



Epichloë spp. and *Serendipita indica* endophytic fungi: Functions in plant-soil relations

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Abstract

Fungal endophytes, by living entire or part of their life inside a plant, are potentially useful in natural ecosystems and agroecosystems to confer multiple benefits to their hosts. These include improvement of water and nutritional status, higher tolerance against biotic/abiotic stresses. In this review, the consequences of infection by *Epichloë* spp., as an obligative symbiont, and *Serendipita indica*, as a facultative one, on plant-soil relations have been discussed. Colonization and infection by both *Epichloë* and *S. indica* results in better plant growth and productivity, including enhanced root proliferation by indole-3-acetic acid production which in turn leads to a better nutrient acquisition. Moreover, the symbionts can confer both local and systemic resistances to pathogens/diseases

through signal transduction. Up-regulation of antioxidant defense system components and reprogramming of stress-related genes in the presence of endophytic fungus can enhance plant resistance against biotic/abiotic stresses. Individual mechanical or drought stresses may impair plant growth and functioning; however, under combined mechanical and drought stresses, drought has little impact on the plant responses and mechanical stress mainly controls physiological attributes including water status and leaf proline. Endophyte-infected hosts usually have higher ability to do osmotic adjustment due to higher proline content. The physical, chemical and biological properties of rhizosphere soil might be changed by the endophyte infection too, presumably resulted in improving soil quality. Altering microbial communication structure and diversity, higher organic carbon storage, enhanced soil fertility and increased aggregate stability due to induced sub-critical hydrophobicity are some important influences of endophyte-host symbiotic relations on soil environment.



1. Introduction to fungal endophytes

The word endophyte, originally proposed by [De Bary \(1866\)](#), is defined as any microbe that spends its entire or part of the life cycle living inside a plant. Fossilized tissues of plant stems and leaves have revealed that plants have been associated with endophytic fungi for more than 400 million years; thus, they play a key role in driving the evolution of life on terrestrial ecosystems. Today, endophytes are more specifically described in terms of their types (fungal and bacterial) and relationships with the host plants (obligative or facultative) ([Rosenblueth and Martínez-Romero, 2006](#)). Fungal endophytes may colonize plant tissues of root, stem and leaves with minimal or no detrimental effects on their hosts ([Arnold and Lutzoni, 2007](#)). They primarily consist of the members of the *Ascomycota* or their mitosporic fungi, as well as some taxa of the *Basidiomycota*, *Zygomycota* and *Oomycota* ([Malinowski and Belesky, 2000](#)). Fungal endophytes have been isolated from many different plants including trees, vegetables, fruits, cereal grains and other crops ([Rosenblueth and Martínez-Romero, 2006](#)) and it is estimated that at least 1 million species of endophytic fungi exist ([Paul et al., 2012](#)). These findings suggest the endophytes as a rich and reliable source of genetic diversity and novel, non-described species.

Endophytic fungi exhibit multifaceted interactions with their hosts including mutualism, neutralism, commensalism and even antagonism ([Dastogeer, 2018](#)) depending on the life history strategies of fungal species and the host plants ([Saikkonen et al., 2016](#)). Regularly, environmental parameters, fungus and plant properties might modify the nature of

plant–fungus associations (Schulz, 2006). For example, the association between asexual *Epichloë* endophytes and cool-season grasses can alter from a mutualistic to an antagonistic symbiosis, when herbivore pressure is low and nitrogen (N) availability for the host is restricted (Saikkonen et al., 2016). Moreover, it is revealed that systemic and vertically transmitted *Epichloë* fungal endophytes and their grass hosts have a higher probability of mutualistic interactions than horizontally transmitted (non-systemic) endophytes in herbs, woody plants and grasses (Saikkonen, 2007). Furthermore, upon leaf aging or senescence, fungal endophytes can shift to the pathogenic side of the continuum, thus becoming more widespread and causing external infections (Saikkonen et al., 2016). However, the relationship between the fungal endophytes and their host plants is usually considered mutualistic because the endophyte-infected plants show promoted growth and higher tolerance to biotic and abiotic environmental stresses. They protect crops against herbivores, suppress or compete with disease causing agents, and combat abiotic stresses. In turn, the host plant provides nutritional support, shelter and propagation opportunities to the fungus (Clay and Schardl, 2002; Schulz, 2006).

In recent years, many scholars have performed descriptive and comprehensive studies to evaluate the influence of fungal endophytes on plant morphological and physiological traits. However, important gaps in our knowledge are evident in the effects of endophyte–plant relations on soil physical, chemical and biological functions. Meanwhile, endophyte–plant associations have a significant impact on soil functions and plant growth (Compant et al., 2016) because, the endophytes regulate many important soil processes and functions like biogeochemical cycling, mineralization and immobilization of nutrients, litter decomposition, and maintenance of plant health and soil quality mainly by changing root architecture and releasing secondary metabolic compounds (Hosseini, 2015; Hosseini et al., 2015a, Hosseini et al., 2017a, 2017b, Hosseini et al., 2018; Ngwene et al., 2016; Slaughter, 2016; Soto-Barajas et al., 2016). Therefore, endophytic fungi, as a significant constituent of natural ecosystems, can play a key role in recycling of material and energy in the environment. Hence, the major points of this chapter are an overview on the roles of fungal endophytes especially *Epichloë* spp. (formerly known as *Neotyphodium*) and *Serendipita indica* (formerly known as *Piriformospora indica*), in plant growth and subsequently to the soil environment with reference to recent developments in endophyte researches.

1.1 Leaf endophytic fungus: *Epichloë* spp.

Endophytic fungi are classified into four functional groups according to their host spectrum, colonized tissue(s), transmission and host colonization pattern and ecological functions (Rodríguez et al., 2009). Class 1 endophytes are defined as Clavicipitaceous including *Balansia* spp. and *Epichloë* spp. associated with insects and fungi or grasses, rushes and sedges. Classes 2, 3, and 4 are included in the non-clavicipitaceous types. The diverse class 2 endophytes include fungi from Ascomycota and a few more fungi belonging to Basidiomycota (Dikarya). Colonizing the root, stem, and leaves of the plants and the formation of extensive plant-fungal infections are the most distinguishing attributes of this group. Class 3 endophytes are enormously diverse and develop highly localized infections mainly in the aboveground parts of tropical trees, nonvascular and vascular plants. Finally, Class 4 endophytes are known as dark septate endophytes [DSE] (Rodríguez et al., 2009).

Cool-season grasses (Poaceae subfamily Pooideae) such as important temperate forage grasses, tall fescue (*Festuca arundinacea* Scherb.), and perennial ryegrass (*Lolium perenne* L.), are frequently colonized with Clavicipitaceous fungal endophytes that include sexual and asexual *Epichloë* species (Card et al., 2014). *Epichloë* endophytes systemically infect aboveground tissues of the host plant especially most abundant in the leaf sheaths and reproductive structures. Previous studies have shown that vertically-transmitted asexual *Epichloë* species (29 species) are efficiently transmitted through host seeds (Leuchtman et al., 2014) and confer numerous benefits to grasses including enhanced stress tolerance and herbivore resistance. However, sexual *Epichloë* species (12 species) produce filamentous ascospores in addition to conidia which are transmitted horizontally by symbiotic flies (Leuchtman et al., 2014; Saikkonen et al., 2016).

As the endophyte-infected seed germinates, the endophyte fungi grow intercellularly into the emerging leaf sheaths and concentrates in the basal parts of plant, but are sparse or not present in the roots (Christensen et al., 2008). In tall fescue, the hyphae of *E. coenophiala* fungus grow up in the stem and into developing ovules and seed head of the reproductive plant. Within the plants, the fungus develops in parallel to the long axes of the plant cells and stays between the cells, in the apoplast space which can be supplied with all of survival sugars and amino acids (Clay and Schardl, 2002). The life cycle of *Epichloë* endophytic fungi is schematically illustrated in Fig. 1. The endophyte infection is usually defined as a systemic

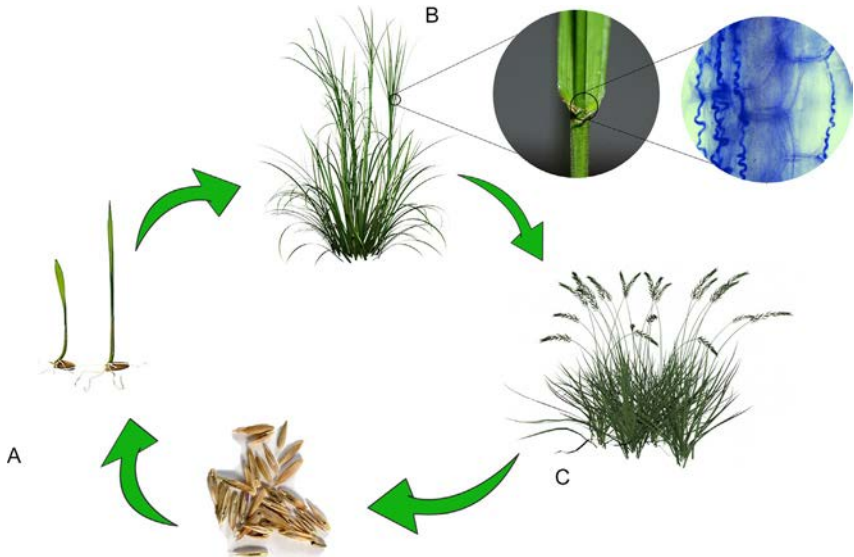


Fig. 1 Schematic illustration of the *Epichloë* endophytic fungus life cycle in host grass. (A) intercellular growth of endophyte into emerging leaf sheaths and host aboveground parts after seed germination, (B) concentration in the basal parts of plant and development of fungus hyphae in parallel to the long axes of the plant, and (C) growth of the *Epichloë* hyphae into developing ovules and seed head of the reproductive plant.

relation, which means that all of tillers or produced seeds by the host plant will be infected. Nonetheless, [Saikkonen et al. \(2010\)](#) have documented some cases in which only some tillers or a portion of the seeds from a given plant are colonized.

1.2 Root endophytic fungus: *Serendipita indica*

Class 4 endophytes (DSE) are limited to roots and characterized by features of having melanized, dark-colored, and septate hyphae ([Rodriguez et al., 2009](#)). Root-inhabiting fungi, containing mycorrhizal and nonmycorrhizal species, form a large part of rhizosphere fungi biomass and affect different aspects of plant life including plant growth and development, plant nutrition and plant tolerance against environmental stresses. Thus, root-endophytic fungi have potential to be used as biological agents for improving plant production systems. There is an increasing attention to the importance of root endophytes during the last decades. Like foliar endophytes, root-associated fungal endophytes are abundant, taxonomically diverse, often

phenotypically plastic, and their ecological functions appears to overlap with soil fungi, saprotrophic and pathogenic fungi, as well as mycorrhizal fungi (Compant et al., 2016).

Serendipita indica, the best-studied member of *Sebacinales* (*Basidiomycota*), was first isolated from the rhizosphere soils of *Prosopis juliflora* and *Ziziphus nummularia* as a contaminant during a routine isolation of arbuscular mycorrhiza fungi (AMF) in the desert *Thar* of Rajasthan, India (Varma et al., 1999). The *S. indica* has ability to penetrate and colonize roots of a wide range of monocotyledonous and dicotyledonous plants (e.g., arabidopsis, wheat, barley, maize, tobacco) under various environmental conditions (Unnikumar et al., 2013). Kost and Rexer (2013) provided a list of tested host plants of *S. indica* and Liu et al. (2019) suggested that root colonization strategies by *S. indica* and changes in the two phytohormone levels (i.e., jasmonate and gibberellin) are highly host-specific. Infestation by *S. indica* results in increased plant growth, enhanced resistance to biotic and abiotic stresses, enhanced phosphate (P) and nitrate uptake, and increased grain yield (Deshmukh and Kogel, 2007; Yadav et al., 2010). Some highlighted recent researches indicating the promoting effects of *S. indica* inoculation on host plant growth and productivity are shown in Table 1.

The *S. indica* exhibits most of the advantageous attributes of AMF by which was first considered as a fungus of the *Glomeromycota*. Similar to AMF, it has a broad host spectrum and exerts plant growth-promoting effects on its host plants (Kost and Rexer, 2013). However, the most important difference between *S. indica* and AMF is that the former is a facultative symbiont and can be easily cultivated on artificial complex media; whereas, *Glomeromycota* have an obligate biotrophic lifestyle and growing in association with host plants only (Kost and Rexer, 2013). Moreover, in contrast to AMF, *S. indica* infests only dead and dying root cells. Its fungal mycelium covers the surface of the roots, and hyphae penetrate into inter- and intracellular spaces of cortical and epidermal cells at the root cap region and finally produce chlamydospores in these cells (Fig. 2C–F); whereas, the central cylinder of the root and stems or leaves of the host plants are always free of fungal hyphae (Deshmukh et al., 2006).

