Chapter

Fungal Endophyte-Host Plant Interactions: Role in Sustainable Agriculture

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Abstract

Fungal endophytes that live inside plant tissues without causing any apparent symptoms in the host plant are important components of plant micro-ecosystems. Endophytic fungi confer profound impacts on their host plants by enhancing their growth, increasing their fitness, strengthening their tolerances to pests and diseases. Moreover, fungal endophytes symbiotic with host plant produce a plethora of bioactive secondary metabolites that are expressed as defensive weapons to protect the host plant against various abiotic stresses. Currently, main focus in endophytic fungi research is associated with the ability of these microorganisms to produce and accumulate biologically active metabolites as these are potent source of novel natural products useful in agriculture sector.

Keywords: fungal endophyte, symbiosis, secondary metabolites, stress, sustainable agriculture

1. Introduction

Over reliance of synthetic pesticides in crop fields from late 1940 to mid-1960s resulted in a number of adverse environmental impacts such as secondary pest outbreak, insect resurgence, effects on non-target organisms, residual problem, environmental pollution, prompted an urgent need for alternative tactics to help make crop protection more sustainable. Biological control using micro-organism has gained much interest, being specific, low relative cost and low risk to ecosystem [1]. Among the various micro-organisms, endophytic fungi can make the chemical intensive crop production system more sustainable as it has ability to enhance plant growth, yield and increase plant fitness by providing biotic and abiotic stress tolerance [2, 3]. Endophytes ("endo" = within, "phyte" = plant) are the microorganisms that inhabit interior of plants especially leaves, stems, roots without causing any apparent harm to the host [4]. These are ubiquitous having rich biodiversity and found in every plant species as nearly 3,00,000 plant species exist on earth with each individual plant host having one or more than one endophytes [5]. Endophytic fungi are considered as plant mutualists as they receive nutrition and protection from host plant while the host plant may benefit from enhanced competitive abilities and increased resistance to herbivores, pathogens and various abiotic stresses [6]. It spends whole or part of their life cycle colonizing inters- and/or intracellularly within the healthy tissues of the host plant without causing visible signs of infection [7, 8]. Moreover, fungal endophytes have gained significant interest in sustainable agriculture due to their great potential to contribute to secondary compounds with unique structure, including alkaloids, benzopyranones, chinones, flavonoids, phenolic acids, quinones, steroids, terpenoids, tetralones, xanthones, etc. [9–11] produced by the fungi or by the plant due to interaction with the fungi. Among the microorganisms, fungal endophytes are the largest group producing secondary metabolites. Fungal toxins produced by these biotic metabolites contribute to plants tolerance towards various biotic and abiotic stresses. Fungal endophytes are known to produce bioactive compounds toxic to insects, nematodes, produces extracellular enzymes (cellulases, proteinase, lipases, esterases) for degradation of dead soil biomass, solubilize insoluble phosphates and produce plant growth-promoting hormones (auxins, cytokinins, gibberellins). Endophyte infected plants manage plant growth under adverse conditions of drought, salinity, temperature and heavy metal stress through different mechanisms. This chapter outlines various approaches for the use of endophytic fungal inoculants to combat various stresses in agricultural fields, thus increasing global crop productivity.

2. Fungal endophyte-host plant association

The association between fungal endophytes and their host plant is due to their unique adaptations which enable the endophytes to harmonize their growth with their host plant [12]. The origin of endophytes is not clear due to complex association between the endophyte and its host plant and the multiplicity of the host's living environment. Exogenous and endogenous are the two hypotheses explaining the origin of endophytes. According to endogenous hypothesis, endophytes are gaged from the mitochondria and chloroplast of the plant, and so it has comparable genetic backgrounds to the host [13], whereas exogenous hypothesis believes that endophytes arrive from outside of the plant and got inserted into the host from root wound, induced channels, or surface [14]. During the long period of co-existence and evolutionary processes, different relationships have been established between endophytic fungi and their host plants ranging from (i) a continuum of mutualism, (ii) antagonism, and (iii) neutralism. As once inside the tissues of a host plant, the endophytic fungi assumed a quiescent (latent) state, either for the whole lifetime of the host plant (neutralism) or for an extended period of time (mutualism or antagonism) until environmental conditions are favorable for endophytic fungi [15]. Endophytes due to its cryptic existence also have its role of decomposers in ecosystem, as they are among the primary colonizers of dead plant tissues [16, 17].

