3 Biotech (2021) 11:399
https://doi.org/10.1007/s13205-021-02931-4

REVIEW ARTICLE

Re-vitalizing of endophytic microbes for soil health management and plant protection

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Received: 6 March 2021 / Accepted: 15 July 2021 / Published online: 5 August 2021

Abstract

Soil health management and increase crop productivity are challenging issues for researchers and scientists. Many research publications have given multiple technological solutions for improving soil health and crop productivity but main problem is sustainability of those technologies under field condition and different agro-climatic zone. Due to the random industrialization, deforestation, mining and other environmental factor reduce soil fertility and human health. Many alternative options e.g., crop rotation, green manuring, integrated farming, biofertilizer (plant-growth-promoting microorganism, microbial consortium of rhizosphere soils), and vermicomposting are available for adapting and improving the soil heath and crop productivity by farmers. Recent trends of new research dimension for sustainable agriculture, endophytic microbes and its consortium is one of the better alternative for increasing crop productivity, soil health and fertility management. However, current trends are focuses on the endophytic microbes, which are present mostly in all plant species. Endophytic microbes are isolated from plant parts—root, shoot, leaf, flower and seeds which have very potential ability of plant growth promotion and bio-controlling agent for enhancing plant growth and development. Mostly plant endophytes showed multi-dimensional (synergistic, mutualistic, symbiotic etc.) interactions within the host plants. It promotes the plant growth, protects from pathogen, and induces resistance against biotic and abiotic environmental stresses, and improves the soil fertility. Till date, most of the scientific research has been done on assuming that interaction of plant endophytes with the host is similar like the plant-growth-promoting microorganism (PGPM). It would be very interesting to explore the functional properties of plant endophytes to modulate the essential gene expression during biotic and abiotic stresses. Endophytes have the ability to induce the soil fertility by improving soil essential nutrient, enzymatic activity and influence the other physiochemical property. In this study, we have discussed details about functional properties of plant endophytes and their mechanism for enhancing plant productivity and soil health and fertility management under climate-resilient agricultural practices. Our main objective is to promote and explore the beneficial plant endophytes for enhancing sustainable agricultural productivity.

Keywords Plant endophytes · Soil fertility · Plant growth promotion · Phytopathogen · Sustainable agriculture · Crop yield · Stress tolerance · Soil health · Plant–microbe interaction

Introduction

Plants are mega species harboring wide diversity of microbes in their different parts such as seed, root, stems, leaf, pollens and flowers, which altogether is known as the plant microbiome (Zhang et al. 2017; Mukherjee et al. 2020). Plant-associated microbes play critical roles in crop yield and plant health through different direct and indirect mechanisms (Mukherjee et al. 2020; Trivedi et al. 2020b). Endophytes are a unique group of plant microbiome that reside asymptomatically inside plant parts and tissues having a symbiotic relationship (Wilson 1995). The group constitutes

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bacteria, fungi, and archaea that inhabit the plant tissue as a whole or a part of their lifecycle (Hassan 2017; Harrison and Griffin 2020). The majority of plant endophytes belong to genera of *Bacillus*, *Pseudomonas*, *Streptomyces*, *Burkholderia*, *Klebsiella*, *Enterobacter*, *Penicillium*, *Aspergillus*, *Alternaria*, and *Fusarium* (Hassan 2017; Khan et al. 2017a, b; Singh et al. 2017a; Mukherjee et al. 2020, 2021). The features of interest of all these endophytic microbial genera are provided in Table 1. However, from newer studies, it has been demonstrated that there is more diversity of plant endophytes which are subject to change according to the host and environmental factors (Kawasaki et al. 2016; Liu et al. 2020). With that being said, some microbial groups are present universally regardless of the environment and are part of the plant's core microbiome (Hamonts et al. 2018). This core group of microbes has co-evolved with the host plant species and is inherited through generations (Song et al. 2020).

Plants in natural communities preserve their symbiotic associations with endophytes that help in growth promotion and protection against different stresses (Rodriguez et al. 2009; Johnston-Monje et al. 2016; Trivedi et al. 2020b). The actinorhizal and rhizobial endophytes enhance nutrient availability especially nitrogen through the process of biological nitrogen fixation (BNF) (Pawlowski and Demchenko 2012) in specialized root structures called nodules (Coba de la Peña et al. 2017). The mycorrhizal endophytic fungal families also help in nutrient acquisition to plant especially phosphorous. Many of the endophytes produce siderophores which increase iron availability to plants (Mukherjee et al. 2020). The enzymatic activities of endophytes mobilize the

Table 1 List of major endophytic microbial genera isolated from plants and their features of interest

