticides, and drought-tolerant crops. Additionally, advances in genomics and biotechnology will enable the creation of customized endophyte strains for specific crops and environments. As research and development continue to uncover the tremendous potential of fungal endophytes, we can expect a paradigm shift in sustainable agriculture that will ensure food security, mitigate climate change, and promote environmental stewardship for future generations.

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