The results of 20 years of intensive and descriptive investigations around the world revealed that *S. indica* is a model species for basic science and technology. In addition, it shows an applicable potential as an important and useful agent in biotechnology and sustainable agriculture. Producing a large number of thick-walled and pear-shaped spores called chlamydospores is one of the beneficial features of the fungus which can be used as bioinoculant

Table 1 *Serendipita indica* (formerly known as *Piriformospora indica*) mediated plant responses for better yield and quality of host plants.

Fungi species	Host plant	Beneficial effects of inoculation	Reference
<i>S. indica</i>	Cucumber (<i>Cucumis sativus</i> L.) Okra (<i>Abelmoschus esculentus</i> L.) Eggplant (<i>Solanum melongena</i> L.) Sweet pepper (<i>Capsicum annuum</i> L.)	<ul style="list-style-type: none">- Vigorous seed germination and growth under in vitro conditions- Enhanced root and shoot production and chlorophyll content of <i>S. indica</i>-inoculated <i>C. sativus</i> compared with auxin and cytokinin treatments	Jisha and Sabu (2019)
<i>S. indica</i>	Chinese arborvitae (<i>Platycladus orientalis</i>)	<ul style="list-style-type: none">- Increased net CO₂ assimilation- Increased biomass of roots, shoots, and whole plants- Greater total root length, total root surface area, and total root volume	Wu et al. (2018)
<i>S. indica</i>	Rapeseed (<i>Brassica napus</i> L.)	<ul style="list-style-type: none">- Increased main root length by 13.8%, root fresh and dry weights by 138.3% and 105.1%, respectively- Higher shoot fresh and dry weights of <i>S. indica</i> inoculated plants by 94.4% and 93.4%, respectively- Higher oil content by 11.1%	Su et al. (2017)
<i>S. indica</i> + AMF	Pineapple (<i>Ananas comosus</i>)	<ul style="list-style-type: none">- Increases in plant height of 70.8 and 65.0% in plantlets inoculated with <i>S. indica</i> and Mix (<i>S. indica</i> + AMF), respectively- Greater number of tillers of 24.7 and 60.2% in plantlets inoculated with <i>S. indica</i> and Mix, respectively- Better nutritional content than control- More photosynthetic efficiency of the plants inoculated by <i>S. indica</i> or/and AMF in comparison with control	Moreira et al. (2015)
<i>S. indica</i>	<i>Coleus forskohlii</i>	<ul style="list-style-type: none">- Overall increase in aerial biomass, chlorophyll contents and enhanced phosphorus acquisition due to more lateral roots- Increased source of metabolites for medicinal application	Das et al. (2012)
<i>S. indica</i> + <i>Paenibarthus lentimorbus</i>	Chickpea (<i>Cicer arietinum</i>)	<ul style="list-style-type: none">- Enhanced plant height of 34.4, 19.7 and 35.3% in host plants inoculated with <i>P. lentimorbus</i>, <i>S. indica</i> and their consortia, respectively compared with un-inoculated plants- Increased dry weight of 64.6, 44.3 and 53.2%, in host plants inoculated with <i>P. lentimorbus</i>, <i>S. indica</i> and their consortia, respectively compared with un-inoculated plants- Higher nutrient uptake of the plants inoculated by <i>S. indica</i> or/and <i>P. lentimorbus</i> in comparison with control	Nautiyal et al. (2010)

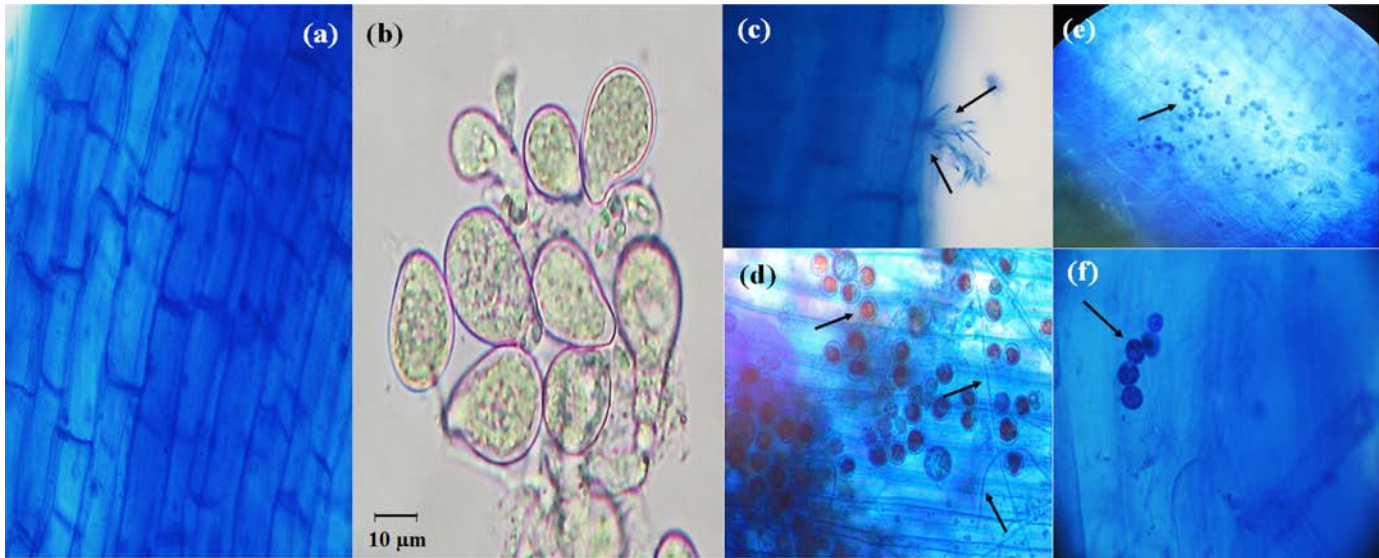


Fig. 2 Pictures of (A) non-inoculated maize plant root, (B) *Serendipita indica* thick walled and pear-shaped chlamydospores, (C) hyphae penetration into inter- and intra-cellular spaces of cortical and epidermal cells, (D) and (E) *S. indica* spores and hyphae, and (F) *S. indica* round bodies in the cortical cells of plant root.

for agricultural crops (Fig. 2B). Easy production, surviving in unfavorable conditions and resuming vegetative growth on several synthetic and complex media under favorable conditions make spores a good candidate and alternative to chemicals for biofertilizers and biopesticides (Casula and Cutting, 2002).



2. The effects of fungal endophytes on host plant growth and tolerance to environmental stresses

2.1 *Epichloë* spp.

2.1.1 Biotic stresses

Biotic stress in plants is caused by living organisms, specifically viruses, bacteria, fungi, nematodes, insects, arachnids, and weeds. Many scientists have focused on the investigation of fungal endophytes as biocontrol factors of pathogen and insects worldwide and have successfully applied endophytes to plant protection (de Silva et al., 2018). Therefore, endophyte-plant symbiotic associations play a key role in determination of microbial community composition in natural ecosystems and yield production in agricultural fields. Here, some of the advances in research on *Epichloë* fungal endophytes impacts on plant tolerance against diseases and pathogens, are summarized and then possible mechanisms for diseases resistance are discussed.

Hume et al. (2016) reviewed the role of *Epichloë* fungal endophyte in grassland ecosystems. They reported that *Epichloë* infection not only reduced survival and performance of more than 40 species of insect herbivores including sap, leaf, and root feeders, but also induced changes in the performance of invertebrates at higher trophic levels, including predators and parasitoids of insect herbivores. Recently, Kauppinen et al. (2018) tested *Epichloë* endophyte effects on leaf blotch pathogen (*Rhynchosporium* sp.) of tall fescue (*Schedonorus phoenix* = *Festuca arundinacea*). They observed that the *Epichloë* endophytes can reduce the pathogen *Rhynchosporium* damages in tall fescues, but resistance to the pathogen depends on grass origin and environmental conditions. Iannone et al. (2017) examined the impacts of seed-transmitted *Epichloë* spp. endophytes on the alleviation of negative effects of head smut of grasses (*Ustilago bullata*) on *Bromus auleticus*. Their results indicated that head smut disease occurrence was almost 0% in endophyte-infected plants while in the endophyte-free counterparts it reached 33%, as a result, the lower biomass production and seeds were observed in the endophyte-free treatments. Xia et al. (2016) studied the effects of an endophytic fungus (*Epichloë gansuensis*) on photosynthetic ability

and yield production of drunken horse grass (*Achnatherum inebrians*) infected by *Blumeria graminis* under four different soil water regimes. Their results showed that while powdery mildew (*B. graminis*) significantly decreased photosynthetic parameters and dry matter of *A. inebrians* in all soil water conditions except severe drought stress (i.e., relative saturation of 0.15). However, the presence of the *E. gansuensis* could lower the damage caused by the pathogen.

Interestingly, the results of Pérez et al. (2016) indicated that the presence of asexual endophyte (*Epichloë occultans*) not only protected the host grasses (*Lolium multiflorum*) against soil pathogens but also had protective side-effect on the neighboring plants (*Bromus catharticus*) in soil infected with *Rhizoctonia solani*. Guo et al. (2016) studied the effect of the *Epichloë* endophyte on soil nematodes and their community characteristics in the rhizosphere of *Achnatherum inebrians*. Their results showed that the presence of the *Epichloë* endophyte significantly affected plant parasite index (PPI), maturity index (MI) and PPI/MI ratio. The MI values of soil nematodes were significantly higher in the endophyte-infected treatments in comparison with the endophyte-free ones, whereas the PPI and PPI/MI were significantly lower in the rhizosphere of endophyte-infected plant than in that of the endophyte-free one. Therefore, they stated that the *Epichloë* endophyte could change the composition of functional groups of soil nematodes, particularly that of plant-parasitic nematodes. Clement and Elberson (2010) and Clement et al. (2005) revealed that symbiotic association of grass-*Neotyphodium* was effective to impede the development and survival of the cereal leaf beetles (*Oulema melanopus*) and other insects. Moreover, Gonthier et al. (2008) have proven that colonization of fowl manna grass (*Glyceria striata*) by the *Epichloë glyceria* endophyte led to fewer fall armyworm caterpillars on the plant, and this enhanced resistance was wound-inducible. Dual-culture experiments of Li et al. (2003) and inoculation of detached leaves of drunken horse grass (*A. inebrians*) indicated that *Neotyphodium gansuense* could constrain growth and disease damage development by some fungal pathogens including seedling rot (*Alternaria alternata*), rust (*Puccinia stipae-sibiricae*), powdery mildew (*Blumeria graminis*), smut (*Ustilago hypodytes*), leaf spot (*Bipolaris sorokiniana*) and ergot (*Sphacelia sp.*). Meister et al. (2006) indicated that colonization of perennial ryegrass (*Lolium perenne*) plants by *Neotyphodium lolii* exhibited reduced aphid population size, and in some cases, the aphids exhibited reduced adult life span and fecundity.

Regardless of the increasing number of researches, the principal mechanism(s) by which endophytes adapt plant defensive system is often

unclear. The recent findings resemble that the endophytes inhibit plant pathogens through several potential mechanisms including direct effects (interaction between endophytes and pathogens), indirect effects (induced plant defense) and ecological effects (occupation of ecological niche). Direct protection against insect herbivores may be as a result of insecticidal compounds like loline alkaloids (N-formyllooline, N-acetylnorloline), and the ergot alkaloid ergovaline or due to insect-detering alkaloidal compounds such as peramine (Popay et al., 2009). *Epichloë* endophytes can produce a range of alkaloids including ergot alkaloids, indole-diterpenes, lolines, and peramine, depending on the presence of complex genes, that may have biological activity against pests or pathogens (Kusari et al., 2012) whereas environmental factors may affect alkaloid levels (Schardl et al., 2013). Some ergot alkaloid and indole-diterpene compounds have deleterious effects on mammals. However, these specific fungal alkaloid compounds from all four classes may cause delayed development and reduced mass and fecundity, which may decrease insect fitness and therefore indirectly reduce insect population sizes and densities (Saari et al., 2014). Moreover, it is documented that fungal endophytes produce several antibiotic compounds having antifungal, antibacterial, nematocidal, and insecticidal properties to strongly inhibit the growth of pathogens in plant (Gunatilaka, 2006). Perhaps production of antifungal compounds and secretion of allelopathic substances could limit fungal infections by pathogenic fungi (Vázquez-de-Aldana et al., 2013).