2.1 Fungal endophytes

2.1.1 Transmission

The life history of endophytes in symbiotum with host plant has three modes of reproduction (**Figure 1**). They can either be transmitted (i) vertically from infected plant to offspring via seeds (*Neotyphodium* spp.), (ii) horizontally by sexual spore s from infected individuals (e.g. *Epichloe* spp.) or (iii) mixture of two life cycles [19]. The pure vertical transmission is asexual reproduction of intercellular hyphae of above ground tissues with no symptoms and transmitted vertically via seeds from infected plants to offspring (e.g. *Neotyphodium* spp.). In contrast, the pure horizontal transmission evolves sexual life cycle, relies on the production of contagious

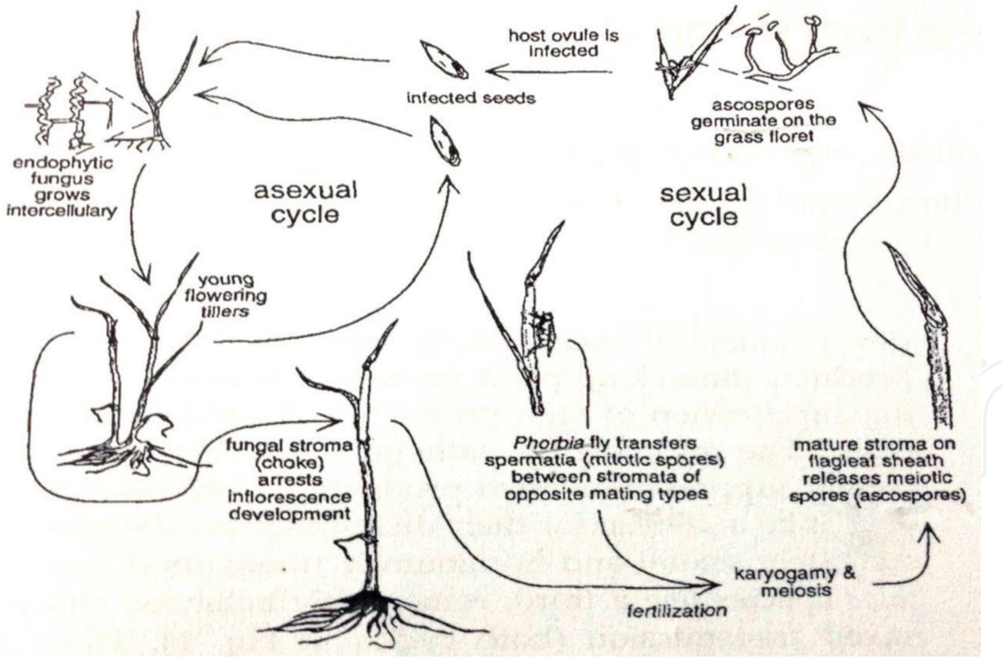

Figure 1.
Asexual and sexual life cycles of Epichloe festucae *symbiotic with* Festuca *spp. [18].*

sexual spores. These spores can only be produced on a fungal structure (stroma) surrounding the grass flag leaf sheath (e.g. some *Epichloe* spp.). Leaves accumulate numerous infections shortly after emergence by means of epiphytic germination of fungal propagules, followed by cuticular penetration or entry through stomata's [20–22] and grow intercellularly within healthy tissues [20, 23]. However, many *Epichloe* spp. use a third mode of reproduction. In this fungi choke some flowering tillers and produce sexual spores leaving majority of tillers uninfected and transmitted asexually via seeds [18]. Endophytes are transmitted vertically (systemic) and horizontally (non-systemic). Vertically transmitted endophytes are mutualistic, whereas those transmitted horizontally depict antagonism to the host [6, 24].

3. Fungal endophytes for sustainable agriculture

In view of escalating pollution and cost due to indiscriminate use of chemical pesticides, diverted researchers interest towards alternative eco-friendly and safe approaches to meet increasing demand of agriculture productivity. Sustainable agriculture requires the use of various strategies to increase or maintain the current rate of food production while minimizing damage to the environment and human health. Symbiotic endophytic fungal associations with crops offer wide range of benefits ranging from the promotion of plant growth to improvements in the tolerance of various biotic and abiotic stresses. Moreover, loss of useful endophytic microbes from crop plants during their domestication and long term cultivation also requires transfer of endophytes from wild relatives of crops to crop species.

4. Fungal endophytes: Biotic stress management

Endophytic fungi have gained importance in the area of agriculture because of their ability to confer resistance to various biotic stress conditions like insect herbivory, nematicidal attack and by aiding plant growth processes.

