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REVIEW ARTICLE **Open Access**

Fungal endophytes of crop plants: diversity, stress tolerance and biocontrol potential

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Abstract

Background There is a growing perception among the scientific community to utilize endophytes in improving crop productivity. The presence of these microorganisms offers benefits to host plants that include enhanced resistance to various insect pests, increased fitness and improved tolerance to abiotic stresses including heavy metal pollutants and higher salinity, albeit with no harm to the environment.

Main body Since reports indicated that fungal endophytes afford protection to cereal crops from a wide variety of pathogenic microbes, in this short review, the diversity and potential of fungal endophytes of some major crop plants including rice, wheat, maize and sugarcane were discussed.

Conclusion Considering the global challenges caused by food security, there is an immediate need to look at effective and environmental friendly solutions to increase crop productivity and endophytes present a solution due to their long-term symbiotic association with their hosts. However, it remains critical to understand their functional significance and overall role in improving the host fitness in natural environments.

Keywords Biocontrol, Fungal endophytes, Crop plants, Diversity, Stress, Tolerance

Background

Globally, due to the growing population, there are major challenges to food security; further, agriculturists face several threats including climate change leading to complex abiotic stresses and other biotic stresses. Thus, there is a pressing need to look at novel solutions to enhancing the crop productivity without harming the environment.

Fungal endophytes are considered as plant mutualists, since host plants harbouring the endophytes are known to derive benefit from enhanced competitive fitness, while the endophytes receive nourishment and protection from the host plants. Plants inhabited with fungal endophytes showed enhanced fitness in stressed (biotic and abiotic) conditions over non-endophytic counterparts (Verma et al. 2022). This is especially true for crop plants, where plant–microbe interaction is considered to be of extreme importance, since their implication on sustainable agriculture is vast (Varma et al. 2017). There is increasing recognition by the scientific community to utilize novel endophytes for the enhancement of crop production (Lugtenberg et al. 2016). In a recent study, *Piriformospora indica*, a root colonizing fungal endophyte, was shown to promote plant growth and performance, and enhance fitness of their host plants to resist against biotic and abiotic stresses (Xu et al. 2018).

It is known that endophytes (often bacteria or fungi) live within their host tissue for certain part of their life, while not eliciting any apparent overt negative effects (Tiwari and Bae 2022). Endophytic fungi generally are grouped under Ascomycetous or Mitosporic fungi; a few (less than 10%) Basidiomycetes also have been reported as endophytes (Rashmi et al. 2019). Fungi belonging to Coelomycetes including *Pestalotiopsis, Diaporthe* and *Phyllosticta* are often reported as endophytes, especially

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in tropical plants, and have been referred to as "almost exclusive" endophytes (Govinda Rajulu et al. 2021). Fungal endophyte species belonging to Clavicipitaceae (Ascomycetes) are widely reported from diverse range of grasses and commonly belong to the genera *Atkinsonella*, *Balansia*, *Blansiopsis*, *Epichloe* and *Myriogenospora* (Kumar and Dara 2021). Further, the *Acremonium* endophytes occurring in all the organs/tissues of grasses including leaves, stems and inflorescences are obligate seed-borne fungi that cause unapparent infections.

Endophytic fungi are known to be ubiquitous and have been recorded from all the groups of Plant Kingdom including Algae, Pteridophytes, Gymnosperms and Angiosperms. Diversity of endophytic fungi is reportedly higher in tropical climates with greater woody angiosperm diversity (Banerjee 2011). The presence of these microorganisms offers benefits to host plants that include enhanced resistance to herbivores and insect pests, increased competitiveness, improved tolerance to abiotic stresses such as occurrence of heavy metals and high salinity and may influence the yield and quality of the crop (Chowdhury et al. 2019). Grasses are colonized by *Acremonium* endophytes, which are known to protect their hosts from insect attack, nematodes, and plant diseases. Further, endophytic fungi also make their hosts more tolerant to drought, and some host plants exhibit enhanced growth and tillering characteristics (Latch 1994).