Endophyte	Host plants	Isolation point(s)	Features of interest	Reference(s)
Alternaria spp.	*Salvia miltiorrhiza*, *Solanum nigrum*, and *Brassica napus*	Root, shoot, and leaf	Increased biomass, chlorophyll content, and secondary metabolite production Abiotic stress tolerance	Khan et al. (2015b) Shi et al. (2017) Zhou et al. (2018)
Aspergillus spp.	*Zea mays*, *Euphorbia indica*, Soybean, and Sunflower	Root and leaf	Production of secondary metabolites for plant growth Stress tolerance	Hamayun et al. (2018, 2019) Mehmood et al. (2019)
Bacillus spp.	*Zea mays*, *Saccharum officinarum*, *Aloe vera*, Cucurbits, and *Oryza sativa*, *Cicer arietinum*	Seed, root, stem, and leaf	Inhibition of phytopathogens Plant growth promotion	Akinsanya et al. (2015) Gond et al. (2015a) Khalaf and Raizada (2018) Kumar et al. (2020) Mukherjee et al. (2020) Wang et al. (2020b)
Enterobacter spp.	*Cicer arietinum*, *Zea mays*, and *Sorghum sudanense*	Seed	Improved productivity Phyto-stabilization of heavy metals Plant growth promotion	Li et al. (2016) Ullah et al. (2020) Mowafy et al. (2021) Mukherjee et al. (2020)
Fusarium spp.	*Brassica napus*, *Oxalis corniculate*, and *Glycine max*	Root	Abiotic stress tolerance Mineral solubilization Biomass production Secondary metabolite production	Radhakrishnan et al. (2015) Shi et al. (2017) Bilal et al. (2018)
Klebsiella spp.	*Zea mays*, *Saccharum officinarum*, and *Triticum aestivum*	Root	Enhance growth and yield N fixation Stress tolerance	Lin et al. (2015) Zhang et al. (2017) Mowafy et al. (2021)
Penicillium spp.	*Triticum aestivum* and *Capsicum annum*	Root	Resistance against abiotic stresses Production of IAA Nutrient mineralization	Ikram et al. (2018) Oses-pedraza et al. (2020)
Pseudomonas spp.	*Pisum sativum*, *Oryza sativa*, *Achyranthes aspera*, *Zea mays* *Brassica napus*, and *Cicer arietinum*	Leaf, root, and seed	Mineral solubilization N fixation Defense against phytopathogens Stress tolerance	Otieno et al. (2015) Devi et al. (2017) Lally et al. (2017) Pham et al. (2017) Sandhya et al. (2017) Mukherjee et al. (2020)
Streptomyces spp.	*Solanum lycopersicum*, *Glycine max*, and Sorghum	Root and stem	Plant growth promotion Biocontrol Production of active secondary metabolites	Goudjal et al. (2016) Patel et al. (2018) Liu et al. (2019)

soil nutrients making them readily available to plants (Behie and Bidochaka 2013; White et al. 2019). In a fashion similar to human gut microbes, the endophytes improve plant health by protecting against phytopathogens. They have the ability to induce systemic resistance and upregulate defense gene expression in the host plant and suppress the growth and fitness of phytopathogens (Hardoim et al. 2015; Irizarry and White 2017; White et al. 2018). Endophytes start modulation of defense gene in host plant right from the seedling stage to maturation (Ongena and Jacques 2008; Gond et al. 2015a, b). Systemic resistance is induced against a broad spectrum of phytopathogen through jasmonic acid, salicylic acid, and ethylene pathways and the production of pathogenesis-related proteins (Bastias et al. 2017). The growth suppression of phytopathogen by endophytes is through the production of antimicrobial compounds such as pyrrolnitrin, pyoleutirin, 2, 4-diacetylphloroglucinol, phenazine-1-carboxylic acid, and hydrogen cyanide (Mousa et al. 2016; Bastias et al. 2017). The different underlying mechanisms of plant endophytes in the improvement of plant and soil health are represented in Fig. 1.

Soil is a mystic resource on this planet harboring both biological and chemical entities. Agricultural soil in particular linked to human health, production economics, water and soil quality, and food safety and security either directly and/or indirectly (Karlen et al. 2019). Healthy soils are the backbone of agricultural productivity as it provides support to healthy plant growth and development. The quantity and quality of about 95% of our food depend on soil functional properties (Kemper and Lal 2017; Brevik et al. 2018, 2020) which indirectly dictates human and animal nourishment as nutrient deficiency of food grains cause many human diseases. It has been known through various studies that the application of organic fertilizers improves soil quality and health by stimulating microbial population and diversity in the soil (Jannoura et al. 2014; Verma et al. 2014; Mukherjee et al. 2019). However, both organic and inorganic fertilizers are applied in common agricultural practices for better

