



Endophytes–Hidden Influences on Nutrient Acquisition and Abiotic Stress Mitigation

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This work was carried out in collaboration among all authors. All authors read and approved the final manuscript.

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Abstract

Climate change and associated fluctuations in rainfall, temperature and water availability place increasing pressure on agricultural production. Sustainable improvements in crop productivity therefore require approaches that support nutrient acquisition and plant performance without increasing dependence on synthetic inputs. Endophytic bacteria and fungi inhabit internal plant tissues and can influence host growth through several direct and indirect mechanisms. This review examines their reported contributions to nutrient acquisition and the mitigation of abiotic stress. Endophytes may assist nitrogen acquisition through biological nitrogen fixation, improve phosphorus availability through solubilisation and mobilisation, and contribute to potassium and micronutrient nutrition. Additional interactions involve siderophore production, changes in root architecture and the modulation of phytohormones. Under drought, salinity and temperature stress, endophyte-associated plants have been reported to exhibit changes in water relations, antioxidant activity, osmotic adjustment and growth responses. The manuscript also discusses endophyte-assisted responses to heavy-metal stress and the practical constraints affecting agricultural use. These include difficulties in isolation, variability in colonisation and performance under field conditions, competition with native microorganisms, pathogenicity concerns and formulation requirements. Although reported findings indicate potential benefits for sustainable crop production, responses vary with the host, microorganism and environmental conditions. Further work is needed to clarify cellular nutrient-transfer processes and optimise reliable, safe and economical applications of endophytes in agricultural systems.

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1. Introduction

Agriculture and the agri-food sector are expected to move towards environmental sustainability by increasing productivity while protecting the natural resource base for future generations. Global agricultural productivity is largely influenced by various abiotic factors including drought, salinity, cold, heat and variations in soil pH, which hamper agricultural yields. Changing climatic conditions and increasing anthropogenic activities associated with growing populations accelerate the challenges of abiotic stresses (Singh *et al.*, 2021). Uncertain climatic conditions, irregular rainfall, heatwaves and rising global temperatures directly affect crop growth and yield by reducing water availability, decreasing photosynthetic rates and creating drought conditions. Greater productivity and competitiveness are anticipated to come from increased efficiency through the acquisition and management of new technologies and crop production strategies. Plant–microbe interactions that promote plant health and development have been the subject of considerable study in sustainable agriculture. Among these organisms, endophytes play an important role in plant-related processes such as colonisation, competition, coexistence and soil nutrient dynamics. Some endophytes promote growth of their host plants by enhancing the host’s ability to take up nitrogen and phosphorus. Recently, endophytic fungi have gained importance in agriculture because of their ability to confer resistance to abiotic stresses, such as temperature extremes, light intensity, drought and salinity, and to biotic stresses, such as pathogen attack and insect herbivory, by supporting several plant growth processes. Recent reviews have described the potential contributions of plant–endophyte interactions to nutrient uptake and plant responses to abiotic stress, while emphasising the complexity of these associations (Sena *et al.*, 2024).

Mechanistic syntheses identify biological nitrogen fixation, mineral nutrient solubilisation, and regulation of stress-associated physiological processes among the pathways through which endophytes may benefit their hosts (Tariq *et al.*, 2025). Plant nutrient acquisition includes both direct uptake mechanisms and microbe-assisted pathways, particularly those involved in nitrogen and phosphorus nutrition (Zhao *et al.*, 2024). In wheat seedlings, an endophytic bacterial isolate was reported to improve growth-related traits under imposed drought stress and to exhibit phosphate-solubilising activity (Dubey & Gautam, 2022). A review focused on floriculture similarly described nutrient solubilisation, phytohormone production, and stress-related benefits associated with endophytes and plant growth-promoting rhizobacteria (Sahu *et al.*, 2025). Despite the reported benefits, the relationships between nutrient acquisition and abiotic stress mitigation by endophytes, together with the limitations affecting their practical agricultural use, warrant an integrated synthesis.

1.1 Objective

This review aims to synthesize the reported roles and mechanisms of bacterial and fungal endophytes in plant nutrient acquisition and abiotic stress mitigation and to outline the practical considerations for their use in sustainable crop production.

1.2 Endophytes

The term “endophyte” was coined by Anton de Bary in 1866 and was derived from two Greek words: “endon” meaning within and “phyton” meaning plant. Wilson (1995) defined endophytes as microbes (typically fungi or bacteria) that inhabit the internal tissues of plants without causing disease symptoms and described their symptomless occupation of plant tissues and their symbiotic or mutualistic relationships with the host. In these organisms, all or a part of their life cycle occurs within their hosts, without causing any apparent symptoms of disease. They are ubiquitous in nature, exhibit complex interactions with their hosts and have been reported in tissues including leaves, stems, roots, flowers and fruits. These interactions involve mutualism, antagonism and, rarely, parasitism (Nair & Padmavathy, 2014).

Endophytes, which are found in almost all plant species (Saikkonen *et al.*, 1998), and colonise internal plant tissues, are valuable in agriculture as a means of improving crop performance (Azevedo *et al.*, 2000). One endophyte species might be associated with many plant species, and many species of endophytes might be present in the same plant species. Some endophytes remain latent within the host plant, while others may interact with other endophytes, whether pathogenic or non-pathogenic (Zabalgogezcoa, 2008).

2. Endophytes- Origin and Evolution

The fossil record shows that endophytes have been associated with land plants for more than 400 million years (Krings *et al.*, 2007). During evolution, plants moved from aquatic (oceanic) to terrestrial habitats and encountered an atmosphere containing high concentrations of carbon dioxide, nutrient-poor soils and fluctuations in temperature and water availability. Under such circumstances, fungi helped plants withstand adverse conditions and establish themselves in soil (Bonfante & Selosse, 2010).