Endophytes indirectly influence the pathogens by strengthening the host plants via production of the secondary metabolites. Mechanisms such as endophyte-mediated changes in host defense chemistry are likely to be implicated in complex endophyte-host-insect interactions (Li et al., 2014). Releasing a set of volatile organic compounds (VOCs) like terpenoids, fatty acid derivatives and phenylpropanoids is one of the important inducible plant responses to biotic and abiotic stresses (Bastias et al., 2017). Li et al. (2014) found that *E. coenophiala* infection of tall fescue (*Schedonorus phoenix* = *Festuca arundinacea*) tended to increase VOCs emissions under intense aphid (*Rhopalosiphum padi*) feeding. They concluded that *Epichloë* colonization may play crucial roles in mediating plant VOCs reactions to herbivorous insects, however, the magnitude and direction of such responses may vary with the type of the *Epichloë*-grass associations. Moreover, Fuchs and Krauss (2019) reported that the altered plant VOCs by the presence of *Epichloë* led to attracting aphid predators and contributed to an increased indirect plant defense. Some of plant hormones including

salicylic acid (SA), jasmonic acid (JA) and ethylene (ET) are responsible for controlling inducible defensive mechanism (Ballaré, 2014). Among these, JA is an important factor regulating responses to necrotrophic pathogens and chewing insect herbivores (Ballaré et al., 2012). Evidences show that *Epichloë* endophyte directly affects the JA pathway by increasing expression of the TFF41 plant gene (Bastias et al., 2017). The TFF41 protein has high similarity to ν -3 FAD enzymes of potato and parsley, which increase the abundance of trienoic fatty acids that are precursors of JA (Johnson et al., 2003). Meta-analysis of Bastias et al. (2017) support the idea that *Epichloë* fungal endophytes would enhance immune system of their host grasses against chewing insects and necrotrophic pathogens by activating or preparing the JA pathway.

In addition, competition for plant space and resources may also occur between inhabitant fungal endophytes and invader pathogens (Zabalgoitia, 2008). The presence of epiphyllous hyphae of *E. festucae* on leaf surfaces may restrict the growth of other fungi (Tadych et al., 2007). Iannone et al. (2017) stated that in triple symbiotic interactions, like when *Bromus auleticus* forage grasses are simultaneously colonized by the smut head disease (*Ustilago bullata*) and *Epichloë*, both systemic fungi compete for photosynthates, plant resources, shoot meristems and ovaries of developing flowers. If the endophytic fungal inhibits *U. bullata* from colonizing the seedlings or the ovaries, both host plant and endophyte benefit.

2.1.2 Abiotic stresses

The main abiotic stresses that plants confront are drought, mechanical resistance, salinity, nutrient deficiency, extreme temperatures, and heavy metals toxicity (Khare and Arora, 2015). Although plants have complex and dynamic resistance mechanisms against environmental stresses, however, abiotic stresses are the most detrimental factors affecting the growth and yield production in natural ecosystems and agricultural fields across the world (Hussain et al., 2019). Most studies of *Epichloë* effects on stress tolerance have focused on osmotic adjustment, water relations and drought recovery, accumulation of drought-protective osmolytes in the grass tissues, and photosynthetic rates under water or heat stress (Malinowski and Belesky, 2000). The most recent advances in research and possible mechanism(s) which endophyte-infected plants apply for coping the deleterious effects of abiotic stresses are highlighted in the following.

Drought is a multifaceted stress which alters the physiological, morphological, biochemical, and molecular traits in plants. Drought stress in plants is

characterized by reduced photosynthesis ability, decreased leaf water potential and turgor pressure, stomatal closure, lowered cell growth and elongation and elevated activities of ROSs (Hussain et al., 2019). The positive effects of endophytic fungi on the drought stress tolerance of plants are well established (Hume et al., 2016). Some of recent studies representing the effects of *Epichloë* on host grass performance under water stress (drought and flooding) conditions are listed in Table 2. Gathering data from all studies to date (i.e., 314 online references) on the influence of endophytic fungi on plant drought tolerance shows that the effect of fungal endophytes on plant function is related to plant water status (Dastogeer, 2018). Interestingly, the extent of endophyte infection effects is higher in host plants grown in water-deficit conditions than those in adequate watering environments. The output of such studies depends on the identity of the plant–endophyte symbiosis associations (Dastogeer, 2018). In contrast to drought stress, there is a little information about the effects of *Epichloë* infection on plant fitness under flooding conditions. However, flooding is one of the major environmental constraint determining the pastures and agricultural productivity, especially in lowlands, while climate change will increase the risk of flood occurrence in the future (Song et al., 2015). Recently, Saedi et al. (2021b) investigated the physiological responses of *Epichloë*-infected tall fescue to oxygen stress in a greenhouse pot experiment. Interestingly, they observed that endophyte infection led to slightly greater root and shoot development, higher leaf chlorophyll content, and lower levels of catalase and ascorbate peroxidase under poor aeration. Moreover, their results showed that non-infected tall fescue coped with poor aeration conditions by the formation of adventitious roots at the soil surface, aerenchyma formation within the root tissue and increased alcohol dehydrogenase activity. Finally, they concluded that *Epichloë* endophyte presence decreases the flooding-induced oxidative stress and prevents the formation and over-accumulation of reactive oxygen species in plant cells.

Enhanced drought tolerance of tall fescue and perennial ryegrass in the presence of *Epichloë* is the most widely recognized model of endophyte-induced drought stress tolerance in hosts (Dastogeer and Wylie, 2017). *Epichloë* infection may increase host resistance to drought stress through *avoidance* and *tolerance* mechanisms (Malinowski and Belesky, 2000). *Avoidance* characterizes the plant ability to increase water uptake and to reduce water loss through developing extensive root systems, leaf rolling, closure of stomata and reducing of canopy area. Whereas, *tolerance* represents the plant ability to preserve its growth and survival under stress conditions,

Table 2 Effects of *Epichloë* fungal endophyte on host plant performance under water stress (drought and waterlogged conditions).

Water stress	Endophyte species	Host grass	Experimental context	Consequences of endophyte infection	Reference
Drought	<i>Epichloë sinica</i>	<i>Roegneria kamoji</i>	Induced water stress by PEG-6000 solutions	<ul style="list-style-type: none">- Higher seed germination and seedling primary root length, shoot height, coleoptile length and number of fibrous roots- Greater total root length, root surface area, average root diameter, root volume, number of root tips, and number of root forks- Notable decline in the H₂O₂ content	Bu et al. (2019)
	<i>Epichloë gansuensis</i>	Drunken horse grass (<i>Achnatherum inebrians</i>)	Controlled-environment pot trial in the greenhouse	<ul style="list-style-type: none">- Increased plant height and chlorophyll content- Decreased plant leaf number, and the CO₂ concentration- Higher biomass, N and P content- Improved water use efficiency	Xia et al. (2018)
	<i>Epichloë</i> spp.	<i>Festuca sinensis</i>	Controlled greenhouse experiment	<ul style="list-style-type: none">- Higher total biomass, plant height, tiller number, blade width, stem diameter, root length, root: shoot ratio and relative water content	Wang et al. (2017)
	<i>Epichloë coenophiala</i>	Tall fescue (<i>Festuca arundinacea</i>)	Controlled greenhouse experiment	<ul style="list-style-type: none">- Increased ability to absorb water at higher soil absolute matric potentials (i.e., lower θ_{PWP} values) especially in soils with lower water holding capacity- Greater survival time, relative water content and leaf water potential at the same time after irrigation stop	Hosseini et al. (2016)

	<i>Neotyphodium coenophialum</i>	Two genotypes (75 and 83) of tall fescue (<i>Festuca arundinacea</i> Schreb.)	Induced water stress by PEG-6000 in a hydroponics system	<ul style="list-style-type: none"> - Higher chlorophyll content and membrane stability - Higher concentrations of K⁺ in the shoots and lower Ca²⁺ and Mg²⁺ in roots - Higher free proline contents - Better drought recovery 	Bayat et al. (2009)
	<i>Neotyphodium</i>	Grove bluegrass (<i>Poa alsodes</i>)	Pot experiment in a controlled greenhouse	<ul style="list-style-type: none"> - 17% more total biomass, and 24% more root biomass and slightly shorter leaves 	Kannadan and Rudgers (2008)
Water-logged conditions	<i>Epichloë</i> spp.	<i>Festuca sinensis</i>	Controlled greenhouse experiment	<ul style="list-style-type: none"> - Higher plant height, tiller number, total biomass, blade width, stem diameter, and root length 	Wang et al. (2017)
	<i>Epichloë</i> spp.	Marsh bluegrass (<i>Poa leptocoma</i>) and nodding bluegrass (<i>Poa reflexa</i>)	Pot experiment in a controlled greenhouse	<ul style="list-style-type: none"> - Increased the root: shoot ratio of <i>P. leptocoma</i> by 58% - No significant effects on aboveground biomass, belowground mass, number of tillers, and number of leaves 	Adams et al. (2017)
	<i>Epichloë</i> spp.	Wild barley (<i>Hordeum brevisubulatum</i>)	A greenhouse experiment	<ul style="list-style-type: none"> - Greater chlorophyll content, higher shoot and root biomass - Higher proline concentration and lower malondialdehyde content and electrolyte leakage 	Song et al. (2015)

mainly through osmotic adjustment and expanding cell wall elasticity to keep the tissue turgid (Malinowski and Belesky, 2000). In the following, we describe some possible mechanisms in which endophyte colonization affects improvement of drought tolerance in host plant exposed to water stress.

Decreased level of photosynthesis, as an important consequence of drought stress, occurs in plants due to reduced production of ATP and some enzymes such as rubisco and sucrose phosphate synthase (Ghannoum et al., 2003). The *Epichloë* infection leads to higher chlorophyll content and leaf area (Hosseini, 2015; Xia et al., 2018) which is concomitant with higher photosynthetic rate. Morse et al. (2002) stated that the presence of endophytic fungi increased the plant photosynthesis rate and stomatal conductance under water-deficit conditions; however, it had no significant effect on initial rubisco activity and carboxylation efficiency. It means that the presence of endophyte might reduce biochemical damage to the photosynthetic machinery of plants exposed to drought (Swarthout et al., 2009).

Foliar endophytes may alter metabolic reactions in the plant, and may be responsible for the changes in net photosynthesis and stomatal conductance by production of plant hormones, glycosidases and proteases (Monnet et al., 2005; Newman et al., 2003). Rozpádek et al. (2015) studied the impact of *E. typhina* on the photosynthesis apparatus of *Dactylis glomerata*. They stated that colonization of *D. glomerata* by endophytic fungi increased concentrations of light harvesting complex proteins (LHCI and LHCII) as well as chlorophyll *b*, and eventually improved the plant growth, PSII photochemistry and C assimilation efficiency. Xia et al. (2018) examined the effects of *E. gansuensis* endophyte colonization on the photosynthetic indexes, including photosynthetic rate, stomatal conductance and transpiration rate, and water use efficiency of *Achnatherum inebrians* plants under limited water conditions. Their results showed that although endophyte-infected *A. inebrians* plants absorbed the same quantity of water as endophyte-free ones, however, water use efficiency of endophyte-infected hosts were greater than endophyte-free counterparts under drought conditions. They concluded that the colonization of *A. inebrians* by *E. gansuensis* endophyte increased the water use efficiency due to enhanced photosynthetic indexes and improved C, N and P accumulation, and thus increased plant biomass.

Decreasing water loss, continuing soil water uptake and maintaining cell turgor pressure by accumulation of various ions, amino acids and sugars, known as osmotic adjustment are crucial processes for preserving plant function and survival under water-deficit conditions (Dastogeer and

Wylie, 2017). Nagabhyru et al. (2013) observed that the presence of *Epichloë* endophytic fungi in tall fescue plants led to significant upregulation of free glucose, fructose, trehalose, sugar alcohols, proline and glutamic acid under drought conditions. *Epichloë*-infected plants can preserve considerably greater water content than the non-inoculated counterparts under drought stress, indicating the ability of endophytes to delay dehydration and plant wilting under stressful conditions. Hosseini (2015) studied the effect of *Epichloë* endophytic fungi on tall fescue water status, physiological characteristics and root morphology under individual and combined drought and mechanical stresses. Based on the results, the plants with endophyte had greater ability to produce proline and enhanced osmotic adjustment under stressful conditions. These results were concomitant with higher values of relative water content (RWC) and leaf water potential (LWP) in the *Epichloë*-infected plants. These results are consistent with the findings of Bayat et al. (2009) who reported that the endophyte-infected plants had better water status than endophyte-free plants due to more efficient osmotic adjustment and higher proline production in roots.