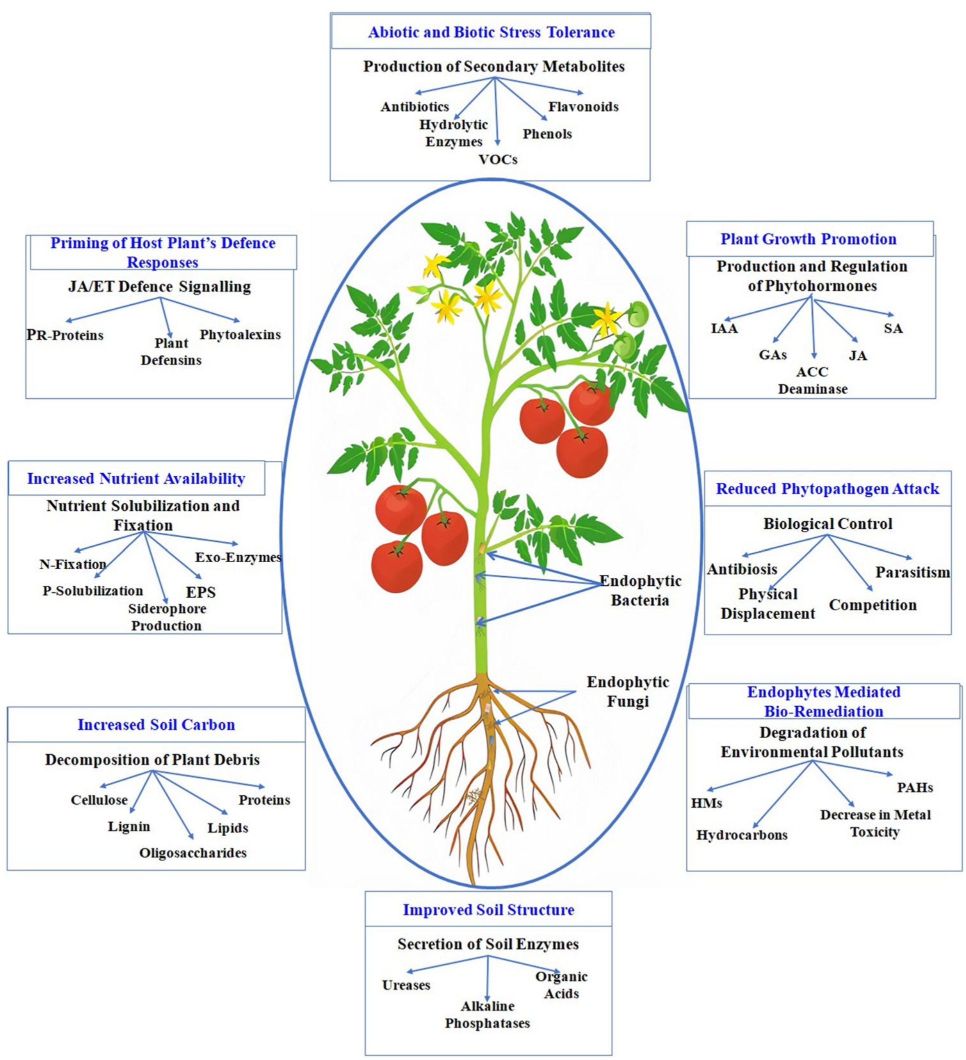

Fig. 1 Diagrammatic representation of plant endophytes' mechanisms involved in improvement of plant and soil health

crop production (Naab et al. 2017; Mukherjee et al. 2021), in which the proportion of the latter is quite higher. Inorganic fertilizers can be replaced with the use of endophytes as a sustainable approach in modern agricultural practices (Kumar et al. 2020). Endophytes possess the ability to solubilize micro and macronutrients in soil without hampering the natural properties and microbial community of the soil. They also play an important role in soil mineral cycling and the removal of pollutants from soil (He et al. 2020; Liu et al. 2020), due to which they are deemed to be a better alternative. Hence, our main aim of this review is to present the functional properties of endophytes keeping in view the current demand of their application as bioinoculants for improvement of soil health, plant productivity, and protection against phytopathogens under a sustainable approach.

Screening and molecular characterization of endophytic microbes from plant material

Before going for screening and molecular characterization, one should have to attain a pure culture of endophytic microbe. Endophytes can be isolated by different plating methods in respective culture media from different plant parts (root, shoot, leaf, flower, fruits, and seeds) after sterilization of that particular part with 1% sodium hypochlorite solution for 1 min and 70% ethanol followed by washing two to three times with sterilized distilled water (Mukherjee et al. 2020). Pure culture of the respective isolated endophyte can be then done by single spore culture for fungi and single colony culture for bacteria. DNA should be extracted from this pure culture of isolated bacteria and fungi as the next step for molecular characterization using polymerase chain reaction (PCR) amplification of conserved regions namely: 16S rRNA or 18S rRNA for bacterial endophytes and ITS for fungal endophytes followed by sequencing. The sequence obtained must be aligned using the Basic Local Alignment Search Tool (BLAST) in National Center for Biotechnology Information (NCBI) for obtaining a similarity index to match the microbial organism from the database. For screening of biochemical and plant growth promotion properties, pure culture of microbes should be grown in respective liquid media. A diagrammatic representation of isolation, identification, and characterization of endophytes from different plant parts is given in Fig. 2. These screening results should be used for the development of potential single inoculants