During the same evolutionary period, endophytes adapted to the plant microenvironment by modifying their genetic make-up through the incorporation of some of the plant’s DNA (Germaine *et al.*, 2004). Through this adaptation and uptake of genetic material, endophytes began producing plant metabolites or their precursors (Zhang *et al.*, 2006). Endophytes are now known to occur in a wide range of habitats and plants such as mosses, ferns, lichens, shrubs, grasses and deciduous and coniferous trees (Sun & Guo, 2012).

The first reports of endophytic fungi isolated from tropical host plants involved plants belonging to the families Araceae, Bromeliaceae and Orchidaceae. Later, in 1984, several endophytic fungi were isolated from members of the same families in France, Brazil and Colombia. Many fungal species colonise living bark, twigs and even small branches of conifers and trees.

2.1 Abundance / Occurrence

The endophytic community is made up of organisms from distinct origins, with organisms possessing larger genomes more likely to live in variable environments, such as soils, whereas those with smaller genomes are more likely to inhabit stable environments and be transmitted vertically (Mitter *et al.*, 2013).

Bacterial endophytes representing more than 200 genera and 16 phyla, including both culturable and unculturable bacteria belonging to Acidobacteria, Actinobacteria, Aquificae, Bacteroidetes, Cholorobi, Chloroflexi, Cyanobacteria, Deinococcus-Thermus, Firmicutes, Fusobacteria, Gemmatimonadetes, Nitrospira, Planctomycetes, Proteobacteria, Spirochaetes and Verrucomicrobiae have been reported (Hallmann *et al.*, 1997). The presence of asymptomatic endophytic fungi in plants has been known since the nineteenth century, and it has been estimated that more than one million endophytic fungal species exist relative to the number of vascular plant species, at a ratio of 1:4–5 fungi per plant (Sun & Guo, 2012).

3. Classification of Endophytes

Endophytes include a wide variety of microorganisms, including fungi, bacteria, actinomycetes and viruses. Endophytes are classified into two categories: systemic (true) endophytes and non-systemic (transient) endophytes. These categories are based on the endophyte's genetics, biology, and mechanism of transmission from host to host (van der Heijden *et al.*, 2015). Systemic endophytes are defined as organisms that live within plant tissues for the entirety of their life cycle and participate in a symbiotic relationship without causing disease or harm to the plant at any point. Additionally, systemic endophyte concentrations and diversity do not change in a host with changing environmental conditions. Non-systemic or transient endophytes, on the other hand, vary in number and diversity within their plant hosts under changing environmental conditions. They have also been shown to become pathogenic to their host plants under stressful or resource limited growing conditions.

Fungal endophytes have been grouped into four classes based on taxonomy and six other criteria, including host range, host tissues colonized, in-plant colonisation, in-plant biodiversity, mode of transmission and fitness benefits (Wani *et al.*, 2015). These four groups are divided into clavicipitaceous endophytes (Class 1) and non-clavicipitaceous endophytes (Class 2, 3, and 4).

Class 1 endophytes are all phylogenetically related and proliferate within cool- and warm-season grasses. They typically colonize plant shoots where they form a systemic intercellular infection. Class 1 endophytes are mainly transmitted from host to host vertically, whereby maternal plants pass fungi to their offspring through seeds and could further be divided into Types I, II and III. These three types of clavicipitaceous endophytes possess different interactions with their plant hosts with interactions ranging from pathogenic to symbiotic and symptomatic to asymptomatic.

Non-clavicipitaceous endophytes represent a polyphyletic group of organisms. Non-clavicipitaceous endophytes are typically Ascomycota fungi. The ecological roles of these fungi are diverse and still poorly understood. These endophyte–plant interactions are widespread and have been found in nearly all land plants and ecosystems. Many non-clavicipitaceous endophytes have the ability to switch between endophytic behavior and free-living lifestyles. Non-clavicipitaceous endophytes are divided into class 2, 3 and 4.

4. Endophytes vs Epiphytes

Endophytes are often contrasted with epiphytes, which live on external plant surfaces (Santamaria & Bayman, 2005). The distinction is that epiphytes can be washed off plant surfaces or be inactivated by surface disinfection, usually with sodium hypochlorite and ethanol, whereas endophytes cannot. Thus, an epiphyte that survives surface disinfection and grows in culture might be assumed to be an endophyte (Arnold & Lutzoni, 2007).

4.1 Endophytes - Colonization in Plants

Endophytes may have vertical transmission (from maternal plant to seeds) or horizontal transmission (from plant to plant). In horizontal transmission, recruitment of microbes from the soil is an important mechanism for plants to gain endophytes (Hallmann *et al.*, 1997). This may occur through passive entry via natural openings and wounds, whereas other microbes use lytic enzymes to enter plant cells and tissues actively (Hallmann *et al.*, 1997).

4.2 Endophytes –Benefits to Plants

Improvements in the growth and yield characteristics of black pepper (Anith *et al.*, 2018) and tomato (Abdelaziz *et al.*, 2019) following inoculation with the root endophytic fungus *Piriformospora indica* have been reported.

Endophytes mediate plant growth promotion through direct or indirect mechanisms (Hardoim *et al.*, 2008). Because some endophytes originate as rhizosphere bacteria, they may retain their attributes inside plants. These beneficial mechanisms are related to those of rhizosphere bacteria, as most endophytes can be cultured and can survive outside their hosts in the rhizosphere. Endophytic microbes function in the following ways: (i) increase nutrient acquisition by plants; (ii) defend plants against pathogens and insects; (iii) increase stress tolerance in plants; (iv) modulate plant development; and (v) suppress weed growth. The specific mechanisms through which endophytic microbes perform these functions in plants are likely to differ depending on the microbe and plant.