Fungal endophytes are prospective source of novel metabolites useful to mankind (Pimentel et al. 2011). According to Wicklow and Poling (2009), *A. zeae* produces polyketide-amino acid-derived antibiotics pyrrocidines A and B, which augment their host defence against pathogenic microbes that cause seedling blights and stalk rots. Kaushik et al. (2014) reported that many fungal endophytes produce secondary metabolites that have the potential to inhibit the growth of the malarial parasite. Bioactive compounds belonging to various classes of antibiotics, antifungal compounds, immune-suppressants and anticancer compounds have been reported from fungal endophytes (Rashmi et al. 2019). Many classes of secondary metabolites are produced by fungal endophytes, including polyketides, terpenoids, flavonoids and lignans. Fungal endophyte, *Neotyphodium* which has been investigated in detail for its secondary metabolite production, has yielded a variety of novel metabolites, it was widely believed that similar investigations on other fungal endophytes from less explored or unexplored habitats would reveal several hitherto unknown compounds of interest (Mousa and Raizada 2013). Though endophytes from various groups of plants including ethnopharmaceutically important plant hosts, mangroves, hosts from tropical forests and grasses have been studied and reviewed extensively, studies on the endophyte assemblages of crop plants and the benefits of their association with their hosts may have a direct impact on mankind, since enhancing agricultural crop production is of profound importance due to concerns about the growing world population. An approach that would be useful to get the solution from nature itself is the usage of fungal endophytes as these organisms are being preferred to ward off or inhibit pests and pathogens without harming the environment. Also, they are known to enhance the productivity. Thus, this review brings insight into the diversity, and bioactive potential of these organisms in crop plants that will help in their effective utilization.

Diversity of endophytes in some major crop plants

As with the other groups of plants, crop plants also harbour Ascomycetes and mitosporic fungi as dominant group of endophytes (Table 1). Potshangbam et al. (2017) studied endophytes belonging to rice and maize and recorded that 99% of the endophytes were dominated by Ascomycota, whereas Zygomycota contributed only 1 percent of the endophyte assemblage. Forty one fungal isolates were obtained from 160 tissue samples including leaves, stems, roots and seeds of *Suwandel* and *Kaluheenati* rice varieties, and fungal genera belonging to the class Ascomycetes dominated the endophyte assemblage (Atugala and Deshappriya 2015). Casini et al. (2019) investigated fungal assemblage of two ancient tetraploid wheat varieties, viz. Perciasacchi (winter wheat) and Tumminia (spring wheat), grown in Sicilian territory of Italy, and revealed a predominance of Ascomycetes and Basidiomycetes including; *Alternaria, Aureobasidium, Cryptococcus, Cystofilobasidium, Filobasidium, Fusarium*, *Mycosphaerella*, *Leucosporidium*, *Dioszegia*, *Puccinia*, *Sporobolomyces*, *Cladosporium*, *Holtermanniella* and *Gibberella.*

Naik et al. (2009) studied the diversity of fungal endophytes of *Oryza sativa* and recorded 570 fungal isolates in 19 species from 2400 leaf and root segments. Also, colonization rate was found to be 50% higher during winter season than in summer season in *O. sativa*. Similar results have been observed in other groups of plants including mangroves (Suryanarayanan et al. 1998), *Eugenia* (Yadav et al. 2016) and other medicinal plants (Rather et al. 2018).

Most dominant fungal endophytes associated with rice and maize grown in Manipur, India, belonged to genera, *Aspergillus*, *Fusarium*, *Penicillium* and *Sarocladium* and their occurrence was not tissue specific (Potshangbam et al. 2017). Generally, only a few endophytes dominate the assemblage of any host species; for instance, Murali et al. (2007) in their study on the diversity of endophytic fungi of tree species of tropical dry thorn and dry