4.1 Fungal endophytes

4.1.1 Biocontrol agents

Fungal endophytes act as biocontrol agents as they can protect their host plants from pathogens and pests [25, 26]. The mechanism whereby endophytes deter herbivory is through production of antiherbivory/bioactive compounds [27–29] or complex interacting factors of metabolic processes in both the fungus and the plant after infection [26, 30]. These defensive compounds may deter feeding (antixenosis) or reduce insect performance (antibiosis) [31, 32]. Endophytic fungi release the specialized biologically active compounds without any observable damage to their host tissues [33]. Defensive compounds may be categorized into various functional groups: alkaloids, terpenoids, isocoumarin derivatives, quinones, flavonoids, chlorinated metabolites, phenol and phenolic acids and many others [7, 34].

1. **Alkaloids:** Alkaloids are the first reported fungal metabolites to have insecticidal activity. Alkaloids produced by the fungus or by plant in response to fungal infection increase host resistance to herbivores [4, 35]. Endophyte infected grasses contain a variety of alkaloids such as peramines, ergot alkaloids, lolitrems, loline alkaloids and which are absent in non-infected conspecifics [36, 37]. Alkaloids are the first reported fungal metabolites to have insecticidal activity. Most of the alkaloids have been detected in the cultures of grass associated endophytic fungi, such as sexual *Epichloe* spp. and asexual *Neotyphodium* spp. Fungal isolate determines the types of alkaloids produced and plant/fungal genotype interaction can modify the quantities of these alkaloids [38]. The alkaloids from fungal endophytes are categorized into three groups, amines and amides, indole derivatives and pyrrolizidines. Among amines and amides, peramine is toxic to insects without being harmful to mammals [39, 40]. It is a strong feeding deterrent for argentine stem weevil and several other insects [41, 42]. The levels of alkaloids and other toxins may be altered qualitatively depending on the plants physiological state. Ball et al. [43] verified that with plant aging, the amount of peramine decreases in leaves and reaches lower levels during inflorescence phase. The second group of amine and amide alkaloids is ergot alkaloids that also provide significant resistance against insect pests [44]. Feeding experiments with a variety of mammals indicate that ergot alkaloids have significant detrimental effects on mammalian health and reproduction [45, 46]. Among indole derivatives, the lolitrem C and F have been shown to confer resistance against a number of insect species [47]. Other indole derivatives namely chanoclavine, agroclavine and elymoclavine isolated from culture of *Neotyphodium* endophyte [34] were reported to be toxic to some insects and mammals [48]. Among Pyrrolizidines, the saturated aminopyrrolizidine alkaloids as norloline, N-formylloline, N-acetylnorloline, N-acetylloline were exclusively found in endophyte infected grasses of *F. arundinacea* (infected with *Neotyphodium coenophialum*) and *Festuca pratensis* (with *Neotyphodium uncinatum*) [49]. A number of feeding experiments have demonstrated the insecticidal and insect feeding deterrent activities of these lolines [50–52]. Lolines in addition to the well documented effect on insects are also nematicidal [53].

2. **Terpenoids:** Second group of endophytic toxins include terpenoids isolated from some endophytic cultures originating from a variety of host plants. Sesquiterpenes and diterpenes are among the identified terpenoids. Sesquiterpenes as of heptelidic acid and hydroheptelidic acid isolated from *Phyllosticta* sp., an endophytic fungus of balsam fir (*Abies balsamea*) exhibited toxicity to

spruce budworm, *Choristoneura fumiferana* (Clemens) larvae [54]. Two insect toxins, pimarane and diterpene were isolated from an unidentified endophytic fungus symbiotic with needle of *A. balsamea* [54]. Two benzofuran carrying normonoterpene derivatives, toxic to spruce budworm larvae were characterized from an endophytic culture obtained from wintergreen (*Gaultheria procumbens*) [55].

3. **Isocoumarin derivatives:** Toxicity of isocoumarin related metabolites from the conifer endophyte cultures showed toxicity against cells and/ or larvae of spruce budworm [56].

4. **Quinones:** Rugulosin, a metabolite of endophytic fungus *Hormonema dematioides* from balsam fir has been reported to have insecticidal activity [54]. An unidentified endophytic culture isolated from eastern larch (*Larix laricina*) produced a quinone derivative, which was toxic to spruce budworm larvae [55].

5. **Flavonoids:** Among the flavonoids, tricin and related flavone glycosides isolated from endophyte infected blue grass (*Poa ampla*) exhibited toxicity against mosquito larvae [56].