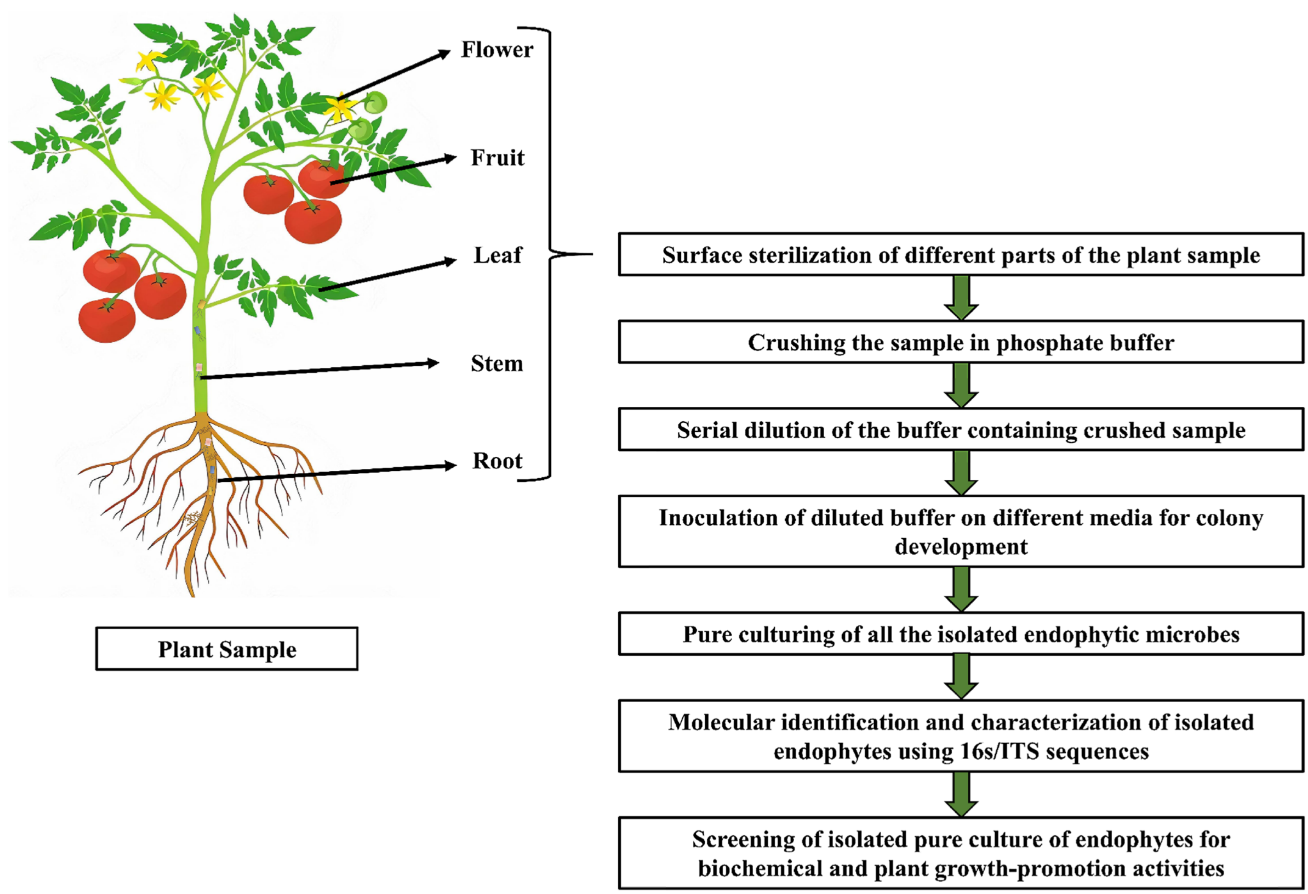

Fig. 2 Flowchart of isolation, identification, and characterization of plant endophytes from different parts

and consortiums. The endophytic microbial consortium is, however, more effective plant-growth-promoting and biocontrol agent for enabling better plant growth under abiotic and biotic stresses (Singh et al. 2018).

Endophytes for agricultural soil health

Almost all the plants have their world of endophytic microbes which are non-aggressive and ubiquitous (Schulz and Boyle 2006). Once colonized, endophytes stimulate the growth and physiology of host plants and properties of soil through various direct and indirect mechanisms (Singh et al. 2018; Mukherjee et al. 2020; Chouhan et al. 2021). Nitrogen fixation, phosphate solubilization, siderophore production, exopolysaccharide (EPS) secretion, exoenzymes' production, and biocontrol activities are some of the functional properties of endophytes (Jasim et al. 2014; Mukherjee et al. 2019, 2020) that aid restoration of soil health and fertility. The exoenzymes produced by endophytes specifically have the capacity of solubilizing essential plant nutrients from their insoluble for to soluble ones (Puri et al. 2020). These exoenzymes also constitute organic acids which lead to lowering of soil pH (Verma et al. 2017). The changes in pH additionally inhibit the activities of phytopathogenic microbes and also alter the growth of some invasive plants thereby increasing nutrient availability (Shahrtash and Brown 2021). Many endophytes synthesize soil invertase, urease, and soil alkaline phosphatases which directly modulate soil organic carbon (SOC), soil nitrogen, and microbial biomass (Hou et al. 2020). Endophytes also degrade plant debris present in soil having macromolecules like lignin, pectin, oligosaccharides, cellulose, hemicellulose, lipids, and proteins with the help of exoenzymes (Wang and Dai 2011; Uzma et al. 2016) into their simpler forms. This adds to the nutrient status of soil, enhancing soil quality, nutrient cycling, and soil micro-environment. Puente et al. (2009) reported in a study on endophytic bacteria associated with *Pachycereus pringlei* produces organic acids which help in weathering and transformation of minerals under in vitro conditions.

Plant–microbe interaction is a complex system that involves a vast array of microbes, the plant, and the soil. The interaction not only affects the physiology of plant but also regulate soil flora and fauna, soil microbial respiration rate, soil health, and nutrient cycling (Chaparro et al. 2012). Plants communicate with the soil microbial community through chemical signals constituting proteins, fatty acids, flavonoids, sugars, aliphatic acids, and amino acids which create a unique environment for the survival of soil microbes. These secreted chemical signals establish interaction with endophytes and neighboring plants leading to the formation of soil aggregates which improves soil porosity by designing the soil structure (Miller and Jastrow 2000). A wide range of endophytic bacteria and fungi viz. *Bacillus*, *Arthrobacter*, *Enterobacter*, *Clostridium*, *Pseudomonas*, *Microbacterium*, *Mucor*, *Microsphaeropsis*, *Phoma*, *Alternaria*, *Steganosporium*, and *Aspergillus* have been reported resistant to metals (Guo et al. 2010; Li et al. 2012). These endophytes can thus be helpful in removing heavy metal toxicity from the soil. Moreover, different studies have suggested that endophytes play a crucial role in the phytoremediation of organic contaminants such as hydrocarbons as well. Most of the soil contaminants are toxic for plants and cannot be degraded by them alone. This problem can be alleviated through plant–endophytes interaction (Li et al. 2012). Endophytes reduce phytotoxicity due to soil contaminants by increasing their immobilization, chelation, and degradation. For this, they secrete organic acids of low molecular weight, siderophores, and enzymes. Siderophores can bind efficiently with iron (Fe), zinc (Zn), cadmium (Cd), gallium (Ga), aluminum (Al), and lead (Pb) to form a stable complex which increases their soluble concentration (Rajkumar et al. 2010).