Table 1 Occurrence of fungal endophytes in some major crop plants

Host and Country	Host tissue	No. of endophyte species	Dominant endophyte(s) genera/species	References
Rice				
Bhadra River project area, Karnataka, India	Leaves	14	*Chaetomium globosum*, *Cladosporium cladosporioides*, *Fusarium oxysporum* and *Penicillium chrysogenum*	Naik et al. (2009)
	Roots	19	*Chaetomium globosum*, *Cladosporium cladosporioides*, *Fusarium oxysporum*, *Penicillium chrysogenum* and Sterile form	
Naranwita, Sri Lanka	Leaves, stem, roots and seeds	41	*Absidia* sp., *Aspergillus* sp. 1, *Aspergillus* sp. 2, *Cylindrocladium* sp., *Paecilomyces* sp. and *Penicillium* sp.	Atugala and Deshappriya (2015)
Manipur, India	Leaves, stems and roots	57	*Fusarium*, *Sarocladium*, *Aspergillus* and *Penicillium*	Potshangbam et al. (2017)
Suphanburi and Chainat Provinces, Thailand	Leaves and roots	21	*Nigrospora oryzae*, *Curvularia lunata*, *Daldinia eschscholtzii* and *Exserohilum* sp. 3	Su-Han et al. (2019)
Maize				
Millands field near Newton Abbott, Devon, England	Stem	23	*Aurebasidium pullulans* var. *melanigerum*, *Acremonium strictum*, *Cladosporium cladosporioides*, *Ustilago* sp.	Fisher et al. (1992)
	Leaves		*Alternaria alternata*	
Semília Genetics and Breeding LTDA, Campo Largo, Paraná, Brazil	Leaves of maize plant lineages (L1 and L2)	15 (L1) 12 (L2)	*Epicoccum nigrum* *Gibberella fujikuroi*	Szilagyi-Zecchin et al. (2016)
Bangalore, India	Leaves Stem Root	10 4 2	*Penicillium* sp. *Epicoccum sorghinum* *Fusarium fujikuroi*	Renuka and Ramanujam (2016)
Manipur, India	Leaves, stems and roots	66	*Fusarium*, *Sarocladium*, *Aspergillus* and *Penicillium*	Potshangbam et al. (2017)
Sugarcane				
Centro de Tecnologia Canavieira S.A. (CTC), Piracicaba, São Paulo, Brazil	Root	21 Genera	*Fusarium* and *Penicillium*	Romão-Dumaresq et al. (2016)
Wheat				
Welgevallen Experiment Farm, Stellenbosch, South Africa	Leaves	55	*Alternaria alternata*, Basidiomycete sp. 1, *Coniothyrium* sp., *Epicoccum nigrum*, *Phoma glomerata* and *Pleospora herbarum*	Crous et al. (1995)
	Culms		*Alternaria alternata*, *Fusarium avenaceum*, *Phoma glomerata* and *Truncatella angustata*	
	Roots		*Coniothyrium* sp., *Fusarium avenaceum Phoma glomerata*	
Buenos Aires Province, Argentina	Leaves	19	*Alternaria alternata*, *Cladosporium herbarum*, *Epicoccum nigrum* and *Rhodotorula rubra*	Larran et al. (2002)
Buenos Aires, Argentina	Leaves, stems, glumes and grains	27	*Alternaria alternata*	Larran et al. (2007)
Israel	Stem and seeds	67*	*Alternaria* spp.	Ofek-Lalzar et al. (2016)

*Number of cultivated endophytes from *A. sharonensis* (Sharon goat grass), *Triticum dicoccoides* (wild emmer wheat) and *T. aestivum* (modern wheat) deciduous forests observed that only few endophytes dominated the assemblage. Similarly, Su-Han et al. (2019) studied Thai rice cultivar for endophytes and recorded 21 species of endophytes of which only four were frequently isolated sporulating endophytic fungi namely: *Nigrospora oryzae*, *Curvularia lunata*, *Daldinia eschscholtzii* and *Exserohilum* sp. 3. *E. rostratum* has also been isolated as an endophyte from Sugarcane plants in Puducherry, India (Fig. 1). Some of the endophytes associated with crop plants have also been reported as pathogens in several hosts; for instance, *N. oryzae* has been reported to cause disease in rice and other hosts including mustard and cotton (Sharma et al. 2013). These may reside in the host as latent pathogens (Suryanarayanan and Murali 2006) and cause visible symptoms, when the host defence weakens.

Tissue specificity has also been observed in endophyte colonization; tissue preference shown by fungal endophytes could be a strategy to decrease competition among them which could be achieved by adapting to the different microenvironment prevalent in the tissues (Suryanarayanan 2017). Similar results were recorded for two rice cultivars in which different fungal communities occurred in different tissue types (Su-Han et al. 2019).

Screening for fungal endophytes from crop plants has also led to the discovery of fungi new to science and new to the host plant. Khunnamwong et al. (2014) discovered novel ascomycetous yeast, *Wickerhamiella siamensis* that was found to occur as an endophyte in sugarcane leaf.