6. **Chlorinated metabolites:** Insecticidal chlorinated metabolite, heptelidic acid chlorohydrins were isolated from cultures of balsam fir needle endophyte *Phyllosticta* spp. [57].

7. **Phenol and phenolic acids:** Phenol and phenolic acids are frequently detected in cultures of endophytes and have pronounced biological activities. Singh et al. [58] purified phenolic compound from ethyl acetate extract of endophytic *Cladosporium* sp. isolated from guduchi (*Tinospora cordifolia*), which induced significant mortality and adversely affected development and survival of tobacco cutworm, *Spodoptera litura* (Fabricius).

Since the 1980s, there is accumulating evidence about factors that influence the outcome of grass–endophyte–insect interactions. Webber [59] was probably the first worker to report plant protection given by fungal endophyte *Phomopsis oblonga* in elm trees (*Ulmus* spp.) against the elm bark beetle, *Physocnemum brevilineum* (Say). Majority of studies for herbivore performance on native grass species symbiotic with endophytic fungi are more consistent showing negative effects including increased mortality [60], reduced mass [61, 62] and decelerated development time [63]. Afkhami et al. [62] reported that bird cherry oat aphid, *Rhopalosiphum padi* (Linnaeus) damaged more endophyte free nodding fescue (*Festuca subverticillata*) than endophyte symbiotic *F. subverticillata*, while positive effect of endophyte infection was reported on eastern lubber grasshopper, *Romalea guttata* (Houttuyn) that preferentially consumed endophyte symbiotic *F. subverticillata* over endophyte free. Similarly increase in growth rate was recorded in third to fifth instars of fall armyworm, *Spodoptera frugiperda* (J.E. Smith) feeding on *N. coenophialum* infected tall fescue [63].

4.2 Fungal endophytes

4.2.1 Nematicidal agents

Fungal endophytes act as nematicidal agents as they are known to produce some compounds which are toxic to nematodes. Diedhiou et al. [64] demonstrated reduced nematicidal activity by an endophytic fungus, *Fusarium oxysporum*, against the plant parasitic nematode *Meloidogyne incognita* in tomato plant. Schwarz et al. [65] reported that several endophytic fungi isolated from above-ground plant organs produced bioactive compound, 3-hydroxypropionic acid (HPA) extracted by bioactivity-guided fractionation of fungal extracts that showed selective nematicidal activity against *M. incognita* with LD50 values of 12.5–15 μg/ml. Similarly, Felde et al. [66] found that combined inoculations of endophytic fungal isolates *Trichoderma atroviride* and *F. oxysporum* is considered an alternative to improve and increase banana yield that reduces the population of burrowing nematode, *Radopholus similis* (Cobb), an important parasitic nematode on banana.

4.3 Fungal endophytes

4.3.1 Phytohormone production

Endophytes can actively or passively regulate the plant growth by solubilization of phosphate, enhance uptake of phosphorus (P), and/ or plant hormones such as auxin, abscisins, ethylene, gibberellic acid (GA), and indole acetic acid (IAA) [67, 68], among these Gibberellic acid is an important phytohormone. The phytohormone GA, a diterpenoid complex, controls the growth of plants, and promotes flowering, stem elongation, seed germination, and ripening [69, 70]. Fungal endophytes *Sebacina vermifera*, *Piriformospora indica, Colletotrichum* and *Penicillium* are distinguished to have better plant growth promoting effects under unfavorable conditions due to their ability to synthesize enzymes and bioactive metabolites [71–73]. Hamayun et al. [69] reported that fungal endophyte, *Cladosporium sphaerospermum* isolated from soybean plant (*Glycine max*) produced gibberellic acid that induced plant growth in rice and soybean. Metabolite pestalotin analogue, isolated from the endophytic *Pestalotiopsis microspora* exhibited significant gibberellin activity in winter-hazel seeds (*Distylium chinense*) and increased their germination rate [74]. Endophytes, *Fusarium tricinctum* and *Alternaria alternata* produced derivatives of plant hormone indole acetic acid that enhanced the plant growth [75]. A study conducted by Johnson et al. [76] on root colonizing endophyte *P. indica* found that association of fungal endophytes with roots modulated phytohormones involved with growth and development of host plant and enhanced nutrient uptake and translocation especially of phosphorus and nitrogen from the soil.