Formation of additional reactive oxygen species (ROSs) including superoxide (O_2^-), hydrogen peroxide (H_2O_2), and hydroxyl radical ($\bullet OH$) are reported as the stress response agents causing oxidative damage and cell death in plants (Rho et al., 2018). However, lower ROS contents are often detected in endophyte-infected plants (Zhang et al., 2010). Multiple lines of evidence indicate that *Epichloë* endophytes produce enzymatic and non-enzymatic antioxidants, which results in degradation of reactive oxygen species leading to oxidative stress tolerance (Dastogeer and Wylie, 2017). For example, higher activity of superoxide dismutase (SOD) is reported in endophyte-infected perennial ryegrass plants subjected to drought (Briggs et al., 2013). Leuchtmann et al. (2014) observed higher ascorbate peroxidase (APX) activity in *Epichloë*-infected perennial ryegrass plants. Moreover, fungal endophytes may produce phenolic compounds, as the principal antioxidant agents in plants, which trigger plant immune system against oxidative damage (Torres et al., 2012; Van de Staaïj et al., 2002). Huang et al. (2007) studied the correlation between total antioxidant capacity and total phenolic content of 292 endophytic fungal isolates. They identified phenolic acids, flavonoids, tannins, hydroxyanthraquinones and phenolic terpenoids as potential phenolic antioxidants and suggested that the endophytes themselves may be producing phenolic antioxidants. Ponce et al. (2009) reported significant qualitative along with quantitative changes in the phenolic composition of endophyte-infected *Lolium*

multiflorum Lam. Also, Qawasmeh et al. (2012) observed that infection with *N. lolii* significantly increased *L. perenne* total phenol content by 3 and 17%, and antioxidant capacity by 7–8%.

Salinity, as the most persistent and progressive problem in arid and semi-arid regions, negatively impacts yield production and plant metabolism. Sodium toxicity induces oxidative damage by overproduction of ROSs which affects plant physiological and biochemical traits such as water use efficiency, photosynthesis, and nutrients uptake, and eventually resulting in cellular structure disruption and plant death (Munns and Tester, 2008). Only a few studies have shown that *Epichloë* endophytes can improve salt tolerance in host plant. Absorbing higher concentrations of K^+ and lower Na^+/K^+ ratios in the aboveground tissues may help *Epichloë*-infected plants to follow their normal metabolism and to compensate toxic effects of Na^+ under salinity stress (Sabzalian and Mirlohi, 2010). Wang et al. (2019) investigated the effects of *Epichloë gansuensis* endophyte on photosynthetic ability, the activity of N metabolism enzymes, N use efficiency, and yield production of drunken horse grass (*A. inebrians*) growing under different salt stress conditions. They showed that the nitrate content, nitrate reductase, nitrite reductase and glutamine synthetase activities, and the photosynthetic ability of *Epichloë*-infected plants, were greater than of *Epichloë*-free hosts under NaCl stress. They concluded that *Epichloë* infection improved the photosynthetic efficiency, increased the activity of N metabolism enzymes and N use efficiency which led to higher total biomass, especially under moderate and severe saline conditions.

Polyamines, small aliphatic N compounds, including diamine putrescine (Put), triamine spermidine (Spd) and tetramine spermine (Spm) can influence several plant physiological processes, including ion channels, antioxidant systems, photosynthesis and nutrient transport systems (Saha et al., 2015). Evidence indicates that accumulation of polyamine content resulting from various abiotic stresses is related to improvement of plant tolerance (Groppa and Benavides, 2008). Chen et al. (2018b) suggested that *Epichloë bromicola* infection improved wild barley (*Hordeum brevisubulatum*) salinity stress tolerance by enhancing conversion of Put to Spd and Spm, as well as improving transformation of free and soluble polyamines to insoluble bound forms of polyamines. Besides, Chen et al. (2018a) stated that the presence of the *Epichloë* endophyte reduced the adverse impacts of salt stress and alkali stress on wild barley (*H. brevisubulatum*) growth by improving photosynthetic ability, increasing total antioxidant capacity and glycine betaine content, increasing nutrient absorption, and osmotic and ionic

adjustment. Song et al. (2015) observed that *Epichloë* infection of *H. brevisubulatum* significantly increased N, P and K^+ concentrations, which resulted to an increase in total biomass. The *Epichloë* colonization also lowered Na^+ accumulation in the endophyte-infected plants compared to endophyte-free counterparts.

Mineral stress, characterized as poor availability of essential nutrients or toxicity of nutrient or non-nutrient minerals, becomes a serious concern in both high-input and low-input agricultural ecosystems. When resources such as soil nutrients are restricted, foliar endophytes may increase nutrient uptake (Shymanovich and Faeth, 2019). Effects of endophyte infection on plant uptake of nutrients other than N and P have received negligible consideration. Nevertheless; increased absorption rates for Ca, P, Mg, K, and some other microelements in endophyte-infected plants have been previously reported (Malinowski and Belesky, 2000).

Generally, plants take up nutrients throughout three main mechanisms including mass flow, diffusion and root interception. Mass flow as a passive process happens when dissolved nutrients reach the root surface by the movement of soil water. Plant transpiration, evaporation and percolation are the main drivers of water movement in soil. This process is mainly responsible for the transport of NO_3^- , SO_4^{2-} , Ca and Mg. Induced changes in leaf area, stomatal conductance, and aboveground biomass by *Epichloë* endophytic fungi could affect plant transpiration and eventually nutrients uptake (Soto-Barajas et al., 2016). Similarly, White et al. (1997) observed that high evaporation from the surface of stomata, a dense mass of fungal hyphae which are usually formed on developing parts of the host, led to the increased flow of nutrients needed by the fungus for reproduction, and those elements mostly transported by the mass flow (i.e., N, Ca, Mg, S, Mn and Mo) were found in higher concentrations in the xylem sap.

Diffusion as an active process is the movement of nutrients towards the root surface driven by concentration gradient. This process is the main mechanism responsible for the acquisition of P, K, Fe and Zn, and is susceptible to any chemical modification in the rhizospheric conditions. Releasing of root exudates including phenolic compounds and organic acids in the rhizosphere of endophyte-infected host plants has a crucial role in solubilization and absorption of some nutrients including K, P and Fe (Khayamim et al., 2010; Malinowski and Belesky, 2000; Soto-Barajas et al., 2016). For instance, roots of endophyte-infected tall fescue plants release phenolic compounds with Fe^{3+} reducing and P solubilizing activities (Malinowski et al., 1998; Malinowski and Belesky, 1999).

Root interception is a possible mechanism for plant nutrient acquisition which happens when essential elements come into physical contact with root surface. This mechanism is usually responsible for absorption of P, Ca, Mg, Zn and Mn (Jungk, 2002). Evidence indicates that *Epichloë* fungal endophyte changes root morphology and architecture, and mycorrhizal colonization (Hosseini, 2015; Omacini et al., 2012) which may affect nutrients uptake through root interception (Soto-Barajas et al., 2016). Increased nutrient content due to *Epichloë* presence was reported for Zn and Mo in perennial ryegrass (Malinowski et al., 2004), and for P, Ca or Zn in *Festuca rubra* (Vázquez-de-Aldana et al., 2013; Zabalgoeazcoa et al., 2006) and tall fescue (Malinowski et al., 1998; Malinowski and Belesky, 2000). Arrieta et al. (2015) investigated the effect of *E. pampeana* on the abundance and diversity of phosphate-solubilizing fungi (PSF), and arbuscular mycorrhizal colonization in *Bromus auleticus* rhizosphere. Their results indicated that endophyte presence had a positive association with mycorrhizal fungi and greater PSF diversity would enhance the phosphorus (P) availability to plants.

Recently, another possible mechanism has been reported for increasing nutrient use efficiency by endophytic fungi. Glucose-6-phosphate dehydrogenase (G6PDH) is recognized as a rate-limiting and key enzyme of the plant pentose phosphate pathway, and is involved in N assimilation (Wang et al., 2019). It is proven that endophyte infection increases activity of G6PDH in host plant leaves and roots than in those of endophyte-free plants. In fact, the presence of *E. gansuensis* played a key role in maintaining the growth of *Achnatherum inebrians* under N deficiency condition by regulating G6PDH activity and the NADPH/NADP⁺ ratio and improving net photosynthesis rate (Wang et al., 2019). Although *Epichloë* infection decreased total N concentration in *Achnatherum sibiricum* shoots, allocation of N fractions to the photosynthetic machinery was significantly higher in the endophyte-infected hosts (Ren et al., 2011). Consequently, *Epichloë*-infected grasses have higher photosynthetic N use efficiency and shoot biomass than those of endophyte-free counterparts when fertilizer is restricted (Ren et al., 2014).

Excessive amounts of nutrient and non-nutrient minerals are toxic for plants, and disrupt photosynthetic functions which finally lead to severely impaired plant growth and performance. For instance, disturbances in chlorophyll biosynthesis and thylakoid electron transport are induced in the presence of Pb, Zn, and Cd (Węźowicz et al., 2017). Endophytic fungi may improve host productivity and competitive abilities under mineral toxicity

stress (Deng and Cao, 2017) by reducing metal availability, altering soil pH, releasing chelating agents along with multiple enzymatic properties (Ikram et al., 2018; Wenzel, 2009). Zhang et al. (2010) examined the effect of symbiotic association of *Achnatherum inebrians* with *Neotyphodium gansuense* on plant growth and antioxidant capacities under high Cd concentrations. They observed that endophyte-infected hosts had better water status, improved growth indices and higher enzymatic antioxidant activities than endophyte-free counterparts, especially under moderate and high Cd concentrations. They concluded that endophyte-infected *A. inebrians* may have better fitness and competitive ability under metal stress conditions because of enhanced antioxidant capabilities. Mirzahosseini et al. (2015) demonstrated that the presence of *Epichloë* confers Ni stress tolerance in tall fescue by avoidance mechanisms including reduction of Ni accumulation and translocation to the plant shoots. Similarly, beneficial impacts of *Epichloë* infection have been reported for tall fescue and ryegrass under Zn stress (Zamani et al., 2015), *Festuca rubra* under arsenic stress (Vázquez-de-Aldana et al., 2013) and, *Festuca arundinacea* and *Festuca pratensis* under Cd stress (Soleimani et al., 2010b).

Extreme temperatures, heat and cold stresses, are becoming the major concerns for plant scientists worldwide due to the climate change. Both high and low temperature stresses cause several changes at the molecular, physiological and cellular levels resulting in irreversible damages to plant growth and development. These include the loss of cell membrane fluidity, photosynthesis impairment, overproduction of ROS, and reduction of water absorption (Nievola et al., 2017). Recent findings indicated that *Epichloë* endophyte positively affects the tolerance of cool-season grasses to cold and heat stresses (Chen et al., 2016; Xu et al., 2017). For instance, Dupont et al. (2015) suggested that perennial ryegrass plants infected with novel *E. festucae* var. *lolii* had increased expression of cold response genes, meaning a better ability to endure cold stress. Moreover, Xu et al. (2017) showed that *Epichloë*-infected tall fescue had significant lower electrolyte leakage and ROS concentration; indicating that endophyte infection confers heat stress tolerance to host plants. Nevertheless, the exact mechanisms of heat and cold stresses tolerance induced by *Epichloë* infection are poorly understood.

Accumulation of various fungal bioactive alkaloids including peramine, ergot alkaloids, indole-diterpenes (especially lolitrems) and lolines, is one of the possible mechanisms for the enhanced tolerance of *Epichloë*-infected hosts in response to temperature stress (Chen et al., 2016). For example,

Zhou et al. (2015) evaluated the effects of cold shock on ergot alkaloid accumulation in three *Festuca sinensis* ecotypes. Their results indicated that ergot alkaloids, ergine and ergonovine were accumulated in endophyte-infected plants, whereas, these substances were not detected in the endophyte-free plants under cold stress treatment. The results showed that endophyte infection altered production of at least two secondary metabolites, the bio-protective alkaloids ergine and ergonovine, in response to short-term cold stress (Zhou et al., 2015). Besides, Xu et al. (2017) proposed that the main mechanism of better drought and heat tolerance of *E. typhina* endophyte infected tall fescue plants is likely related to less ROS production and promotion of particular antioxidant enzyme activity in the host plant.