Many of the endophytic bacteria and fungi are antagonistic and are drawing special attention as an alternative for the management of soil-borne diseases with minimal environmental impact and soil pollution. These antagonistic endophytes control the population of soil-borne phytopathogens through different mechanisms namely: parasitism, competition, production of lytic enzymes, and antibiosis (De Silva et al. 2019). EPS produced by endophytes plays important role in plant–endophyte interactions and also exhibit many biological functions. EPS of endophytic origin have antioxidative, antiallergic, and prebiotic properties (Liu et al. 2017) along with metal complexation ability (Liu et al. 2021). Thus, EPS can be helpful in regulating the population of soil phytopathogens and reducing the bioaccessibility of heavy metals. From the above-presented statements, it can be very well concluded that augmentation of soil with specific endophyte or endophytic consortium can be significantly supportive in restoring soil health. A list of identified endophytes that have studied in the management of soil health, their host plant(s), and features of interest is provided in Table 2.

Endophytes for sustainable plant protection and its stress management

Many appreciative efforts have been made to study the role of endophytes in a plant's defense system against different stresses. Application of different endophytes can assist in the adjustment of plant's tolerance to various abiotic and biotic stresses (Wani et al. 2015). Biofertilization, biocontrol, and phytostimulation are the three mechanisms through which endophytes help plants in combating unfavorable conditions.

Table 2 Endophytes in improvement of soil health

Endophytes	Host plant	Features of interest in soil health management	Reference(s)
Neotyphodium coenophialum	*Festuca arundinacea*	Enhancement of soil carbon and nitrogen	Franzluebbers et al. (1999)
Neotyphodium occultans	*Lolium multiflorum*	Modulation of soil catabolic activity Enhancement of soil microbial (fungal) population and their activities	Casas et al. (2011)
Bacillus spp.	*Solanum nigrum*	Hyperaccumulation of metal (Cu, Cd, and Cr) in soil	Guo et al. (2010)
Burkholderia cepacia	*Zea mays*	Phytoremediation of organic contaminants (toluene and phenols)	Wang et al. (2010)
Phomopsis liquidambari	*Bischofia polycarpam*	Promotion of litter mass degradation Alleviation of soil nitrogen concentration	Chen et al. (2013)
Phialocephala fortinii	*Asparagus officinalis* *Chamaecyparis obtusa* and *Rubus* spp.	Degradation of organic compounds Improvement of nutrient cycling in the soil	Narisawa (2017) Surono and Narisawa (2017)
Enterobacter spp., *Microbacterium arborescens*, and *Pantoea stewartii*	*Leptochloa fusca and Brachiaria mutica*	Enhancement in the uptake, translocation, accumulation, and phytostabilization of heavy metal (Cr) in contaminated soil	Ahsan et al. (2018)
Phomopsis liquidambari	*Oryza sativa*	Increment in decomposition of straw and total soil nitrogen	Sun et al. (2019)
Epichloë gansuensis	*Achnatherum inebrians*	Improvement of soil fertility and soil nutrients availability by inducing soil enzyme activity such as invertase, alkaline phosphatase and urease	Hou et al. (2020)
Serratia spp., and *Arthrobacter* spp.	*Brassica juncea*	Improvement in organic matter content of soil Phytoremediation of vanadium contaminated soil Improvement of plant growth and soil health	Wang et al. (2020a)
Phomopsis liquidambaris	*Acharis hypogaea*	Alleviation of soil health through improved root exudation Improvement of soil carbon metabolism Increment of rhizospheric bacterial community	Xie et al. (2020)
Acrocalymma vagum and *Paraboeremia putaminum*	*Glycyrrhiza uralensis*	Ensure plant growth under drought stress conditions by structuring soil microbiome and maintaining soil water content, soil organic matter, and nutrient availability	He et al. (2021)

It is a well established fact that plants regulate their defense system through phytohormonal signaling and its crosstalk. The phytohormones induce innate immunity in a plant for protection against different phytopathogens. As per Waqas et al. (2015), endophytic fungus *Penicillium citrinum* provided protection to *Sclerotium rolfsii* (phytopathogen) by increasing the level of jasmonic acid (JA) and salicylic acid (SA)-mediated hormone signaling. In addition, they also reported that another endophytic species of the same fungus, *P. formosus*, increased plant growth by lowering the level of phytohormones associated with stress signaling namely abscisic acid (ABA) and JA during heat stress. They also regulated other phytohormones levels and produced different secondary metabolites for alleviating the same stress. Similarly in another study, endophytic *Aspergillus niger* increased the level of gibberellins and auxin to promote plant growth under stress (Lubna et al. 2018). During stress conditions, the level of ethylene increases in plants causing inhibition in root length, root hair, and lateral root development. During such instances, endophytes produce an enzyme known as 1-aminocyclopropane-1-carboxylate (ACC) deaminase which functions in lowering ethylene levels and promoting plant growth (Santoyo et al. 2016). Sun et al. (2009), compared ACC deaminase production capacity in mutated and wild type endophytic *Burkholderia phytofirmans* and their impact in canola. They observed that the mutated strain was unable to promote the growth of canola seedlings while the wild type strain showed remarkable growth promotion. The result ascertains that endophytes affect the growth and development of plants through ACC deaminase enzyme production.