5. Endophytes and Nutrient Acquisition

Nitrogen, phosphorus and potassium are major nutrients acquired by plants through their roots, and their limited availability in soil affects plant productivity. The availability of these nutrients in the rhizosphere depends in part on plant symbioses with microbes involved in nutrient acquisition. Symbioses with beneficial fungi and bacteria are known to be vital for nutrient acquisition by the root systems of most plants (Sirrenberg *et al.*, 2007). Thus, application of beneficial microorganisms as biofertilisers plays a key role in today's agricultural scenario by enhancing soil fertility and crop production. For example, mycorrhizal fungi of the order Glomales are known to have symbiotic relationships with the majority of terrestrial plant species, whereby the fungi facilitate plant access to soil nutrients, mainly phosphate (Harrison, 2005).

5.1 Nutrient Acquisition Symbiosis

Endophytic microbes that supply nutrients to plants include those that fix atmospheric nitrogen in plant tissues. These types of endophytes include actinorhizal and rhizobial symbioses.

Because nitrogenases are sensitive to oxygen, the few families of plants that engage in nitrogen-fixing symbioses sequester microbes in low-oxygen nodules, where nitrogen is fixed and transferred to root tissues. Another type of nutritional endophytic symbiosis involves microbes that inhabit internal plant tissues and extend into the soil. Dark septate endophytes and mycorrhizal fungi establish this kind of symbiosis with many families of plants. The hyphae of these fungi grow endophytically in roots, while mycelia extending into the soil acquire nutrients and mobilise them for plants. Another nutrient acquisition mechanism involves the liberation of nutrients from insects by microbes that extend between, or cycle between, plants and decaying insects. In this process insects consume plants and accumulate nitrogen and other nutrients in their bodies; the degradation of insects by microbes that are also symbiotic with plants results in the transfer of nutrients to plants.

In another symbiosis, the "rhizophagy cycle" or "rhizophagy symbiosis", microbes (often bacteria or yeasts) cycle between an endophytic/intracellular protoplast phase in root cells and a free-living walled phase in the soil. Microbes acquire nutrients in the free-living soil phase and nutrients are extracted oxidatively from microbes in the endophytic/intracellular protoplast phase (White *et al.*, 2018). Nitrogen fixation by microbes involved in the rhizophagy cycle occurs in the free-living soil phase because high levels of reactive oxygen secreted from root cell plasma membranes onto microbes inhibit nitrogenases. In the rhizophagy cycle, microbes receive nutrients from plants through root exudates (e.g., carbohydrates, proteins, vitamins, organic acids) around the root tip meristem.

5.2 Nitrogen Fixation

Nitrogen supply is a major limiting nutritional factor for plant growth. Plants cannot reduce atmospheric N and therefore require an external supply of fixed N. Biological N fixation has considerable potential as an alternative to chemical fertilisers. Several symbiotic prokaryotic endophytes capable of fixing atmospheric nitrogen have potential agricultural applications. Diazotrophic endophytes can directly transport nitrogen to plants. Nitrogen-fixing, free-living endophytic bacteria have been studied for several decades (Döbereiner & Pedrosa, 1987). The most famous and well-studied legume-Rhizobium symbiosis is still the subject of worldwide research which is directed towards enhancing the N₂ fixation efficiency through plant and bacterial genome manipulation.

A study reported the effects of inoculating sugarcane plants with a consortium of five different endophytic diazotrophic bacteria belonging to *Gluconacetobacter diazotrophicus*, *Herbaspirillum*, and *Burkholderia* (Schultz *et al.*, 2014). In this study, the consortium was evaluated with regard to the agronomic performance and N nutrition of sugarcane in the field against chemical N fertiliser, and found that the consortium increased sugarcane stalk yield to a level similar to that obtained with chemical fertilisation. *P. indica*-colonised tomato plants showed improved N acquisition, which was not affected by increases in soil P levels or the degree of colonisation when compared with AMF-colonised plants (Cruz *et al.*, 2010).

Twenty-three endophytic bacteria were identified as potential ammonia producers in chilli; Audipudi *et al.* (2017) reported that *Pseudomonas*, *Curtobacterium* and *Bacillus* sp. isolated from chilli were among the highest producers of ammonia. Christian *et al.* (2019) reported that colonization by foliar endophyte *Colletotrichum tropicale* in leaves of *Theobroma cocoa* significantly affected nitrogen uptake and distribution. They found significantly higher concentrations of N¹⁵ in endophyte-inoculated plant leaves than in uninoculated plants in the same pots.

5.3 Phosphate Solubilization

Apart from N₂ fixation, several endophytes release organic acids into the soil that solubilise phosphate complexes and convert them into orthophosphate for plant uptake and utilisation. Although phosphorus is abundant in soils, most of it remains unavailable in insoluble forms. Several studies discuss the role of endophytes as phosphate solubilisers. Endophytic bacteria possess the ability to solubilise inorganic phosphate and extracellular tri-calcium phosphate effectively in the presence of glucose (Kuklinsky-Sobral *et al.*, 2004). Plants take up phosphate either directly through their own transporters or indirectly through endophytic or mycorrhizal associations. For example, the endophyte *Pantoea* spp associated with root nodules of groundnut have been shown to possess phosphate solubilizing activity. Endophytic *Bacillus*, *Pseudomonas*, *Klebsiella* and *Acinetobacter* are also re-reported as potential phosphate solubilizers (Kuklinsky-Sobral *et al.*, 2004).