Soil contamination, referred to over-accumulation of organic and inorganic chemicals or other changes in the natural soil environment, typically causes toxic effects on plant growth and beneficial soil organisms and acts as a source of groundwater pollution (Hernandez-Soriano, 2014). Heavy metals, polycyclic aromatic hydrocarbons associated with petroleum hydrocarbons, and herbicides/insecticides are most common soil contaminants (Bashiri et al., 2015). Due to the great damage caused by soil contamination, there is an increasing interest to utilize the potential of plant-endophytes interactions for the remediation of a variety of contaminated soils worldwide. Symbiotic relations of plants and endophytic fungi can improve plant growth and enhance the biodegradation of organic contaminants in the rhizospheric soil by possessing proper degradation pathways and metabolic capabilities (Weyens et al., 2009). Some fungal endophytes and endophyte-infected plants can produce chelating agents, siderophores, biosurfactants, low molecular weight organic acids, and various detoxifying enzymes, which are favorable for eliminating organic contaminants from soils (Soleimani et al., 2010a).

As far as known, there is little evidence about the effects of *Epichloë*-infected hosts on polluted soils. Soleimani et al. (2010a) evaluated the effects of two grass species (*Festuca arundinacea* and *Festuca pratensis*) infected by endophytic on degradation of petroleum hydrocarbons in an aged petroleum contaminated soil. Their results suggested that *Epichloë* infection increased host root and shoot biomass and generated higher levels of water-soluble phenols and dehydrogenase activity in the soil. As a result, more amount of total petroleum hydrocarbons (TPHs) were degraded, indicating that endophyte-infected grass have more potential for removal of TPH from oil-contaminated soils. In fact, higher root biomass of

endophyte-infected plants coincides with enhanced release of root exudates and water-soluble phenols, which trigger microbial degradation of TPHs (Soleimani et al., 2010a).

2.1.3 Combined stresses

Plants are often confronted with combination of several abiotic and biotic stresses and the plant response to combined stresses differs from that caused by individual stresses. For instance, the combination of drought and heat stress induces greater detrimental effects on growth and productivity of crops than when each stress was applied individually (Hussain et al., 2019). As mentioned in previous sections, several studies have revealed how fungal endophytes impact plant response to individual stress. Nonetheless, the outcome of endophyte–grass interactions under combined biotic and abiotic stresses remains poorly explored. Bultman and Bell (2003) mentioned that the protective effect of endophytic fungi infection on the host may be the most when environmental stresses, like drought and herbivore damage, are present. Advantages of host–endophyte symbiosis become most apparent in complex conditions where plants are exposed to multiple stresses (Miranda et al., 2011). In this regard, Hosseini (2015) investigated the interactive effects of mechanical and drought stresses on water status and leaf proline content of tall fescue in a greenhouse study. A sand growth medium was used and the dead-load technique was utilized to apply mechanical stress to plant roots. The results showed that in the presence of mechanical stress, drought has little impact on the plant responses and mechanical stress is the main controlling factor of water status and leaf proline content. It was shown that *Epichloë* infection improved plant water status by producing more proline especially under combined severe drought and mechanical stresses (Hosseini, 2015).

Some host tolerance mechanisms induced by endophyte infection such as production of fungal secondary metabolites and alkaloids, developing extensive root systems and increasing of antioxidative capacities in response to single stresses are discussed in previous sections (see Sections 2.1.1 and 2.1.2). It can be suggested that the fungal loline alkaloids may play a dual role in grass defense system against insect pests and drought stress. Additionally, *Epichloë* infection causes an increase in root length and a decrease in root diameter (Hosseini, 2015; Malinowski and Belesky, 2000), which are certainly expected to play a key role in drought tolerance and/or nutrient acquisition. Carson et al. (2004) stated that endophyte

infection was associated with production of dehydrins, a group of intrinsically unstructured proteins abundant during late embryogenesis, which led to protection from drought and temperature stresses in several grasses, including tall fescue.

2.2 *Serendipita indica*

2.2.1 Biotic stresses

Plants colonized with *S. indica* show an improved resistance against many soil-borne and root pathogens and also exhibit induced systemic resistance (ISR) to different foliar pathogens (see Table 3). Here we describe some involved mechanisms of host tolerance to pathogens/diseases after root colonization by *S. indica*.

Plant hormones such as indole acetic acid (IAA), gibberellin (GA), cytokinin (CK), abscisic acid (ABA), ethylene (ET), salicylic acid (SA) and jasmonic acid (JA) show a significant influence on increasing plant growth as well as improving plant defense system against biotic/abiotic stresses (Xu et al., 2018). Several evidences suggest that these phytohormones play a vital role in the generation of ISR, where the microbes initiate processes in roots which induce systemic tolerance in the aerial parts of plants against microbial pathogens or insects (Verhagen et al., 2004). For instance, SA signaling pathways restrict the growth of biotrophic pathogens by killing the infested cells via programmed cell death (Panda et al., 2019). Moreover, alternative defense mechanism against necrotrophic pathogens is associated with JA signaling pathways (Glazebrook, 2005). *S. indica* interferes with phytohormones synthesis and signaling to enhance growth, flowering time, differentiation and local and systemic defense responses (Xu et al., 2018). The results of some studies have proven that *S. indica* inoculation is effective on conferring ISR against powdery mildew fungi in some crop plants by regulating JA, JA-responsive genes, ET and ET-responsive genes (Khatabi et al., 2012; Serfling et al., 2007; Stein et al., 2008; Waller et al., 2005). Cosme et al. (2016) investigated the effects of *S. indica* on rice water weevil (RWW) root herbivore (*Lissorhoptus oryzophilus*) by monitoring of the changes in GA and JA signaling. Their results suggested that *S. indica* is able to protect plants against RWW adults and larvae through endophyte-elicited GA biosynthesis which repressed the herbivore-induced JA in roots and recovered plant growth.

The presence of *S. indica* helps activating both enzymatic and non-enzymatic antioxidants and suppressing induced oxidative damage by pathogen/herbivore attacks (Ansari et al., 2013). Kumar et al. (2013) stated

Table 3 A list of plant diseases and pathogens controlled by *S. indica* in different host plants according to recent researches.

Disease/symptoms	Pathogen	Host plant	Reference
Stem rot	<i>Phytophthora cinnamomi</i> and <i>P. plurivora</i>	Rhododendron (<i>Rhododendron ferrugineum</i> L.)	Trzewik et al. (2020)
Panama disease	<i>Fusarium oxysporum</i>	Banana (<i>Musa</i> spp.)	Cheng et al. (2019)
Bacterial wilt	<i>Ralstonia solanacearum</i>	Anthurium (<i>Anthurium andraeanum</i>)	Lin et al. (2019)
Early blight	<i>Alternaria solani</i>	Tomato (<i>Solanum lycopersicum</i> L.)	Panda et al. (2019)
Root-knot nematode	<i>Meloidogyne incognita</i>	Tomato (<i>Solanum lycopersicum</i> L.)	Varkey et al. (2018)
Botrytis gray mold disease	<i>Botrytis cinerea</i>	Chickpea (<i>Cicer arietinum</i> Linn.)	Narayan et al. (2017)
Sheath blight disease	<i>Rhizoctonia solani</i>	Rice (<i>Oryza sativa</i> L.)	Nassimi and Taheri (2017)
Soybean cyst nematode	<i>Heterodera glycines</i>	Soybean (<i>Glycine max</i>)	Bajaj et al. (2015)
Bakanae disease	<i>Fusarium fujikuroi</i> Nirenberg	Rice (<i>Oryza sativa</i> L.)	Hajipour et al. (2015)
Crown rot	<i>Fusarium culmorum</i> or <i>F. graminearum</i>	Winter wheat (<i>Triticum aestivum</i>)	Rabiey et al. (2015)
Root rot	<i>Fusarium culmorum</i>	Barley (<i>Hordeum vulgare</i>)	Harrach et al. (2013)
Verticillium wilt or viral pathogen	<i>Verticillium dahlia</i> or pepino mosaic virus-Sav E397	Tomato (<i>Solanum lycopersicum</i>)	Fakhro et al. (2010)
Root rot of barely	<i>Fusarium graminearum</i>	Barley (<i>Hordeum vulgare</i> L.)	Deshmukh and Kogel (2007)

that *S. indica* has a key role in triggering secondary metabolite biosynthesis and eliciting lignans production in hairy root cultures of flax (*Linum album*) which activates antioxidant machinery of the plants. Dehghanpour-Farashah et al. (2019) proved that *S. indica* restricted the wheat crown rot disease caused by *Fusarium pseudograminearum* due to enhanced enzymatic activities of guaiacol peroxidase (GPX) and catalase (CAT). They concluded that sodium nitroprusside (as a donor of nitric oxide) and spermidine (as a polyamine compound) significantly improved the impact of *S. indica* on host ISR by increasing H₂O₂ production, antioxidant enzymatic activities and callose deposition.

Gene expression regulation in response to *S. indica*, evidently reveals that this root endophytic fungus targets different genes and subsequently induces different physiological reactions in host plant under biotic/abiotic stress conditions (Gill et al., 2016). Up-regulation of pathogenesis related genes, JA (VSP, PDF1.2, LOX2) and ET (ERF1) signaling genes were reported in *S. indica*-inoculated host plants, in response to pathogen infection (Camehl and Oelmüller, 2010; Molitor et al., 2011). Hajipour et al. (2015) proved that *S. indica* can diminish the damage of bakanae disease (*Fusarium proliferatum*) in rice by up-regulating of some pathogenesis-related genes such as NPR1, PR1, PR4 and PR5, as well as two transcriptional factor genes namely WRKY62 and WRKY85. Similarly, Lin et al. (2019) reported that *S. indica* inoculation stimulates up-regulation of both the PR1 and PR5 (SA-responsive related genes) significantly in anthurium leaves infected by *Ralstonia solanacearum*, by about 0.5-fold levels. This suggests that the endophytic fungus has critical role in activation of JA-dependent defense processes and ISR mechanism in plant upon bacterial infestation.

2.2.2 Abiotic stresses

Drought: *S. indica* has been beneficially implicated in conferring plant protection against drought and salinity stressors (see Table 4) that threaten plant survival and functioning, worldwide. In the case of drought stress tolerance, *S. indica* modifies ROS detoxifying enzyme system, lipid peroxidation, osmolyte contents and expression of drought-related genes (Gill et al., 2016). Investigations at the cellular level indicate that *S. indica* colonization leads to up-regulating of 14–3–3 proteins responsible for both the stress tolerance and nutrient metabolism in host plants (Ghaffari et al., 2019). In plants exposed to drought stress, these proteins regulate plant transpiration through controlling of stomatal closure (Sun et al., 2013). In another study, Zhang et al. (2018) reported that the number of *S. indica*-responsive genes

Table 4 Summary of *S. indica*-mediated responses of various host plants to drought and salinity stresses according to representative recent studies.