Following a long course of coexistence, endophytes have developed the ability to mimic host plant metabolism and produce effective bioactive compounds similar to their host in vitro as a result of close contact and horizontal gene transfer (Wang et al. 2010). Endophytes produce a vast array of secondary metabolites constituting antibiotics, hydrolytic enzymes, toxins, and volatile organic compounds (VOCs) that play a significant role in alleviating a plant's defense system for mitigation of stresses (Afzal et al. 2019). Hence, endophytes are also considered as an emerging source of novel bioactive compounds (Singh et al. 2017a). Endophytic *Streptomyces* spp. provides resistance in chickpea by enhancing the level of defense-related compounds such as phenols and flavonoids (Singh and Gaur 2017). Kang et al. (2018) observed an increased level of nematicidal compounds such as 4-vinyl phenol, L-methionine, palmitic acid, and piperine in plants colonized by *Bacillus simplex*, inhibited soybean cyst nematode. Co-inoculation of endophytic fungi *Beauveria bassiana* and mycorrhizae increases terpenoids levels in tomato plant leaves, reducing the foliar feeding by herbivores (Shrivastava et al. 2015). Endophytes also activate the defense pathway by modulating systemic acquired resistance in the plant. Endophyte actinobacteria isolated from the wheat plant induced the genes of SAR such as *PR-1* and *PR-5* genes and *PDF-1.2* and *Hel* genes to regulate JA and ethylene pathway and confers resistance against several fungal phytopathogens in *A. thaliana* (Conn et al. 2008). A similar study was also reported by Gond et al. (2015a), that endophytic bacteria, *Bacillus amyloliquefaciens* activate JA-dependent defense pathway by increasing the expression of *PR-1* and *PR-10* genes against the attack of fungal pathogens and enhanced the growth and development of maize plant. Endophytes also protect plants from oxidation through excessive pesticidal application by producing antioxidants (Jan et al. 2020).

Quorum sensing (QS) is responsible for communication between host and pathogenic microbes as well as other bacterial symbionts via signaling molecules like N-acyl-homoserine lactone (AHL). Quorum sensing is a density-dependent gene expression in bacteria. As the density increases, the signaling also increases and all cells act somewhat like multicellular organisms (Rosenblueth and Martínez-Romero 2006). The regulation of gene expression in phytopathogenic bacteria needs to produce antibiotics, virulence factors, and exoenzymes to degrade cell walls and to infect plants (Von Bodman et al. 2003). Plant under stress conditions produce signal molecules or mimic the bacterial QS to manipulate the QS-regulated behavior of phytopathogenic bacteria (Bauer and Mathesius 2004). Endophytic bacteria isolated from *Cannabis sativa* were investigated to disrupt cell-to-cell quorum sensing signals in *Chromobacterium violaceum* and were proved to act as biocontrol agents for bacterial phytopathogens (Kusari et al. 2014). In the same way, endophytic isolates of phylum *Actinobacteria* isolated from *Phaseolus vulgaris* provide resistance from phytopathogenic Gram-positive bacteria disruption of QS (Lopes et al. 2015). A detailed list of endophytes that have been studied in plant protection and stress management and their respective features of interest is provided in Table 3.

Endophytes for sustainable management of environmental pollution

Detoxification of heavy metals (HMs)

Rapid industrialization and urbanization without proper planning is adversely affecting the environment through contamination or pollution. One such pollution is the increasing deposition of HMs and pesticides in soil which is has a direct impact on crop production and human health. HMs and their isotopes are categorized under elemental pollutants while residual pesticides are categorized under organic pollutants. As per WHO (1996), the maximum permissible limit of HMs is (0.8, 50, 36, 100, 85, and 35 mg kg^{-1}) in soils and (0.02, 0.6, 1, 1.3, 2, and 10 mg kg^{-1}) in plant with respect of Cd, Zn, Cu, Cr, Pb, and Ni. However, the amount of these HMs is ever-increasing in the soil and the plants leading to several fatal human diseases. Endophytes perform the remediation process more effectively than rhizospheric microbes because of their close contact with host plants, since plants growing in HM contaminated soil naturally employ endophytes with HM-degrading genes. Siciliano et al. (2001) support this fact as they reported that endophytes perform degradation of nitroaromatic compounds more effectively than the rhizospheric microbial community. This was due to the presence of nitro-aromatics degradation genes being prevalent in endophytes than other soil microbes. Microbes and/or genetically engineered microbes have the capacity of reducing soil contamination (Pilon Smits et al. 1999). Research studies have reported that endophytes such as *A. calcoaceticus*, *B. cereus*, *P. putida*, *Trichoderma* spp., *Cladosporium* spp., *P. polymyxa*, *P. fluorescens*, *Paecilomyces* spp., *B. subtilis*, *Rhizobium* spp., *E. pisciphila*, *R. rubrum*, *P. agglomerans*, *Aspergillus* spp., *Mucor* spp.,