Stress tolerance induced by fungal endophytes

Endophytes provide protection to host plants under hostile environmental conditions that experience heat, stress and prolonged periods of drought (Ganie et al. 2021). Therefore, these endophytes may mitigate the impact of climate change which is a major challenge facing agricultural sector, since these factors could substantially influence the food production and thereby global economy. Sudden and rapid changes in climatic conditions have threatened the food security at global scale (Arora 2019). It is known that climate change has contributed to reduced rice productivity in many regions due to decreased availability of water, and soil salinization. According to Redman et al. (2011), the endophytes conferred salt, drought and cold tolerance to host plants grown in growth chamber and greenhouse conditions. Even though not adapted to drought or salt stress, two commercial varieties of rice achieved tolerance to these stress conditions, when colonized with Class 2 endophytic fungi isolated from plants growing across moisture and salinity gradients. A rice endophyte, *Penicillium simplicissimum,* was found to tolerate salt concentration up to 10% (Potshangbam et al. 2017), suggesting that the endophyte may play an important role in imparting salt stress tolerance to their hosts. In another study, a salt-tolerant endophytic fungus, *Fusarium* sp., isolated from salt-adapted Pokkali rice, was found to promote the growth of the salt-sensitive rice variety IR-64, when exposed to salinity stress (Sampangi-Ramaiah et al. 2020). Fungal endophytes of wheat increased the percentage of germination, energy of germination and hydrothermal time values, while reducing the host's susceptibility to heat and drought based on seedling fresh weight values (Hubbard et al. 2012). Similarly, in the case of dicot plant species, *Penicillium* sp. was shown to confer resistance to salinity stress as reported by Khan et al. (2011). They showed that the endophytic fungus, *Penicillium minioluteum* could enhance the production of Flavonoids, Daidzein and Genistein in soybean grown under conditions of salinity stress, when compared to control plants

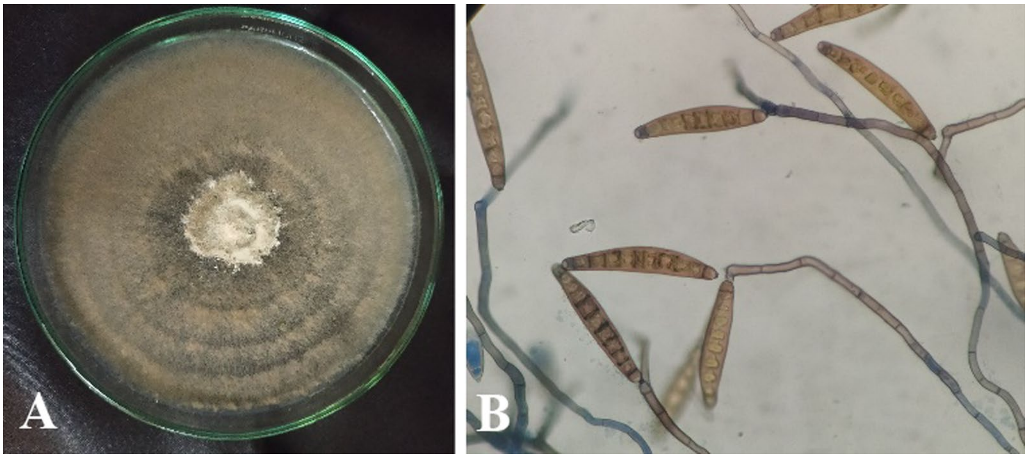

Fig. 1 *Exserohilum rostratum* **A** Growing on PDA medium. **B** Conidiophores with conidia

and could positively influence the growth characteristics of the plant host including shoot length and chlorophyll content. Colonization by *Piriformospora indica*, an extensively studied root endophyte, minimized the usage of chemical fertilizers and provided increased resistance and tolerance to plants to overcome abiotic and biotic stresses, further increased the yield (Unnikumar et al. 2013). In barley plants exposed to low temperature-stress, *P. indica* was shown to improve the crop yield and was suggested as an effective crop treatment strategy in improving crop productivity (Murphy et al. 2014). Also, the ability of *P. indica* to increase the biomass of maize plant, especially under low phosphate condition, was recorded by Gill et al. (2016).