In soybean, endophytic bacteria generally occur during the vegetative (V6) stage, when Enterobacteriaceae and species of *Pseudomonas* and *Ralstonia* involves in phosphate solubilization (Kuklinsky-Sobral *et al.*, 2004) and improve P nutrition, potentially helping to reduce phosphate fertiliser use. Endophytic *Bacillus cereus* and *B. megaterium* isolated from Ginseng plant also showed significantly high P solubilisation (Thamizh Vendan *et al.*, 2010).

Arbuscular mycorrhizal fungi (AMF) form symbiotic associations with roots of most terrestrial plants. Host plants transfer carbohydrates to AMF for mycelial growth and spore development; on the other hand, mycorrhizal hyphae absorb nutrients from the soil and transfer them to the host, thus promoting plant growth and nutrient acquisition (Aggarwal *et al.*, 2011; Yamawaki *et al.*, 2013). *Pseudomonas aeruginosa* strain PM389 isolated from pearl millet was found to exhibit mineral phosphate solubilisation, siderophore production, and antagonistic activity against several pathogenic bacterial and fungal species (Gupta *et al.*, 2013).

P. indica is an efficient phosphate mobilizer and produces phosphatase enzymes which cleave phosphate ester bonds of insoluble polyphosphates and organic phosphates (Malla *et al.*, 2004) and different organic acids which, in turn, solubilise insoluble polyphosphates. The ability of the fungus to grow on various P sources, including inorganic, organic and polyphosphate forms, also indicates its role as an active P solubiliser as well as a P mobiliser.

5.4 Potassium Mobilization and Micronutrients

Potassium is another nutrient important for plant growth and development. According to Baghel *et al.* (2020), inoculation with the endophytic bacterium FDN2-1 in soil amended with glauconite could significantly increase available K.

Saddique *et al.* (2018) found that rice seeds inoculated with the endophytic fungus *Piriformospora indica* showed significantly higher concentrations of P and zinc (Zn) in plant roots and shoots compared with uninoculated controls.

5.5 Siderophore Production

Some endophytes produce small molecules called siderophores, which are iron-chelating compounds that can make iron available to plants and deprive pathogens of iron (Compant *et al.*, 2005). Among the siderophores produced by endophytes, those with biocontrol properties include catecholate, hydroxamate and/or phenolate types. Also, siderophores specifically help iron-deficient plants in fixing nitrogen since diazotrophs require Fe^{2+} and Mo factors for nitrogenase synthesis and functioning. In the case of plant growth-promoting bacteria, Fe^{2+} is oxidised to an Fe^{3+} -siderophore complex in the bacterial membrane, which is later introduced into the cell by endophytes through a gating mechanism (Gao *et al.*, 2010). The concentration of soluble metals increases when siderophores bind to the metal surface (Rajkumar *et al.*, 2010). After heavy metal contaminants have been removed, plants employ different mechanisms to acquire iron from bacterial siderophores.

A siderophore-producing endophyte, *Pseudomonas* strain GRP3 was tested on *Vigna radiata* for its effects on iron nutrition. After 45 days, plants inoculated with strain GRP3 showed reductions in iron-deficiency-related chlorotic symptoms and increased chlorophyll a and chlorophyll b contents compared with the control (Sharma *et al.*, 2003).

Streptomyces acidiscabies E13 was also reported to be an effective siderophore producer that enhances the growth of *Vigna unguiculata* under nickel stress conditions (Sessitsch *et al.*, 2013). Certain endophytic actinomycetes such as *Streptomyces* sp. GMKU 3100, *Streptomyces* sp. mhcr0816, *Streptomyces* sp. UKCW/B, and *Nocardia* sp. have been reported to produce siderophores (Singh & Dubey, 2018).

5.6 Modulation of Root Architecture

As soil is a reservoir of nutrients and water, roots are crucial for plant access to these resources. Variations in root characteristics have been observed under different stress conditions. Endophytes produce plant growth regulators that affect root architecture (Lamont, 2003). Maggini *et al.* (2019) reported that in Echinacea plants, indole-3-acetic acid-producing endophytes affected the physiology and function of the root.

Endophyte-mediated enhancement of root development in cuttings and seedlings was reported in Scots pine and Norway spruce (Doty, 2011). Colonization of fungal endophytes improves nutrient solubilisation, nutrient uptake and water-absorption efficiency in plants by increasing root surface area (Yakti *et al.*, 2018).

5.7 Phytohormone Production

Endophytic microbes enhance plant growth through their ability to synthesize enzymes and various bioactive metabolites (Huang *et al.*, 2010). Endophytic microbial associations may also enhance the production and signalling of phytohormones that promote plant growth (Pinski *et al.*, 2019) and may activate host gene expression related to nutrient metabolism (Bajaj *et al.*, 2018). *P. indica*-mediated growth promotion has been attributed to altered levels of primary metabolites, particularly putrescine, which increased IAA and gibberellin levels in tomato (Kundu *et al.*, 2022). Putrescine is also important for hyphal growth of *P. indica* indicating that it is co-adapted by both host and microbe. The authors therefore concluded that putrescine is an essential metabolite and its biosynthesis in plants is crucial for *P. indica*-mediated plant growth promotion and fungal growth.

6. Endophytes as Abiotic Stress Controller in Plants

Abiotic stress is a major threat to agriculture and has been associated with productivity reductions of more than 50 per cent in major crop plants worldwide (Bray *et al.*, 2000) and with morphological, physiological, biochemical and molecular changes in plants (Wang *et al.*, 2003). Plant growth and development are restricted by different extreme conditions which include environmental stresses as well as stresses caused by living communities.