4.4 Fungal endophytes

4.4.1 Agriculturally important enzyme production

Degradation of the dead soil biomass by fungal endophytic is a major step in bringing the utilized nutrients back to the ecosystem that improves soil quality. Endophytic fungi is reported to produce various extracellular hydrolases including cellulase, laccase, pectinase, phosphatase, lipase, xylanase, and proteinase as a resistance mechanism against pathogenic invasion [77] and to obtain nutrition from host as these enzymes break macromolecules such as lignin, sugar-based polymers, proteins, organic phosphate, and carbohydrates to micromolecules that are transported throughout the cells for metabolism and help in host symbiosis process [78]. Sunitha et al. [79] isolated and identified approximately 50 endophytic fungal strains having amylase, laccase, cellulase, pectinase, lipase and protease enzymes. Study conducted by He et al. [80] explained that endophytic fungal species have ability to decompose organic components, including lignin, cellulose, and hemicelluloses that facilitates nutrient cycling. Chathurdevi and Gowrie [81] reported that the endophytic fungi species isolated from medicinal plant *Cardiospermum halicacabum* can support plant growth to overcome the adverse conditions through producing different extracellular enzymes. Fungal chitinases enzyme have vital role in degradation and cycling of carbon and nitrogen from chitin molecule. Chitin molecule is a linear homopolymer of β-1,4N-acetylglucosamine can be obtained from insect's exoskeleton, crustacean's shells, and fungal cell wall. Many fungal endophytes isolated from leaves of trees of Southern India have shown the production of chitinases [82]. An endophyte, *Acremonium zeae*, isolated from maize is reported to produce the extracellular enzyme hemicellulase, which may be used in the bioconversion of lignocellulosic biomass into fermentable sugars [83].

5. Fungal endophytes: Abiotic stress management

Agricultural productivity is significantly threatened by various abiotic stresses. Environmental stresses such as drought, salinity, temperature can collectively cause more than 50% yield losses worldwide [84]. Plants can tolerate abiotic stress by two mechanisms: (i) via activation of response systems directly after exposure to stress [67] (ii) biochemical compounds that are synthesized by fungal endophytes, acts as anti-stress agents [85]. Experimental studies also confirmed that endophytic fungi can help the host plants from environmental stress conditions such as drought, salts, high temperatures and heavy metals and can thus increase the plant growth.

5.1 Drought stress

Among the abiotic stresses, water stress commonly, known as 'drought', is considered as one of the major challenges to crop production worldwide [86]. Drought has a negative impact on the plant growth rate, germination rates, membrane loss of its integrity, repression of photosynthesis, and increase in the productivity of reactive oxygen species [87, 88]. Fungal endophyte infected plants enhance drought tolerance by increased accumulation of solutes in tissues, or by reduced leaf conductance and a slowdown of the transpiration stream, or due to formation of thicker cuticle as compared to non-infected plants [67]. Chippa et al. [89] reported that endophytic, *Neotyphodium* spp. is reported to enhance drought tolerance in grass plant by stomatal and osmoregulations and protect plants in drought and nitrogen starvation. Experimental studies on lavender plants inoculated with *Glomus* spp. showed that these plants accumulated solutes in tissues thereby exhibiting better drought tolerance by improving water contents, N and P contents and root biomass [90, 91]. Moreover, plants harboring endophytes consumes significantly less water and had enhanced biomass than non-symbiotic plants. For instance, endophytes *Chaetomium globosum* and *P. resedanum* isolated from sweet pepper (*Capsicum annuum*) plants enhanced shoot length and biomass of the host plants challenged by drought stress [92, 93]. Similarly, Redman et al. [72] found that inoculation of endophytes *Fusarium culmorum* and *Curvularia protuberata* in drought-affected rice plants resulted in increased biomass than of non-inoculated plants. Fungal endophyte colonization also results in higher chlorophyll content and leaf area in plants under drought stress than non-colonized plant. Higher chlorophyll concentration is related with higher photosynthetic rate [94]. For instance, enhanced photosynthesis rate was recorded in drought stressed *C. annuum* plants colonized by endophytes *C. globosum* [95] and *P. resedanum* [96].

5.2 Salinity stress

High salinity due to extreme climatic conditions and misuse of agricultural land over the past few decades has led to high salinity, which is a limiting factor to global agricultural productivity [97]. Soil salinity is the accumulation of water soluble salts in soil that affects its physical and chemical properties thereby reducing soil's agricultural output [98]. Reactive oxygen species (SOD, CAT, APX) are formed in plants on onset of salt and osmotic stress. Endophytic *Piriformospora indica* induces salt stress tolerance by elevation of antioxidant enzymes [99]. These are involved in the removal of reactive oxygen species either directly or indirectly via regeneration of ascorbate and glutathione in the cell. Experimental studies by Rodriguez et al. [100] reported that constant exposure of non-symbiotic plants dunegrass (*Leymus mollis*) to 500 mmol/l NaCl solution, became severely wilted and desiccated within 7 days and were dead after 14 days. In contrast, symbiotic plants infected with *F. culmorum* showed wilting symptoms only after they were exposed to 500 mmol/l NaCl solution for 14 days.