Table 3 Endophytes in plant health and defense

Endophytes	Host plant	Features of interest	Reference(s)
Neotyphodium coenophialum	*Festuca arundinacea*	Alteration of root activity and mineral transport from root to shoot under phosphate limited condition	Malinowski et al. (2000)
Penicillium verruculosum RS7PF	*Potentilla fulgens L.*	Promotion of seed germination in green-gram and chickpea by IAA modulation	Bhagobaty et al. (2010)
Acinetobacter johnsonii	*Beta vulgaris*	Production of IAA for plant growth and development Production of phosphatase enzyme for enhanced nutrient absorption by host plant	Shi et al. (2011)
Bacillus weihenstephanensis, *Serratia marcescens*, and *Cornyebacterium minutissimum*	*Solanum lycopersicum* and *Capsicum annum*	Antagonism against wilt-causing bacteria *Ralstonia solanacearum* Production of secondary metabolites for increased plant growth	Amaresan et al. (2012)
Sporosarcina aquimarina	*Avicennia marina*	Promotion of plants growth by IAA production Enhancement of nutrient availability by production of siderophore and phosphatase	Janarthine and Eganathan (2012)
Piriformospora indica	*Hordeum vulgare L.*	Increased grain yield and shoot biomass under low temperature condition	Murphy et al. (2014)
Trichoderma brevicompactum	*Allium sativum*	Production of bioactive compound (trichodermin) Antifungal activity against fungal phytopathogens	Shentu et al. (2014)
Bacillus spp.	*Zea mays*	Inhibition of phytopathogens through antifungal lipopeptide Regulation of genes associated to production of pathogenesis-related (PR) proteins	Gond et al. (2015b)
Pantoea spp. and *Paenibacillus* spp.	*Triticum aestivum*	Biocontrol activity against *F. graminearum* by biofilm formation Modulation of plant growth through production of IAA, siderophore, and phosphatase	Herrera et al. (2016)
Pseudomonas aeruginosa, *Bacillus* spp., *Enterobacter* spp., *Shinella* spp.	*Saccharum officinarum*	Promotion of plant growth by IAA production, phosphorous solubilization, siderophore production, and biocontrol activity	Taulé et al. (2016) Pirhadi et al. (2018)
Bacillus subtilis	*Cicer arietinum L.*	Improvement in plant growth under salinity condition Protection against root rot causing fungal phytopathogen (*F. solani*)	Egamberdieva et al. (2017)
Stenotrophomonas maltophilia, *Prototheora geniculata*, *Bacillus amyloliquefaciens*, *Stenotrophomonas maltophilia*, and *Bacillus licheniformis*	*Solanum lycopersicum*	Production of IAA and phosphatase for increased plant growth and development	Abdallah et al. (2018)
Hypocrea lixii F3ST1	*Allium cepa*	Boosting of plant immunity and reducing damage caused by *Iris yellow spot virus* and its vector *Thrips tabaci*	Muvea et al. (2018)
Curtobacterium spp., *Methylobacterium* spp., *Microbacterium* spp., and *Bacillus amyloliquefaciens*	*Urochloa ramosa L.*	Inhibition of fungal phytopathogens by lipopeptide Promotion of seedling growth Regulation of expression of defense-related genes	Verma (2018)
Acinetobacter calcoaceticus, *Enterobacter cloacae, and Bacillus cereus*	*Glycine max*	Promotion of plant growth through IAA and siderophore production Fixation of atmospheric nitrogen Phosphate solubilization	Zhao et al. (2018)

Table 3 (continued)

Endophytes	Host plant	Features of interest	Reference(s)
Acinetobacter baumannii	*Capsicum annum*	Induction of secondary metabolites production having antioxidant property	Monowar et al. (2019)
Pseudomonas aeruginosa	*Cucumis sativus*	Suppression of damping off phytopathogen (*Pythium aphanidermatum*) Plant growth promotion activity	Priyanka et al. (2019)
Bacillus subtilis, *Bacillus pumilus*, and *Klebsiella pneumoniae*	*Oryzae sativa*	Antagonism against fungal phytopathogens	Kumar et al. (2020)
Enterobacter cloacae, *Enterobacter* spp., *Bacillus subtilis*, *Pseudomonas aeruginosa*, *Bacillus subtilis*, *Enterobacter* spp., *Enterobacter hormaechei*, *Staphylococcus equorum*, *Pantoea* spp., and *Mixta intestinalis*	*Cicer arietinum L.*	Production of plant growth-promoting components (IAA, mineral solubilization, NH3 production, siderophore production, protease activity) Antagonism against phytopathogens	Mukherjee et al. (2020)

Microsphaeropsis spp., *Alternaria* spp., *Phoma* spp., *Peyronellaea* spp., *Steganosporium* spp., and *Azotobacter* spp. have the ability to produce different extracellular oxidase enzymes such as manganese peroxidase, laccase, and lithium peroxidase that helps to degrade various phenolics substance and it directly linked to the remediation process (Ongena and Jacques 2008; Nandy et al. 2020). The removal of HMs is mostly done through absorption, transformation, phytoextraction, hyperaccumulation, and translocation. The organic pollutants are mostly removed by the process of mineralization, degradation, and detoxification (Meagher 2000). A list of endophytes studied for HMs detoxification and their respective host(s) is provided in Table 4**.**

Detoxification of pesticides

Injudicious use of fertilizers and pesticides has caused many physical and physiological discomforts in plants as well as in animals. Discolouration, necrosis, and deformation are the major physical impact of excessive pesticides on plants (Geetha 2019) which have significant effects on physiological and biochemical processes (Chaudhary et al. 2020; Giménez-Moolhuyzen et al. 2020). The pesticides accumulate in soil mostly through the process of leaching which leads to deterioration of soil fertility and soil microbial community. Endophytic microbes play an important role to minimize and degrade inside the plant body. A study on bark, xylem tissue, and leaves of tea plants showed that there are no significant changes in community structure and number of endophytic colonies in the phyllosphere after pesticide treatment (Win et al. 2021). Seed treatment with pesticides resulted in alteration of rhizosphere fungal and bacterial community in maize plant but leaf fungal endophytic colonies remain unaffected (Nettles et al. 2016). Another study on the community-level effect of different concentrations of pesticide N-(3,5-dichlorophenyl) succinimide on *Nicotiana tabacum* phyllosphere showed that there was no significant impact on alpha and beta diversity of beneficial endophytic bacterial community, viz., *Alphaproteobacteria*, *Gammaproteobacteria*, *Sphingomonas*, and *Pseudomonas* (Chen et al. 2021). All these reports suggest that leaf endophytes are more resistant to pesticides and are well-suited candidates for degradation agrochemicals.