Plants may tolerate abiotic stress *via* two mechanisms: the activation of response systems following exposure to stress and the production of biochemical compounds by endophytes that act as anti-stress agents (Schulz *et al.*, 2002).

The symbiotic interactions between plant and endophyte may result in several outcomes depending on the fitness benefits experienced by each partner. Changes in the external environment disrupt plant metabolic homeostasis, creating a need for genetic and metabolic mechanisms within plant cells (Gill & Tuteja, 2010). The importance of microbes, especially the endophytes, at this point increases immensely. Over the past decade, studies have shown that fungal endophytes confer stress tolerance to host species and play a significant role in plant survival under abiotic stress (Rodriguez *et al.*, 2009) and this could be an alternative strategy to overcome the abiotic stress in plants. Endophytic microbes aid in plant health by deterring herbivory and pathogenesis while also facilitating plant growth through nutrient uptake (modification of root morphology, alteration of nitrogen accumulation and metabolism), water use efficiency (osmotic adjustment, stomatal regulation) and mitigation of environmental stresses. In turn, endophytes obtain access to the host plant's nutrients and dissemination to the next generation.

6.1 Drought Stress Management

Plant growth is greatly affected by drought stress and plants must adapt to this stress to survive. Drought is a major abiotic stress, adversely affecting crop productivity and distribution worldwide and affecting up to 45% of global agricultural land (Hussain *et al.*, 2018). Drought stress induces a range of physiological and biochemical responses in plants such as stomatal closure, repression of growth and photosynthesis, and activation of respiration. Plants experience drought conditions when water supply to the roots is limited or transpiration is very high.

Diurnal water stress normally occurs in most plant species around midday and in the afternoon in temperate climates, even though soil water content is normal. This temporary drought stress has a negative impact on the growth rate and can reduce germination rates, disrupt membrane integrity, suppress photosynthesis and increase the production of reactive oxygen species (Greenberg *et al.*, 2008). Furthermore, drought and salinity are the main causes of osmotic stress to plants. While drought leads to osmotic stress, salinity causes both ionic toxicity and osmotic stress in cells (Zhu, 2002).

All fungal endophytes conferred drought tolerance to plants regardless of the habitat of origin (Rodriguez *et al.*, 2008). Endophytes may influence plant metabolism to promote the accumulation of soluble sugars, amino acids such as proline, polyols, and alkaloids that contribute to cell-wall elasticity and osmotic adjustment under drought conditions. Endophyte-associated plants have been reported to use significantly less water and possess increased biomass than the non-symbiotic plants. The drought tolerance phenomenon may be explained as enhanced accumulation of solutes in tissues of endophyte-infected plants as compared to non-infected plants, reduced leaf conductance and a slower transpiration stream, or thicker cuticle formation (Malinowski & Belesky, 2000).

The central response to water deficits is increased biosynthesis of the plant hormone ABA and/or reduced ABA breakdown (Bray, 2002). In plants suffering from drought, ABA acts as a signal regulating plant responses to water deficits, principally by controlling water loss and stomatal closure. Also, other evidence suggests that ABA plays a role in root branching, enhancing the plant water absorption capacity (de Smet *et al.*, 2006).

Piriformospora indica, an endophytic fungus co-cultivated with Arabidopsis plants, was associated with earlier upregulation of drought-stress-related mRNAs and proteins in leaves of colonised seedlings than in uncolonised seedlings. *P. indica* colonisation of Chinese cabbage roots promotes root and shoot growth and lateral root formation. When *P. indica* colonized plants were exposed to polyethylene glycol to mimic drought stress, the activities of peroxidases, catalases and superoxide dismutases in the leaves were upregulated within 24 hours (Rodriguez *et al.*, 2008). *P. indica* colonization was found to retard the decline in photosynthetic efficiency and prevent the degradation of chlorophyll and thylakoid proteins of colonized plants under drought stress condition (Sun *et al.*, 2010).

Seed treatment (1%) followed by foliar application (2%) of PPFM, twice, at 30 and 50 days after sowing, enhanced the growth and yield of aerobic rice (Aswathy, 2020). The significant role of *P. indica* inoculation in rice grown under different levels of moisture stress has been documented.

As part of investigations into PPFM and plant growth regulators under drought (Sivakumar *et al.*, 2017), a study by Sivakumar *et al.* (2018) reported that tomato plants grown under drought or water stress were treated with pink-pigmented facultative methylotrophs (PPFM) or plant growth regulators (PGRs). PPFM (2%) produced the greatest root length of 25.90 cm, followed by brassinolide (25.20 cm) and salicylic acid (22.93 cm). Root length increased by up to 26.34 per cent with PPFM (2%) compared with the control, followed by brassinolide (22.93%). Among the treatments, PPFM (2%) resulted in the highest lycopene content (5.92 mg) followed by brassinolide (5.88 mg).

Xu *et al.* (2017) imposed drought stress on maize seedlings both naturally and by applying PEG-6000. Twelve plants per treatment were grown in a plastic pot containing sterilised sand. Water was withheld to impose natural drought stress. For PEG-6000 treatment, seedlings were carefully removed from the sand, washed and transplanted into a pot containing half-strength Hoagland solution containing 20% PEG-6000 (with or without *P. indica* inoculation). Control plants were grown in half-strength Hoagland solution for the duration of the experiment. Samples were harvested within 24 h. The effects of *P. indica* colonisation on maize seedlings are depicted in Fig. 1.