5.3 Temperature stress (low and high)

High temperature is a major obstacle in crop production that results in major cellular damage such as protein degradation and aggregation [101]. Whereas, low temperature can cause impaired metabolism due to inhibition of enzyme reactions, interactions among macromolecules, changes in protein structure, and modulating cell membrane properties [102]. Endophytic, *Curvularia* spp. is proven to confer thermal tolerance ability plants like tomato, watermelon, and wheat [103]. Herbal plant wooly rosette grass (*Dichanthelium lanuginosum*) that lives in the areas where soil temperatures can reach up to 57°C, the presence of endophytic fungi *Curvularia* sp. protects the plant from temperature stress better than endophyte free plants [104]. Experimental demonstration by Redman et al. [103] showed that grass *D. lanuginosum* survival in soil temperatures ranging between 38 and 65°C is directly linked to its association with the fungus *C. protuberata* and its mycovirus, *Curvularia* thermal tolerance virus (CThTV). Moreover, cold stress tolerance was conferred in germinated seeds of rice under laboratory conditions by *C. protuberata* isolated from *D. lanuginosum* thriving in geothermal soils [72].

5.4 Heavy metal stress

Heavy metal contamination due to increased industrialization has recently received attention because heavy metals cannot be itself degraded [105]. Toxicity by heavy metals can cause the loss of about 25–80% of various cultivated crops. Heavy metals being very toxic to roots of cultivated crop plants can cause poor development of the root system [106]. Endophytic fungi possess metal sequestration or chelation systems that increases tolerances of their host plants to heavy metals via enhancements of antioxidative system thereby changing heavy metal distribution in plant cells and detoxification of heavy metal, thus assisting their hosts to survive in contaminated soil [107, 108]. For instance, dark septate root endophytes (DSEs), *Phialocephala fortinii* can produce the black biopolymer melanin, which can be synthesized from phenolics and binds heavy metals [109] that keep heavy metal ions away from living, plant cells [110]. Siderophores being metal-chelating compounds [111, 112] released from roots into the rhizosphere can be helpful in inhibiting absorption of heavy metals into plant cells as siderophores can form complexes with heavy metals which are not easily absorbed by plant roots. Yamaji et al. [113] recorded that endophytes *P. fortinii* and *Rhizodermea veluwensis* showed an ability to produce siderophores that probably affects heavy metal exclusion in the rhizosphere.

6. Conclusion

Fungal endophytes can be a significant component of sustainable agriculture, being safe, cost-effective, have ability to produce various compounds like phytohormones, defensive compounds, solubilize phosphates, extracellular enzymes, siderophore production, inhibiting plant pathogens, and promoting plant growth. Over the last decade, sharp rise in study of fungal endophytes is seen as they hold huge potential in agricultural sector. However, most of the research on endophytes is still at an experimental level in lab or greenhouse. For permitting the practical use of these endophytes in agriculture it is extremely necessary to encourage field experiments to determine the effectiveness of the endophytes under real world conditions. Simultaneously, it is also necessary to build awareness of this new research field among farmers to improve interactions and collaboration with scientists working in different fields, thereby encouraging the adoption of endophytes in agriculture and maximizing their benefits. If endophytes become feasible in agricultural sector, their practical aspects will also have to be researched so that farmers can learn how to integrate these endophyte species within pre-existing eco-friendly agricultural methods so as to ensure continuity in the approach to sustainability. Moreover, scientific research has to be also focused on use of genetically modified endophytes made by combining endophytes having two or more different ecological roles, such as the suppression of diseases and insect pests to simultaneously improve plant yields and its defensive properties. Thus, optimization of microbial functions to enhance crop production and protection is also required.

Conflict of interest

No conflict of interest is indulged.

Abbreviations

HPA	3-hydroxypropionic acid
P	phosphorus
GA	Gibberellic acid
IAA	indole acetic acid
SOD	superoxide dismutase
CAT	catalase
APx	ascorbate peroxidase
CThTV	*Curvularia* thermal tolerance virus
DSEs	dark septate root endophytes

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