Stress type	Host plant	Experimental context	<i>S. indica</i> beneficial roles	Reference
Drought	Barley (<i>Hordeum vulgare</i> L.)	Pot experiment	<ul style="list-style-type: none"> - Greater shoot dry biomass by 1.1-fold and 1.3-fold in moderate and severe drought stresses, respectively - Enhanced activities of both the photosystem and the electron transfer chain - Enhanced production of sugars and organic compounds 	Ghaffari et al. (2019)
	Maize (<i>Zea mays</i> L.)	Controlled experiment in laboratory	<ul style="list-style-type: none"> - Decreased root diameter by 39% and 12% under moderate and severe water stresses - Increased maximum root growth force and maximum root growth pressure by 1.1-fold and 1.7-fold, respectively 	Hosseini et al. (2019)
	Rice (<i>Oryza sativa</i> L.)	Pot experiment	<ul style="list-style-type: none"> - Increased seedling biomass and enhanced phosphorus and zinc acquisitions - Higher chlorophyll fluorescence, proline content and improved antioxidant capacity 	Saddique et al. (2018)
	Maize (<i>Zea mays</i> L.)	Pot experiment	<ul style="list-style-type: none"> - Increased root fresh weight by 15% and 30% under mild and severe drought stresses, respectively - Increased enzymatic activity of ascorbate peroxidase by 2.7-fold 	Hosseini et al. (2018)
	Wheat (<i>Triticum aestivum</i> L.)	Pot experiment	<ul style="list-style-type: none"> - Increased root volume by about 36% and 72% under moderate and severe drought stresses, respectively - Increased chlorophyll content and decreased catalase activity under severe drought stress 	Hosseini et al. (2017a)
	Maize (<i>Zea mays</i> L.)	Pot experiment	<ul style="list-style-type: none"> - Increased root fresh and dry weights, leaf area, SPAD value, and leaf number under PEG-induced water stress - Enhanced antioxidative activities of catalases and superoxide dismutases - Up-regulation of drought-related genes DREB2A, CBL1, ANAC072, and RD29A 	Xu et al. (2016)

Continued

Table 4 Summary of *S. indica*-mediated responses of various host plants to drought and salinity stresses according to representative recent studies.—
cont'd

Stress type	Host plant	Experimental context	<i>S. indica</i> beneficial roles	Reference
	Chinese cabbage (<i>Brassica campestris</i> L.)	Pot experiment	<ul style="list-style-type: none">- Increased root fresh weight by 38% and leaf fresh weight by 46%- Promoted development of the main and lateral plant roots- Decreased accumulation of malondialdehyde, as a biomarker of oxidative stress in cells- Enhanced antioxidative capacity	Sun et al. (2010)
Salinity	Melon (<i>Cucumis melo</i> L.)	Pot experiment	<ul style="list-style-type: none">- Increased plant fresh weight, chlorophyll content and reduced the electrolyte leakage under severe salt stress- Higher relative water content under moderate and severe salt stress- Increased proline content by 25.2% under 200 mM NaCl treatment	Hassani et al. (2019)
	Tomato (<i>Solanum lycopersicum</i> L.)	Pot experiment	<ul style="list-style-type: none">- Improved root branching, fresh and dry weight of salt-stressed plants- Increased levels of chlorophyll b, indole acetic acid, catalase and superoxide dismutase in leaves- Reduced abscisic acid and proline levels	Abdelaziz et al. (2019)
	Maize (<i>Zea mays</i> L.)	Pot experiment	<ul style="list-style-type: none">- Higher biomass, higher stomatal conductance, lower K⁺ efflux from roots and higher K⁺ concentration in shoots	Yun et al. (2018)
	<i>Medicago truncatula</i>	Pot experiment	<ul style="list-style-type: none">- Improved plant growth under severe saline condition- Higher antioxidant enzymes activities and hyphae density in roots under high salt concentration- Reduced malondialdehyde activity, Na⁺ content and relative electrolyte conductivity	Li et al. (2017)
	Barley (<i>Hordeum vulgare</i> L.)	Pot experiment	<ul style="list-style-type: none">- Increased total shoot dry weight by 1.5-fold in 300 mM NaCl treatment- Changes in carbohydrate metabolism, nitrogen metabolism, and ethylene biosynthesis pathway	Ghaffari et al. (2016)

increased from 464 (under no stress condition) to 1337 and 2037 after 6 and 12 h exposures to drought stress induced by polyethylene glycol 6000 (PEG-6000), respectively. Their results suggested that endophytic fungus stimulated genes for hormone functions, including those responsible for the production of IAA, ABA, SA and CK. As a result, *S. indica* promotes plant functioning under drought stress. In addition, Sun et al. (2010) stated that the reprogramming of drought-related genes such as DREB2A, ANAC072, and CBL1 in addition to RD29A in the leaves of *S. indica*-colonized plants, is responsible for plant survival under drought stress condition.

Higher antioxidant capacity and accumulation of secondary metabolites in *S. indica*-inoculated plants protect them against the detrimental effects of drought stress. Xu et al. (2016) pointed out that maize plants exposed to PEG-6000-induced drought stress had greater SOD and CAT activities and higher proline accumulation. They concluded that elevated ROS scavenging system was a reason for the observed better survival of maize after inoculation with *S. indica*. In contrast, Hosseini et al. (2017a, 2018) observed that *S. indica* inoculation markedly lowered the APX (i.e., 2.7-fold) and CAT (i.e., 2.1-fold) in maize and wheat plants under severe drought stress, respectively. They concluded that *S. indica*-inoculated plants had higher proline concentration rather than non-inoculated counterparts. As a result, the inoculated plants had more ability to perform osmotic adjustment and eventually, to overcome harmful effects of drought stress and tolerate lower oxidative damage than non-inoculated ones. Therefore, the activities of antioxidant enzymes decreased in *S. indica* host plants.

Salinity: The promoting effects of *S. indica* endophytic fungus on plant resistance to salt stress, are well documented (Table 4). In the majority of cases, reprogramming of salt stress-related genes, elevated enzymatic and non-enzymatic antioxidant capacities, reduced membrane electrolyte leakage and promoted osmotic adjustment are the three main mechanisms for salt tolerance (Baltruschat et al., 2008; Khalvandi et al., 2019; Lanza et al., 2019). Abdelaziz et al. (2019) reported that *S. indica* reduced Na^+/K^+ ratios by increasing K^+ concentration in the tomato leaves and roots of colonized plants under salt stress. They also observed that colonization of roots by *S. indica* increased antioxidant enzymatic activity and expression of LeNHX1–4 genes of tomato leaves. As a result, *S. indica*-inoculated plants had better functioning and growth (Table 4). Kord et al. (2019) investigated the impact of *S. indica* inoculation on regulation of small RNA (sRNA) molecules including microRNAs (miRNAs) which play important roles in eukaryotic gene expression and plant adaption to environmental stresses

as documented by [Brant and Budak \(2018\)](#). According to results of sRNA-seq analysis, they identified 193 target genes in inoculated rice plants, which most of them were responsible for encoding either genes or transcription factors involved in nutrient uptake, sodium ion transporters, growth regulators, and auxin-responsive proteins.

Mineral stress: Acquisition of P, as the second most important macronutrients for plant growth and development, is one of the major features of symbiotic host plant-*S. indica* interactions ([Jisha et al., 2019](#); [Ngwene et al., 2016](#); [Wu et al., 2018](#)). However, the positive effects of *S. indica* on mobilization, extraction and acquisition of other essential elements such as N, Mg, S, Zn and Fe are proven ([Johnson et al., 2014](#)).

Phosphorous is absorbed by plants either directly through diffusion and interception mechanisms or indirectly through endophytic/mycorrhizal associations. *S. indica* fungus is able to produce phosphatase enzymes and organic acids which contribute to solubilization and mobilization of phosphate from insoluble polyphosphates and organic phosphates ([Johnson et al., 2014](#)). [Jisha et al. \(2019\)](#) examined the effect of *S. indica* inoculation on *Centella asiatica* (L.) under phosphate limitation, and reported that *S. indica*-colonized plants had better growth parameters and higher production of asiaticoside (a major nutraceutical secondary metabolite) at low P concentrations. They concluded that *S. indica* infestation increased plant tolerance against phosphate limitation due to higher acid/alkaline phosphatase activity, enhanced total phenolic content, increased SOD activity and higher level of IAA. [Wu et al. \(2018\)](#) stated that *S. indica*-inoculated *Brassicae napus* plants had greater capability to take up P from different sources because of higher phosphatase activities and higher organic acids (i.e., oxalic, malic and citric acids) in rhizosphere soil. They observed higher expression of the BnPht1; 4 and BnACP5 genes in inoculated roots under P limitation conditions which demonstrates the involvement of the fungus in mitigating P deficiency by promoting its uptake.

Magnesium is another essential macronutrient required for the chlorophyll formation and photosynthesis. *S. indica* plays crucial role in the Mg acquisition from soil and supports the plant growth under Mg deficiency conditions ([Johnson et al., 2014](#); [Prasad et al., 2019](#)). Phylogenetic analysis revealed that PiMgT1, a member of Mg transporters family, is actively involved in Mg uptake by the *S. indica* fungus and may be helping in the nutritional status of the host plant particularly under Mg-limited conditions ([Prasad et al., 2019](#)). In the case of sulfur (S), [Nongbri and Oelmüller \(2013\)](#) comprehensively reviewed the role of *S. indica* in S metabolism and

assimilation. Summarily, they stated that *S. indica* fungus targeted genes involved in S uptake and metabolism and signals from the fungus activate processes in the roots which strongly promoted the S acquisition especially under S deficiency conditions.

In contrary to essential micronutrients and macronutrients, excess levels of some heavy metals such as cadmium (Cd), lead (Pb), copper (Cu) and arsenic (As) are poisonous for plants and cause oxidative stress which consequently leads to lipid peroxidation, and DNA and protein damage. Several studies have confirmed that *S. indica*-plant symbiotic relations are an excellent system for mitigating adverse consequences of heavy metals stress (Hui et al., 2015; Johnson et al., 2014; Sartipnia et al., 2013). Nanda and Agrawal (2018) observed higher Cu accumulation in roots, elevated enzymatic antioxidant activities (SOD, CAT, APX, and GPX) and reduced lipid peroxidation and hydrogen peroxide with *S. indica* under Cu stress conditions. Similarly, Dabral et al. (2019) suggested that *S. indica* inoculation decreased cell death and ROS accumulation in rice plant roots as compare with non-inoculated roots under Cd stress. Their results revealed that significantly greater accumulation of Cd in fungal spores could diminish ROS accumulation in root cells leading to lower cell death. Mohd et al. (2017) suggested that *S. indica* inoculation increased rice tolerance against arsenic toxicity due to three different mechanisms including reducing the availability of free arsenic in the plant environment, bio-transformation of the toxic arsenic salts into insoluble particulate matter and modulating the antioxidative system of the host cell.

Extreme temperatures: Although *S. indica* was originally isolated from the rhizosphere of xerophytes growing in a hot desert area, but it has ability to endure both the extreme cold and hot conditions (Varma et al., 2014). There is little information about the effect of *S. indica* inoculation on plant tolerance against both heat and cold stresses. The cold tolerance was demonstrated by an experiment in the cold deserts of Leh-Ladakh (Varma et al., 2014). Interestingly, RNA-Seq analysis of soybean root tissue showed that *S. indica* inoculation led to down-regulation of heat shock and other proteins involved in heat, high light, and hydrogen peroxide stress tolerance (Bajaj et al., 2018; Lahrmann et al., 2013). It can be concluded that *S. indica* may reduce the deleterious effects of abiotic stressors using other mechanisms and thus do not need to up-regulate heat shock proteins (Bajaj et al., 2018). However, the exact mechanisms are not understood and should be investigated in future studies.

2.2.3 Combined stresses

As mentioned in the previous section, plants respond differently when they are exposed to combination of stressors rather than to individual ones. Hosseini et al. (2018) examined maize morphological and physiological responses as affected by *S. indica* inoculation under individual and combined drought and mechanical resistance stresses. Under exposure to individual stress, drought had more destructive impacts on plant water status and growth parameters rather than individual mechanical stress. However, under combined drought and mechanical stresses conditions, mechanical stress played the dominant role in controlling plant responses. The *S. indica* inoculation protected plants against both individual and combined stresses so that the inoculated plants had greater root volume (RV), leaf area (LA), RWC, LWP and proline content compared to the non-inoculated plants under stressful conditions. The same results were observed for *S. indica*-inoculated wheat plants under individual and combined drought and mechanical stresses Hosseini et al., (2017a). Fig. 3 schematically shows the beneficial effects of *S. indica* inoculation on host plant resistance against biotic and abiotic stresses.