Table 1. Effect of PPFM and PGR on the root length, root volume and fruit yield of tomato under drought

Treatments	Root length (cm)	Root volume (cm ³)	Fruit yield (g/ plant)
Absolute control (100% FC)	27.90	122.80	674.10
Control (50% FC)	20.50	97.90	409.30
PPFM (1%)	22.60	101.00	463.40
PPFM (2%)	25.90	117.00	552.90
PPFM (3%)	22.10	110.00	428.80
Brassinolide (1ppm)	25.20	118.90	509.40
Salicylic acid (100 ppm)	22.93	119.70	472.60
BAP (100 ppm)	21.50	108.70	419.20
GA ₃	22.10	106.76	425.60
SEd	0.48	2.73	11.03
CD (P = 0.05)	1.02	5.73	23.18

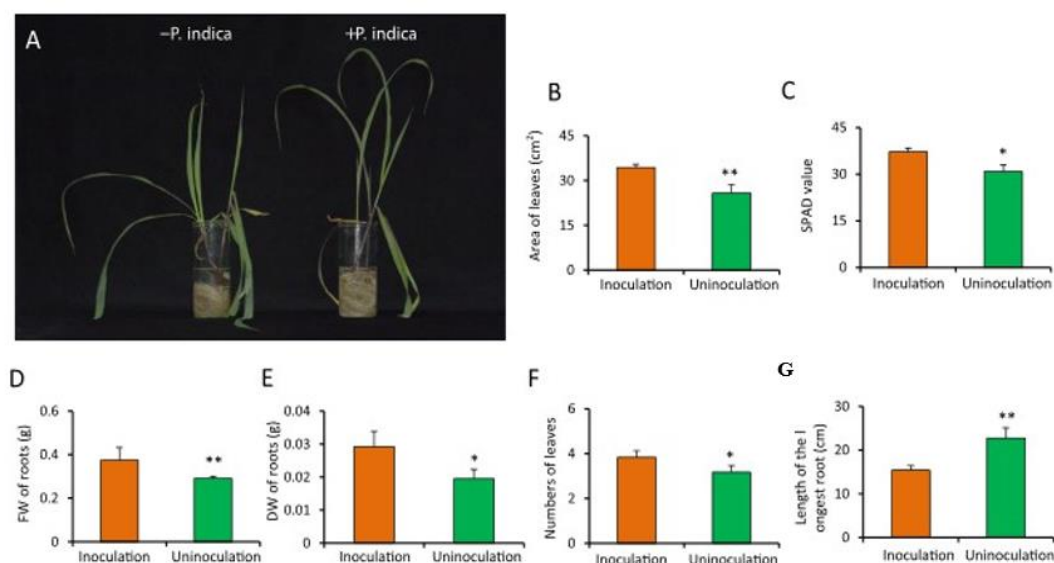


Fig. 1. (A). Picture showing the impact of *P. indica* on maize seedlings. (B). Effect of *P. indica* on the leaf area (C). Effect of *P. indica* on SPAD value. (D, E). Effect of *P. indica* on fresh weight and dry weight of maize seedling roots, (F). Effect of *P. indica* on number of leaves and (G). Effect of *P. indica* inoculation on root length

In another study, *Gluconacetobacter diazotrophicus* strain PAL 5 and a strain belonging to the genus *Herbaspirillum* were inoculated into sugarcane plants to evaluate their drought stress recovery (Aguilar *et al.*, 2016). After being subjected to 21 days of drought stress, bacteria-inoculated plants had significantly higher shoot and root dry weight (50 and 70%, respectively) and total N content in leaves (77%). It was also reported that these diazotrophic strains help preserve leaf water potential and relative water content through efficient stomatal closure, resulting in plant water preservation during the drought, which highlights the ability of these endophytic diazotrophic bacteria to protect the plant from abiotic stresses.

AMF have been reported to increase water absorption, nutrient absorption, photosynthesis, root structure, antioxidant defence systems, polyamine and fatty acid homeostasis, osmotic adjustment, aquaporin expression, soil structure, and hormone balance to resist soil water deficit (Zou *et al.*, 2021).

6.2 Salinity and Alkalinity Stress Management

Salinity is a major abiotic stress that restricts yields on almost 40 m ha of irrigated land, which is approximately one-third of the irrigated land on earth. It is estimated that about 50 per cent of arable land will be affected by salinity stress by the year 2050 (Munns & Tester, 2008). Salinity severely affects plant growth and metabolism, resulting in reduced biomass production (Sekmen *et al.*, 2007).

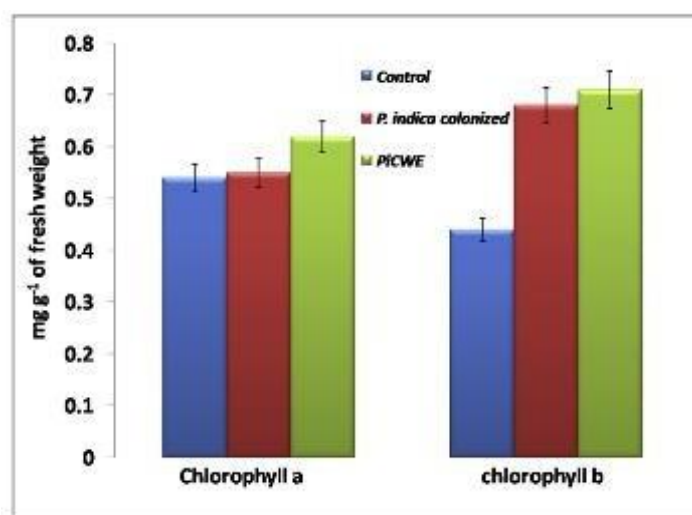


Fig. 2. Effect of *P. indica* colonization on stress imposed *Centella asiatica* plants in a study conducted by Jisha et al. (2018)

The fungus *P. indica* has been shown to grow even under conditions of high salt concentration of 219.14 mM whereas its growth was inhibited at a salt concentration of 438.27 mM (Chordia, 2011). Khan et al. (2011) reported that the endophytic association of *Penicillium minioluteum* significantly ameliorated the negative effects of abiotic salinity stress damage and supported soybean growth and metabolism. The low level of ABA and high level of salicylic acid (SA) in endophyte-treated soybean plants compared with untreated plants under salinity stress suggests favourable effects of *P. minioluteum* association. *P. indica* induces salt tolerance in barley by increasing the levels of antioxidants (Baltruschat et al., 2008).