Biocontrol potential of fungal endophytes

To safeguard a sustainable and productive agricultural system, agrochemicals are widely used in plant disease control strategies. But, the intensive use of chemicals causes adverse effects on humans and functioning of the ecosystem, further reducing agricultural sustainability (De Silva et al. 2019). Several studies indicated that endophytic fungi play an important role in protecting cereal crops against a number of pathogenic fungi (Lee et al. 2009). Thus, use of endophytes could be preferred in agriculture due to the fact that the synthetic insecticides are expensive and can have adverse effects on the environment, non-target microorganisms and integrated plant disease management strategies (Albajes et al. 2002). Thus, microorganisms including endophytes are being preferred to ward off or inhibit pests, which may not harm the environment. Ramesh et al. (2021) showed that fungal endophytes of rice could be potential biocontrol agents of blast disease of rice and also act as plant growth promoters.

Trichoderma virens is considered an effective biological control agent and has also been isolated as a plant endophyte from several plant hosts (Tsavkelova et al. 2005). Since *T. virens* is capable of colonizing plant roots, it suggested its potential to protect plant health, inhibit pathogenic microorganisms or bring about systemic resistance (Romão-Dumaresq et al. 2016). *Trichoderma virens* parasitizes and colonizes the potential site of infection including fungal resistance structures (Howell 2002). Other than its antifungal activity, it also produces extracellular enzymes like chitinase, a wide array of antibiotics and was also reported to elicit production of phytoalexins in their hosts (Howell 2006). In maize, colonization by the fungal endophytes, *T. harzianum*, *Hypocrea lixii* and *T. atroviride* and their presence in different tissues including root, stem and leaves clearly demonstrated that these endophytes can establish association with maize, which is not their original host while their increased colonization rates in the roots compared to other parts of the plant indicated the possibility of their root/rhizosphere colonization (Kiarie et al. 2020).

Piriformospora indica can be utilized as a bio-fertilizer, bio-protector, bio-regulator, plant promoter and biotization agent (Gill et al. 2016) and was also reported to ward off plant pathogens of crop plants. It was found to be an effective microorganism in biocontrol of take-all disease of *Triticum aestivum* (Ghahfarokhi and Goltapeh 2010). As a potential biocontrol agent, *P. indica* was effective in managing various root diseases in maize (Kumar et al. 2009), wheat (Rabiey et al. 2015) and barley (Waller et al. 2005).

Fávaro et al. (2012) demonstrated the facultative endophytism of *Epicoccum nigrum* that inhibited the growth of sugarcane pathogens including *Fusarium verticillioides, Colletotrichum falcatum, Ceratocystis paradoxa* and *Xanthomonas albilineans*, at least in vitro. Joshi et al. (2019) identified endophytic, *Trichoderma* strains with higher bioactive potential that can be used in future as tool for management in sugarcane diseases.

Potshangbam et al. (2017) studied fungal endophytes of rice and maize for their interactions with phytopathogens of cereal crops, viz. *Rhizoctonia solani*, *Pyricularia oryzae*, *Pythium ultimum* and *Sclerotium oryzae*. The interactions of test pathogen and host endophytes were evaluated macro-scopically and micro-scopically, and it was observed that *Acremonium* sp. (ENF 31) and *Penicillium simplicissimum* (ENF22) potentially inhibited the growth of all the pathogens included in the study. Muvea et al. (2018) reported that endophyte-colonized onion plants showed resistance against onion thrips which are known to transmit Iris yellow spot virus (IYSV). More studies on crop plants with regard to biocontrol potential of endophytes included those of endophytes of rice against *Magnaporthe grisea* (Atugala and Deshappriya 2015), protective effects of wheat endophytes against *Stagonospora* infection (Sieber et al. 1988), protection against *Fusarium graminearum* by six different species of wheat endophytes (Comby et al. 2017) and potential of endophytes, *Sarocladium strictum*, *Anthracocystis floculossa* and *Penicillium olsonii* against *Fusarium* head blight in wheat (Rojas et al. 2020).

Conclusion

Since endophytes have evolved with their hosts over a long evolutionary time scale and are already established to provide immense benefit to the hosts, they offer an interesting and viable solution in overcoming the challenges associated with increasing crop productivity and their protection against pests without significantly affecting the environment and other non-target hosts. However, several aspects of their biology still remain not well deciphered and the immediate challenge would be to understand their biological role and devise newer techniques to effectively utilise these symbiotic microorganisms.

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Author contributions

KM collected the data for writing the review under various headings and did the preliminary preparation of the manuscript. TSM has given input for the review and fine-tuned the article to reduce plagiarism. VK guided Malarvizhi K (Ph.D. scholar) in the work on fungal endophytes of sugarcane and in writing this review.

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Competing interests

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