3. The effects of endophytic fungi on soil quality indicators

The complex relations between plants and endophytic symbionts can significantly affect soil ecosystem characteristics and functions. It is proven that the symbiotic interaction of foliar and root endophytic fungi with host plants influences belowground biogeochemical reactions controlling nutrient cycling and soil organic matter dynamics. These processes play key roles in the productivity and function of both natural ecosystems and agroecosystems (Compant et al., 2016). Moreover, the endophytic symbiosis such as *Epiclloë*-grass relations has long-term and constitutive nature which makes it suitable for ecosystem studies of plant-microbe interactions and their consequences on ecological processes (Slaughter, 2016). Omacini et al. (2012) conducted a meta-analysis to study the available information on the effects of endophytes on soil. Their comprehensive and quantitative study indicated that there were significant variations in root biomass, root exudates, and AMF colonization of infected plants compared to the endophyte-free counterparts, suggesting that these foliar endophytes can alter the host plant rhizosphere by multiple pathways. Here we aim to

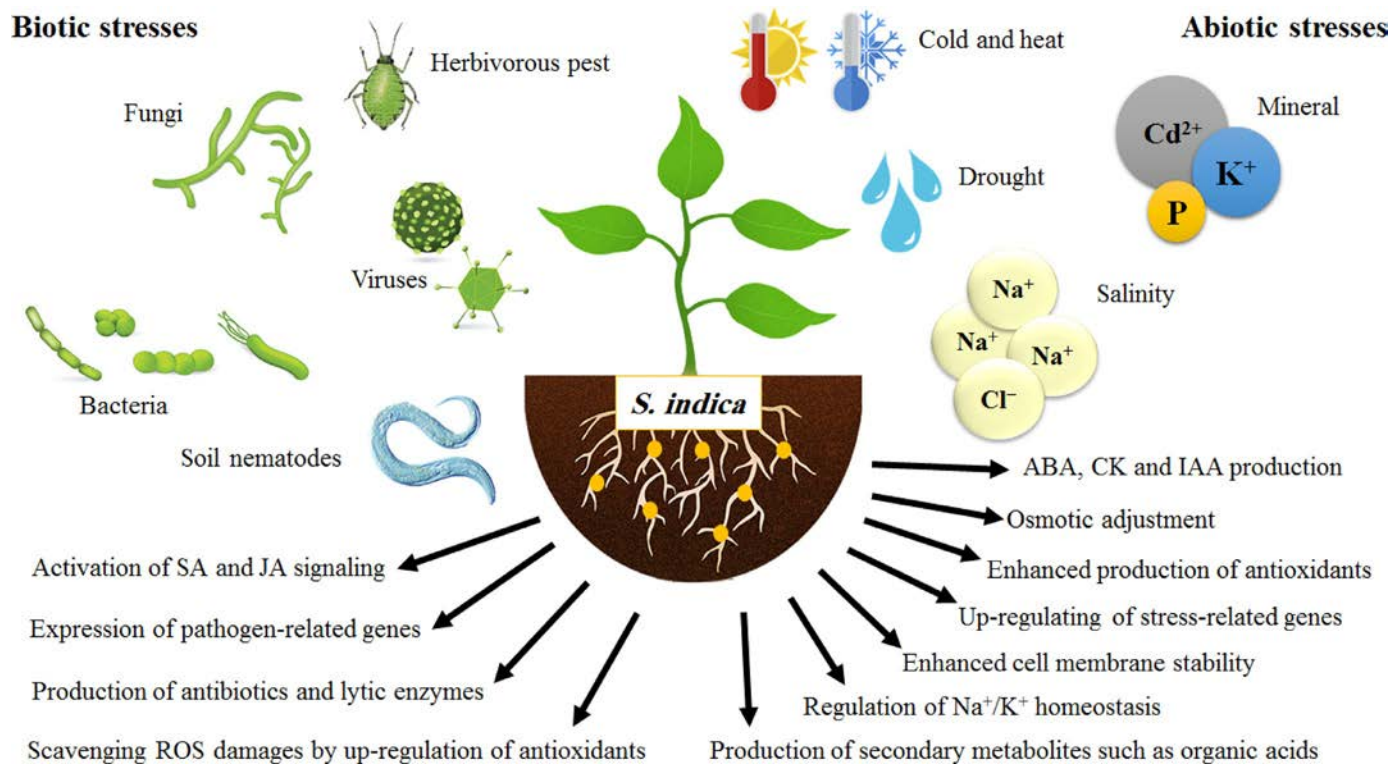


Fig. 3 Underlying mechanisms of host tolerance to biotic and abiotic stresses mediated by *S. indica*. Fungi confer plant tolerance to abiotic stresses [i.e., drought, salinity, mineral (nutrients deficiency and toxicity of heavy metals) and temperature extremes] mainly through production of phytohormones, activation of antioxidants to metabolize ROS, reprogramming of stress-related genes and osmotic adjustment. Additionally, *S. indica*-inoculated plants benefit from up-regulation of pathogenesis-related genes, enhanced enzymatic and non-enzymatic antioxidant capacity, production of antimicrobial compounds and JA and SA signaling against biotic stresses. ABA, abscisic acid; ROS, reactive oxygen species; IAA, indole acetic acid; JA, jasmonic acid; SA, salicylic acid and CK, cytokinin.

review some representative researches which have studied the effect of endophyte-plant symbiosis on different aspects of soil environment and the underlying mechanisms for these alterations over the past 20 years.

3.1 Soil biological indicators

Changing in the composition of soil microbial communities and soil microbial respiration in the presence of foliar endophytic fungi are established in a limited number of publications (Buyer et al., 2011; Rojas et al., 2016). There are a number of contradictions about the effects of fungal endophyte presence on soil microbial parameters (Iqbal et al., 2012). For instance, lower soil microbial activity and consumption of certain substrates, lower abundance of gram-positive bacteria, AMF and other microbial groups have been reported in the rhizosphere of endophyte-infected tall fescue (Buyer et al., 2011). In contrast, some studies have reported stimulatory effects of endophyte-infected tall fescue or no change on soil microbial community composition (Iqbal et al., 2012). Slaughter et al. (2019) stated that *Epichloë*-grass relations had no significant effect on total AMF colonization; however, altered AMF arbuscule presence and extraradical hyphal length in soil were observed under different grass-endophyte combinations. The CTE45 genotype hosted the fewest AMF arbuscules regardless of endophyte presence, and endophyte-infected (E^+) clones within NTE19 supported significantly greater soil extraradical hyphae compared to endophyte-free (E^-) clones. Because AMF are often associated with improved soil physical characteristics and C sequestration, our results suggest that development and use of unique grass-endophyte combinations may cause divergent effects on long-term ecosystem properties. Rojas et al. (2016) investigated the effect of the *E. coenophiala*, on the biomass and structure of soil bacterial, archaeal and fungal communities in both rhizosphere and bulk soils associated with tall fescue plants. Their results showed that *E. coenophiala* infection altered soil fungi composition by increasing phylum Glomeromycota and reducing phylum Ascomycota and other fungal genera. However, soil prokaryotic (bacterial and archaeal) communities were not significantly affected by the presence of foliar endophytic fungi.

In addition to soil microbial communities, *E. coenophiala* symbiosis in tall fescue may impact soil macro- and micro-fauna communities, too (Omacini et al., 2012). Increased number of earthworms (Humphries et al., 2001), decreased abundance of root-knot nematodes (Elmi et al., 2000) and altered community composition of springtail species (Lemons et al., 2005) have

been reported in response to foliar endophyte infection. Rabiey et al. (2017) observed that *S. indica* presence in both wheat root and soil samples led to detectable variations in the microbial community composition and increased diversity in the fungal and bacterial communities.

A few studies have examined the effects of endophyte-infected host plants on soil microbial biomass and activities. Iqbal et al. (2012) observed higher total microbial biomass in endophyte-infected tall fescue plots in comparison with endophyte-free counterparts. Nevertheless, Hosseini (2015) investigated the effects of endophyte-infected and endophyte-free tall fescue residues on soil organic carbon and basal microbial respiration in four texturally-different soils. She observed that endophyte-infected residues increased soil organic carbon storage and decreased microbial respiration in different soils. Similarly, Handayani et al. (2011) and Franzluebbers and Hill (2005) reported lower microbial respiration in pastures with high *Epichloë* infection frequencies compared to areas with low endophyte occurrence.

The symbiotic interactions between host plant-endophyte can modify the microbial features of rhizosphere or even bulk soil in both direct and indirect pathways. Directly, endophyte-infected grasses produce and release some secondary metabolites like ergot and loline alkaloids and phenolic compounds (Yan et al., 2015). In a great portion of studies, secreting of these compounds to rhizosphere is responsible for reduced microbial biomass and activities (Mikola et al., 2016; Omacini et al., 2012). Indirectly, endophyte presence can contribute to changing of soil structure and functioning of soil microbial communities through improved plant growth and nutrient status (Guo et al., 2016). An increase in root biomass and exudates and also enhanced soil fertility as a result of endophyte infection, may affect qualitative and quantitative characteristics of microbial communities (Gundel et al., 2017; Hosseini, 2015). Moreover, changes in the amount and soil-to-atmosphere fluxes of soil gases (i.e., O₂ and CO₂) may be associated with the alterations in the structure of soil microbial communities in grassland ecosystems (Iqbal et al., 2013).

3.2 Soil C and N cycling

Plant-microbe symbiotic interactions play crucial roles in natural and agroecosystems such as litter decomposition, soil aggregation and N cycling (Slaughter, 2016). *Epichloë*-mediated variations in plant rhizodeposition and soil microbial structure and functioning may lead to higher soil carbon

sequestration (Iqbal et al., 2012) and altered N dynamics in grasslands (Franzluebbers and Hill, 2005; Franzluebbers and Stuedemann, 2005). Several studies revealed that the grass-endophyte symbiosis had inhibitory effect on litter decomposition (Hosseini, 2015; Lemons et al., 2005; Omacini et al., 2012). These observations are often related to *Epichloë*-mediated alkaloids production which negatively affects decomposers. However, Gundel et al. (2017) stated that the presence of *Epichloë* endophytic fungus can be associated with higher decomposition rate of plant litter. They also observed lower N and P contents in endophyte-infected *Schedonorus* (= *Festuca*) *pratensis* plant litter. They concluded that *Epichloë* infection could alter plant residues decomposition by several ecological pathways rather than production of toxic alkaloids. These ways included changing of plant leaf chemical composition or modifying the structure of the plant community and microclimate (Gundel et al., 2017).

Soil organic carbon (SOC), a key factor in preserving soil quality and health, indicates the sustainability of soil resources exposed to different land management practices. Although the benefits of endophyte infection to host grasses are well documented, limited studies have investigated the effect of plant-microbe interaction especially endophytic symbiosis on soil quality, particularly organic matter accumulation and dynamics. Hosseini et al. (2015a) examined the effects of foliar fungal endophyte infection in tall fescue on rhizosphere chemical, biological, and hydraulic properties in different soil textures. The results showed that *Epichloë* endophytic fungus significantly enhanced soil organic carbon storage and hot-water soluble carbohydrates (HWSC), especially for the medium- to fine-textured soils, and decreased the basal soil respiration. Likewise, Handayani et al. (2011) tested how *Epichloë* infection altered active soil C pools such as particulate organic matter C (POM-C), microbial biomass C (MBC), mineralizable C (Min-C), and C content in macro-aggregates and micro-aggregates. They observed that endophyte presence effectively increased MBC ($\approx 26\%$) and percent of micro-aggregates ($\approx 46\%$), and decreased Min-C ($\approx 43\%$) and C associated with micro-aggregates ($\approx 15\%$). They concluded that *Epichloë*-infected tall fescue has potential to modify C sequestration and soil structure, particularly in short-time periods that can be used to examine conservation efforts to improve pasture productivity and the consequences of pasture restoration strategies.

As far as known, there is only one study which examined the effects of *S. indica* inoculation on SOC storages, so it yields a field ripe for research. Moballeggh (2017) studied the effects of wheat and maize inoculation with

S. indica and addition of its extract on soil structural stability indices and physicochemical properties. Her results indicated no significant difference between SOC of rhizosphere of *S. indica* inoculated and non-inoculated plants, however, the fungus extract addition effectively increased basal microbial respiration and consequently reduced SOC pool. She concluded that the fungus extract can be considered as a microbial substrate which would trigger microbial activities and then reduced SOC in the rhizosphere.

3.3 Soil aggregate stability

Aggregate stability, a representative index for resistance of soil structure against destructive physical stresses, is affected by plant-microbe interactions. The impact of *Epichloë*-grass symbiotic interactions on soil aggregate size distribution were investigated in previous studies (Franzluëbbers and Stuedemann, 2005; Handayani et al., 2011). In a descriptive and comprehensive study, Hosseini et al. (2015a, 2015b and 2017b) examined the influences of *Epichloë* infection on soil aggregate stability in texturally-different soils via different methods. They quantified soil structure stability by high energy moisture characteristic (HEMC), as a novel and useful method for determining the structural stability of different soil textural types (Levy and Mamedov, 2002), and also by water dispersible clay (WDC), as a common method for evaluating aggregate instability.

In the HEMC method, an index of aggregate stability against slaking defined as stability ratio (SR) is determined by quantifying differences in water retention curves of fast- and slow-wetted aggregates (between 0.5 and 1.0 mm) at high energies (i.e. absolute matric potentials of 0 to 50 cm). The SR ranges from zero to one in which higher values indicate greater stability of soil aggregates. Moreover, Hosseini et al. (2015b) proposed the slope of HEMC at its inflection point (S_i) as an alternative structural stability index. This index is conceptually similar to Dexter's S-theory (Dexter, 2004). The value of S_i represents the extent of aggregate porosity which is concentrated into a narrow range of pore sizes. Higher values of S_i and also S_iR (i.e., the ratio of S_i values of fast- to slow-wetted aggregates) are consistent with improved aggregate stability. The results indicated that foliar endophyte presence (*E. coenophiala*) increased soil organic carbon (SOC) pools especially for the fine-textured soils. As a result, values of SR and S_iR and structural stability of the tall fescue rhizosphere soils, particularly in medium- and fine-textured ones, significantly increased (Hosseini et al., 2015b). The same trend was observed when endophyte-infected tall fescue

residues were added to different soil textures (Hosseini et al., 2017b, 2017c). Evaluating of aggregate stability of rhizosphere soil using WDC also revealed that *Epichloë*-infected tall fescue rhizosphere had a lower WDC value when compared to the endophyte-free one. This means that endophyte-infected associated soils had greater structural stability due to higher concentration of HWSC and SOC storage (Hosseini et al., 2015a). Similarly, Moballegh (2017) reported lower WDC and greater HWSC upon addition of *S. indica* extract to soil. However, she found no significant effects of *S. indica* inoculation or its extract addition on HEMC stability indices of rhizosphere. Recently, Saedi et al. (2021a) studied the effect of endophyte-tall fescue symbiosis on the rhizosphere quality indicators under different aeration conditions in a greenhouse pot experiment. The results showed that soil structure degradation was intensified under oxygen-limited conditions. However, endophyte symbiosis increased the aggregate stability through the water-repellent exudates and enhanced organic carbon storage especially under oxygen-limited conditions.