In a study conducted by Radhakrishnan et al. (2013), four endophytic fungi (GM-1, GM-2, GM-3, and GM-4) were tested for their ability to improve soybean plant growth under salinity stress conditions. The seed germination and plant growth were higher in seeds pre-treated with endophytic fungal cultures than in the controls. Sallaku et al. (2019) showed that arbuscular mycorrhizal fungi (AMF) alleviate the salinity stress in cucumber plants by extending their root length and root surface area and photosynthetic rate (NAR) compared with untreated plants. Improved root systems enable the plant to utilise water and minerals from non-saline areas until exploitation of areas affected by salt cannot be avoided.

Waller et al. (2005) demonstrated that *P. indica* could diminish the adverse effects of salt stress in barley seedlings by increasing ascorbic acid levels and antioxidant enzyme activities. Redman et al. (2011) evaluated the role of the endophytic fungus *Fusarium culmorum* (FcRed1) in cultivated rice varieties var. M-206 (subspecies Japonica) and Dongjin (subspecies Indica). The results showed that the symbiotic rice seedlings under stress conditions such as salinity and drought performed better with respect to plant height, root length, biomass and higher osmolyte accumulation than non-symbiotic rice seedlings, indicating a beneficial effect of *Fusarium culmorum*.

6.3 Temperature Stress Management

Temperature is among the abiotic stresses that severely affect plant growth and metabolism, resulting in reduced biomass production and plant death. Plants have developed mechanisms to cope with these stresses through signal-transduction pathways that adjust their metabolism. Crop plants are highly sensitive to ambient temperature, with a 1° C difference in temperature sufficient to affect development and yield. Monocot crop plants are particularly vulnerable to higher temperatures during the reproductive and grain-filling phases. The critical temperature above which plants get killed is called thermal death point. Temperatures above 50°C kill many annual crops. Temperature stress may occur at either low or high temperatures.

Cold stress tolerance was conferred to germinated seeds under laboratory conditions by TempSym1 (*Curvularia protuberata*) isolated from *Dichanthelium lanuginosum* thriving in geothermal soils (Redman et al., 2011). In a study conducted by Murugan (2011), cabbage, cauliflower and beetroot plants treated with *P. indica* grew better when compared with the untreated control plants, and after approximately three months of growth in microplots, significant increases in the growth of all three plants were recorded. Endophytes enhance cold tolerance by altering photosynthetic activity and metabolism of carbohydrates resulting in deposition of cold-stress-related metabolites like starch, proline and phenolics.

High temperatures are a major obstacle in crop production as well as microbial colonization, which results in major cellular damage such as protein degradation and aggregation (Hussain et al., 2018). High temperature adversely affects mineral nutrient acquisition, shoot growth and pollen development and disrupts photosynthesis and respiration, resulting in lower yields. The fungal endophyte *Curvularia protuberata* was found to confer thermo-tolerance (over a 12-month field trial and under laboratory conditions) to the monocot *Dichanthelium lanuginosum* (panic grass) (Rodriguez et al., 2008).

6.4 Heavy Metal Stress

Endophytes can break down complex compounds and thereby aid phytoremediation. Phytoremediation can be considered a form of bioremediation. Phytoremediation of organic contaminants is based on the combined actions of plants and their associated microorganisms, such as mycorrhizal fungi and bacteria. Sheng *et al.* (2008) found that water-soluble Pb increased significantly and pH decreased in a solution containing growing endophytes and proposed that these changes might be due to the organic acids produced by the endophytes. Kuffner *et al.* (2010) also found that some Actinobacterium endophytes could release metal-mobilizing metabolites into the contaminated soil, mobilised Zn and/or Cd, and enhanced the metal accumulation in the leaves of *Salix caprea*.

7. Endophytes' Desirable Characters

Endophytes must possess the following attributes for agricultural use.

a. They must not induce plant disease; b. they should be capable of spreading within plant parts; c. they should be culturable; and d. they must colonise plant parts naturally, with species specificity.

7.1 Patents

Approximately 88 patents have been granted for the effectiveness of endophytes in stress alleviation, 90 for their use in controlling biotic stress and seven for phytoremediation.

7.2 Hurdles and Future Prospects

Externally applied endophytes have shown promise for ameliorating abiotic stress in multiple studies; however, their performance is not always maintained under field conditions. To ensure their efficiency in large-scale application and commercialisation of the endophyte-based products for amelioration of abiotic stress, several factors should be optimized as indicated below.

- ✓ Lack of a standard protocol for surface sterilization and endophyte isolation: Isolation of endophytes is a primary step towards developing applications in crops using endophytes. However, there is still a lack of consensus for standard surface-sterilization techniques to remove the epiphytic microbiota from the plant surface. Existing sterilisation techniques have been shown to be harmful to endophytes. Experiments using non-culturable microbes are also difficult, which limits the practical application of endophytes.
- ✓ Endophytes should ameliorate multiple abiotic stresses and should be effective plant colonisers with broad host ranges: Under laboratory conditions, endophytes can be screened for a single abiotic stress such as drought or salinity, but under field conditions, the host plant may face multiple stresses simultaneously. To cope with field stresses, endophytes should confer tolerance to multiple abiotic stresses. Endophytic microbes should be able to colonize diverse plants and crops so that their application is not limited to a few crops.
- ✓ Endophytes should compete effectively in soil and plants with native soil and plant microbes for entry into plant tissues: One major impediment to the use of endophytes under field conditions is the presence of native soil microbes and endophytes that would compete with applied biostimulant microbes for entry into plants. Microbes that are poor competitors with other plant or soil microbes may be excluded from entry into plants because of the presence of other microbes that are in much higher concentrations in soils and in root tissues, effectively blocking their entry. For application under field conditions, biostimulant microbes should be better at entering into plant tissues than many other soil microbes. The qualities that make an endophytic microbe a better competitor are not yet fully understood.
- ✓ Endophytes should not be plant or animal pathogens: Before commercialisation, endophytes should be screened in plants for pathogenicity or production of toxins. Some fungal and bacterial endophytes may not produce toxins in culture, but in plants or in the presence of other microbes, they may produce toxic metabolites. Many stress-tolerance-conferring endophytes, including *Colletotrichum* sp., *Alternaria* sp., *Fusarium* sp. and *Aspergillus* sp., may also be producers of mycotoxins and cause disease in many plants.
- ✓ Endophyte-based formulations should be optimized for economical and sustained delivery under field conditions: For application of endophytes or endophyte-derived metabolites, they may be formulated in liquid or powder form. Under field conditions, the activity of biostimulant microbes or metabolites depends on the type of formulation, humidity and temperature of the environment and the type of active ingredients. For the successful application of formulations, it is necessary to optimize every parameter, specifically for abiotic stress conditions. Further, for a successful product, it should be economical. Cost-effectiveness is improved when a single application of a microbial product results in persistence in the field. Multiple applications increase the cost of the biostimulant product. Several carriers such as chitosan, milk protein and maltodextrins have been used in formulations to increase shelf life and support initial inoculum growth after application to plants.
- ✓ Better public awareness, biological product-friendly government policies and streamlined registration processes are needed: The consumers of an endophyte-based product are commercial growers, gardeners and homeowners. Uncertainty regarding an unfamiliar biological product may discourage the use of new biological technologies including those based on endophytes. Articles for general audiences, awareness programmes, workshops and outreach activities should be conducted at grassroots level to educate potential consumers and local vendors regarding endophyte modes of action and benefits to the environment and human health. Government policies and the registration process for agricultural biostimulants differ from country to country. Governments should support endophyte-based biostimulants by changing policies and laws and allowing easier registrations of biological products. Government and industry partnerships to fund research on endophyte-based technologies could help move endophytes from the laboratory to the market. The results of this effort would be a less contaminated environment and a more sustainable agricultural system that has increased resilience to confront future climate perturbations.

The use of endophytic fungi to improve nutrient absorption in plants may influence the optimal use of organic and inorganic fertilizers. The capability of endophytic fungi to increase biotic and abiotic stress tolerance in plant hosts remains an area requiring further agricultural investigation. Studies of fungal species capable of developing resistance to environmental changes may support their application in pest and disease management under climate change and in food production in resource-limited areas.

Many endophytes are now recognised as symbionts with unique and intimate interactions with the plant host. The use of endophytic fungi in the remediation of contaminated land is yet another area to be explored.

8. Conclusion

Endophytic microorganisms offer potential approaches to improving crop nutrient acquisition and mitigating abiotic stresses while supporting more sustainable agricultural management. The studies reviewed describe contributions from bacterial and fungal endophytes to nitrogen fixation, phosphorus solubilisation, potassium mobilisation, iron acquisition and changes in root architecture. These interactions may also influence plant growth through phytohormone production and the regulation of physiological and biochemical responses. Under drought, salinity and temperature stress, several host–endophyte associations have been associated with improved water relations, antioxidant activity, osmotic adjustment or growth. Their relevance also extends to heavy-metal stress and phytoremediation. Nevertheless, beneficial outcomes observed under controlled conditions do not necessarily translate into consistent field performance. Efficient agricultural use requires suitable host colonisation, the ability to function alongside native microorganisms, the exclusion of pathogenic or toxin-producing strains, and formulations that remain effective under variable environments. Research on nutrient exchange during the rhizophagy cycle and on interactions between shoot and root endophytes remains necessary. A clearer understanding of these processes, together with field-oriented evaluation, may help identify applications that reduce reliance on external inputs without overstating their expected benefits.

9. Limitations

This review synthesises published descriptions of endophyte-associated nutrient acquisition and abiotic stress mitigation across different host plants and microbial groups. The reported responses are context-dependent, and evidence obtained under controlled conditions may not predict performance in diverse field environments. Differences in host compatibility, microbial colonisation, native microbial competition and formulation persistence limit direct generalisation among cropping systems. Mechanistic understanding of nutrient transfer, including the rhizophagy cycle, also remains incomplete. Consequently, the discussion identifies potential agricultural applications but does not establish universally effective inoculants or consistent responses across stresses.

Declaration of AI Use

This manuscript was prepared through the intellectual contributions of the author(s) to the study design, data analysis, interpretation of results, and scholarly content. Grammarly and ChatGPT were used solely to assist with grammatical refinement and reference formatting during manuscript revision. The author(s) accept full responsibility for the accuracy, integrity, and final content of the manuscript.

Competing Interests

Authors have declared that they have no known competing financial interests or non-financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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