3.4 Soil water repellency and hydraulic properties

Among the fungi, the role of AMF on soil hydrophobicity and hydraulic properties is commonly investigated (Rillig et al., 2010). A great number of these researches indicates an increase in soil water repellency and percentage of water-stable aggregates is linked with the production of glomalin by AMF (Rillig et al., 2010). However, there is little information about the impact of foliar and root endophytic fungi on these soil fundamental properties. For the first time, Hosseini (2015) and Hosseini et al. (2015a) investigated the effect of *Epichloë* endophytic fungus presence on water repellency and hydraulic properties of tall fescue rhizosphere soil. They hypothesized that the presence of *Epichloë* endophytic fungus in the aboveground parts of tall fescue can change the soil water repellency and aggregate stability by alteration of the chemical and biological properties of rhizospheric soil. They applied the intrinsic sorptivity method as suggested by Hallett and Young (1999). Summarily, in this method ethanol (S_E) and water (S_W) sorptivities, repellency index (RI) and contact angle (θ) are measured to characterize the soil hydrophobicity. The results revealed that endophyte-infected treatments had greater S_E , RI and θ and lower S_W (Hosseini et al., 2015a). It can be concluded that the differences in the rhizosphere hydrophobicity and hydraulic properties of the endophyte-infected and endophyte-free plants may be due to changes in pore structure (quantified

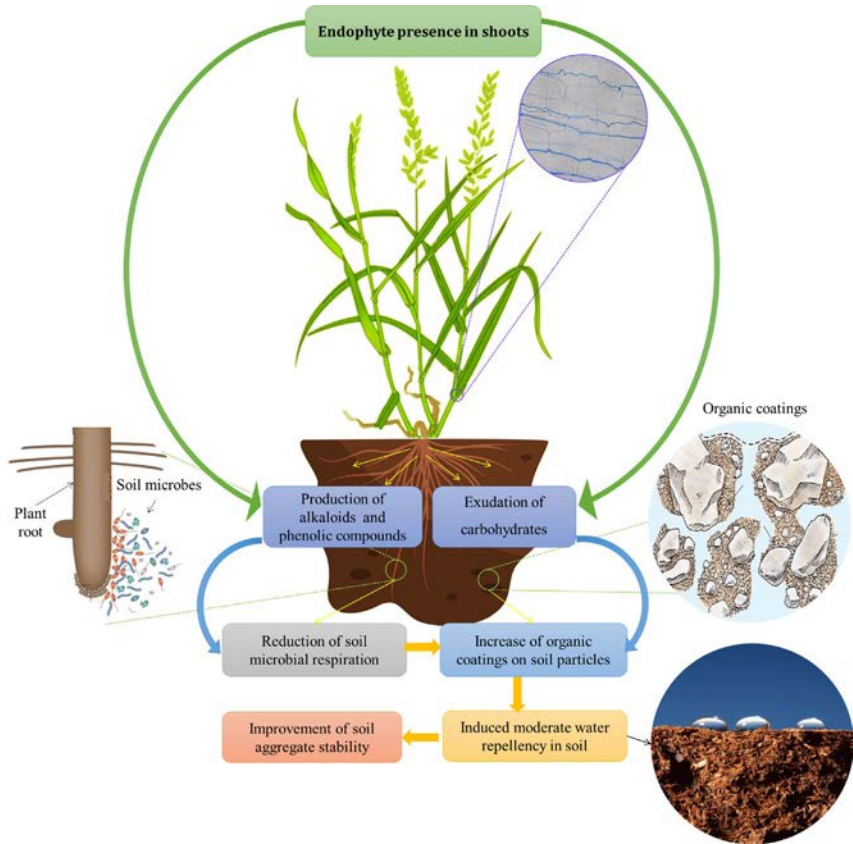


Fig. 4 Schematic view of possible mechanisms in which foliar *Epichloë* of tall fescue affects the water repellency and aggregate stability of the rhizosphere. Proposed by Hosseini, F., Mosaddeghi, M.R., Hajabbasi, M.A., Sabzalian, M.R., 2015a. Aboveground fungal endophyte infection in tall fescue alters rhizosphere chemical, biological, and hydraulic properties in texture-dependent ways. *Plant Soil*. 388, 351–366, with permission from Springer Nature.

by S_E) and hydrophobic coatings (quantified by S_W), which are positively correlated with SOC storage. A conceptual schematic view was presented to show how and in which ways the foliar endophyte affects the water repellency and aggregate stability of the rhizosphere (Fig. 4). In accordance with their findings, Moballegh (2017) reported the highest value of RI in the rhizosphere of *S. indica*-inoculated plants. She suggested that the outer wall layer of the fungal hyphae consists mainly of polysaccharides or some hydrophobic proteins (Varma et al., 2007) which resulted in higher water repellency in the associated soils.

Soil hydraulic properties including water content at permanent wilting point (θ_{PWP}), absolute matric potential at PWP (h_{PWP}), plant available water (PAW) and its corresponded integral energy (E_{I-PAW}) were affected by *Epichloë*-grass symbiotic interactions (Hosseini et al., 2016). The E_I concept is applied to quantify the energy required for plants to take up a unit mass of water at a certain water content range (i.e., PAW range). Practically, it is calculated by integration of soil water retention curve over the PAW range. Lower value of E_I indicates that plants can easily take up water from the soil. These results showed that h_{PWP} of tall fescue is remarkably greater than the conventional value (i.e., 15,000 hPa) and its mean value was greater in endophyte-infected plant associated soils ($\approx 27,572$ hPa) compared to endophyte-free ones ($\approx 21,780$ hPa). This means that endophyte-infected plants had more ability to take up water at higher h values under similar conditions presumably due to induced drought-tolerance mechanisms (see Section 2.1.2). Moreover, endophyte-infected treatments, especially in the coarse- and medium-textured soils, had higher PAW and lower E_I , indicating that for similar PAW values, the host plant requires lower energy to take up a unit mass of water from the PAW range because endophyte presence can facilitate soil water release path in this range by increasing SOC and improving soil structural stability (Hosseini et al., 2016). In a separate lab study, it was examined whether addition of endophyte-infected tall fescue residues had considerable effects on different soil available water (SAW) quantities including PAW, least limiting water range (LLWR) and integral water capacity (IWC) and their corresponded integral energies [i.e., E_{I-PAW} , E_{I-LLWR} , E_{I-IWC}] in four texturally-different soils (Hosseini, 2015). Although endophyte presence had no significant effect on the SAW quantities, their corresponding integral energies except for E_{I-IWC} , significantly increased by addition of endophyte-infected residues. This finding is interpreted as follows: the presence of *Epichloë* reduced soil penetration resistance in the dry range by increasing SOC and improving soil physical quality, and as a result, host plant is able to take up water in a wider range of soil water content, and integration over a broader soil water content range resulted in greater values of E_I .

3.5 Soil mechanical properties

Drought, extreme temperatures, poor aeration and high penetration resistance are four main physical limitations for root development and plant growth. Among these physical constrains, high soil mechanical impedance

is very important especially in dry environments because decreasing water content dramatically increases soil penetration resistance which is simultaneous with severely reduced root development and impaired plant functioning (Bengough et al., 2011). Despite the importance of soil penetration resistance on root system extension, few studies have investigated the impact of plant-endophyte symbiosis on soil mechanical properties and host responses to mechanical stress.

The probable effects of endophyte presence on modifying soil mechanical properties were studied by Hosseini (2015). She examined the effects of endophyte-infected and endophyte-free tall fescue residues on mechanical properties of texturally-different soils. Addition of endophyte-infected residues significantly lowered soil penetration resistance especially in the dry range (i.e., absolute matric potentials higher than 8000 hPa). An increase in SOC and greater aggregate stability (i.e., lower WDC content) in endophyte presence treatments, were possible reasons for reduced penetration resistance and increased soil physical quality especially in dry conditions (Hosseini, 2015).

Maximum axial root growth pressure (σ_{\max}) is a quantity to identify plant root ability to penetrate into hard soils (Materchera et al., 1992). The extent of σ_{\max} is controlled by internal (i.e., osmotic potential, cell wall extensibility and cell wall pressure) and external (i.e., soil matric potential, penetration resistance and temperature) conditions (Greacen and Oh, 1972). As endophyte-host interaction has considerable effect on plant responses to stressful conditions, Hosseini et al. (2019) hypothesized that *S. indica* may be effective on the σ_{\max} and root penetration ability into hard soils, especially under drought stress conditions. For the measurement of σ_{\max} , the maximum axial force (F_{\max}) exerted by the *S. indica*-inoculated and non-inoculated roots of maize seedlings were measured under control and PEG-induced water stress conditions. After measuring root diameter (d), σ_{\max} was calculated by dividing the F_{\max} by the corresponding root cross-sectional area. Interestingly, the results showed that *S. indica* inoculation exerted a temporary stress on root growth leading to greater lag time (T_{lag}) for force development and the time to reach F_{\max} (T_{\max}) in inoculated plants. Greater values of T_{lag} and T_{\max} in the inoculated plants can be attributed to destruction and decomposition of the cell wall of root cells by fungal enzymes (Kost and Rexer, 2013) and consuming a portion of the host cellular energy for development of compatibility with the fungus presence in the root. However, the establishment of a symbiotic relationship between maize roots and *S. indica* resulted in greater F_{\max} and σ_{\max} especially under moderate and severe water stresses. It means that *S. indica* inoculation can

moderate adverse impacts of stressful conditions on growth and elongation of plant roots especially during the initial growth stages by improving osmotic adjustment and/or by altering cell wall properties. Further studies are recommended for identifying the exact mechanisms.



4. Concluding remarks and future prospects

The advantages of both foliar and root endophytic fungi (*Epichloë* spp. and *S. indica*) for host plants are predominantly observed under harsh environmental conditions. Endophyte can improve mineral nutrition, biotic and abiotic stress tolerance and competitive ability of host plants in comparison with endophyte-free counterparts. This leads to better functioning and productivity in both natural ecosystems and agroecosystems. Production of various secondary metabolites including alkaloids, antibacterial and fungicide compounds, better osmotic adjustment, up-regulation of stress-related genes, enhanced antioxidant capacities for ROS scavenging and modifying phytohormones are the most important induced mechanisms applying by the endophyte-infected plants to cope with stressors. Although most of studies are focusing on drought and mineral stresses, the outcome of endophyte infection against some individual and combined stressors like water-logged conditions, extreme temperatures and high soil mechanical resistance in ecosystems has been scarcely considered. However, under global changing climate, gathering information and gaining knowledge regarding the plant-microbe feedbacks to these stressors are totally necessary.

The recent information derived from studies in the last two decades are useful to realize the utility of plant-endophytic fungi interaction in sustainable agriculture production. Plant-endophyte interactions may have the capability to reduce the need for application of pesticides, chemical fertilizers, help weed management, phytoremediation, and desalinization of agricultural soils. However, the probable consequences of endophyte infection to engineer agroecosystems in these ways remain to be explored. Moreover, most studies during the last decades have been performed under controlled greenhouse conditions. Nonetheless, plant-fungi feedbacks may be different under natural field conditions. Therefore, it is recommended to investigate the potential effects of endophyte infection on plant performance under field conditions.

Several lines of research have revealed that both foliar and root endophyte infections have enormous consequences on the belowground processes such as microbial community composition and functions, litter

decomposition, carbon sequestration and nutrient cycling, and different aspects of soil quality and health. Generally, endophyte infection improved soil physicochemical quality by increasing SOC storage, structural stability and facilitating of water and nutrient release pathways. However, this field of study is an area of attention and further investigations should be performed to clear underlying processes and mechanisms in molecular and cellular levels.

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