There are a number of studies on endophytes revealing that these microbes establish a symbiotic relationship with their host and secrete enzymes to metabolize and detoxify various pesticides. For example, an endophytic *Pseudomonas* spp. possesses gene encoding organophosphate hydrolase enzyme which is responsible for degradation of 97% of organophosphate pesticide such as chlorpyrifos (Barman et al. 2014a, b). A group of endophytes having a symbiotic relationship with *P. fugax* (one of the major winter weeds in the oilseed rape field in China) helped

Table 4 Endophytes in bioremediation of heavy metals (HMs)

Host plant	Microbes	HMs bioremediated	Reference(s)
Salix variegate Franch	*Chromosporium* spp., *Fusarium* spp., and *Gonatobotrysi* spp.	Cd	An et al. (2015)
Solanum lycopersicum L.	*P. janthinellum* LK5	Al	Khan et al. (2015a)
Populus spp.	*Serenpidita vermifera* P04	Cd, Zn, Pb, and Cu	Lacercat-Didier et al. (2016)
Dysphania ambrosioides L.	*Plectosphaerella* spp., *Cladosporium* spp., and *Verticillium* spp.	Pb and Zn	Li et al. (2016)
	Penicillium spp. FT2G59 and *P. columnaris* FT2G7		
Imperata cylindrica L. and *Bothriochloa ischaemum* L.	*Leotiomycetes* and *Pezizomycetes*	Pb and Cd	Tong et al. (2017)
Solanum nigrum L.	*Colletotrichum* spp., *Alternaria* spp., and *Fusarium* spp.	Cd	Khan et al. 2017a, b
	F. tricinctum, and *A. alternata*	Cd	
Brassica napus L.	*Fusarium* spp., *Penicillium* spp., and *Alternaria* spp.	Cd and Pb	Shi et al. (2017)
Zea mays	*Westerdykella* spp.	Hg	Pietro-Souza et al. (2020)

to promote resistance from quizalofop-p-ethyl, an acetyl CoA carboxylase-inhibiting herbicide (Liu et al. 2020). In another study, it was shown that endophytic bacteria *Pantoea ananatis* Sd-1 degrade carbaryl by secreting hydrolytic enzyme carbohydrate esterase (Yao et al. 2020). This enzyme esterase is a major enzyme in hydrolysis of other pesticidal compounds as well namely: organochlorines, pyrethroids, and carbamates (Sharma et al. 2018). Since endophytes exhibit significant growth and multiplication rate within plant tissue, they can be used as a potential tool for the bioremediation of environmental contaminants such as xenobiotics and pesticides (Gupta et al. 2020; Win et al. 2021). Moreover, plant–endophyte interaction not only enhances phytoextraction or phytoremediation of environmental pollutants but they perform an excellent job for plant growth promotion even under biotic and abiotic stress conditions (Waller et al. 2005; Becerra-Castro et al. 2013). A detailed list of endophytes studied in the bioremediation of pesticides and their respective host(s) and properties is provided in Table 5.

Endophytes for human health

Endophytes are a very precious source of secondary metabolites of which many are antioxidant, antimicrobial, and anticancerous. They are just like a treasure house of bioactive molecules that needs to be explored. Many of these bioactive molecules can be used for the management of human diseases either directly or after transformation (Devi and Prabakaran 2014; Gouda et al. 2016). The trait of producing bioactive molecules have been incorporated in them through the transfer of genetic information from higher plants during evolution as explained earlier. The classical example of this fact is taxol-producing endophyte *Metarhizium anisopliae* isolated from the bark of *Taxus* spp., which

Table 5 Endophytes in bioremediation of pesticides

Endophytes	Host plant	Pesticide bioremediated	Properties	Reference(s)
Sphingomonas spp.	*Cytisus striatus*	Hexachlorocyclohexane	Phytoremediation of HCH Enhancement of plant growth	Becerra-Castro et al. (2013)
Pseudomonas spp.	Balloon flower	Chlorpyrifos	Synthesis of organophosphate hydrolase enzyme	Barman et al. (2014a, b)
	Polypogon fugax	Quizalofop-p-ethyl	Degradation of acetyl-CoA carboxylase-inhibiting herbicide	Liu et al. (2020)
Rhizobium leguminosarum	*Pisum sativum*	Kitazin	Production of plant growth-promoting bioactive compounds to enhance plant growth under pesticide stress condition	Shahid et al. (2018)
Alphaproteobacteria, *Gammaproteobacteria*, *Sphingomonas*, and *Pseudomonas* spp.	*Nicotiana tabacum*	N-(3,5-Dichlorophenyl) succinimide	Negative responders of broad-spectrum pesticide treatments	Chen et al. (2020)
Pantoea ananatis	*Oryza sativa*	Carbaryl	Secretion of carbohydrate esterase to hydrolyze carbaryl	Yao et al. (2020)

is a very important life-saving anticancer agent (Zhang et al. 2009). Going by the classical example, endophytes associated with medicinal plants can be a very eminent source of bioactive molecules and can be utilized for producing natural drugs (Singh and Dubey 2015). Several bioactive compounds constituting vinblastine, paclitaxel, camptothecin, hypericin, etc. are already produced at a commercial scale from the endophytes isolated from their respective plants and are of pharmaceutical importance (Nicoletti and Fiorentino 2015). Endophytes are also gaining the limelight for human health because many studies suggest that novel bioactive molecules produced by them are important for combating antibiotic resistance by human pathogenic microbes (Fadiji and Babalola 2020).

Endophytes are also a good source of antioxidant compounds that are now deemed to be a potential alternative for the prevention and treatment of human diseases linked with reactive oxygen species (ROS). Thus, diseases such as diabetes, hypertension, cancer, Alzheimer, ischemia, and Parkinson can be treated with the help of antioxidants derived from endophytes (Mishra et al. 2014). Many prevalent human deficiency diseases can be overcome by taking that particular nutrient through diet. Plants form a major part of the diet and their biofortification with nutrients can help in providing the deficient nutrient to the human population naturally as a replacement of chemical supplements. Endophytes can be an integral part of this concept as well, since, many of the reports have proved that endophytic microbes associated to crop also helps in biofortification (Singh et al. 2017b; Trivedi et al. 2020a). The underlying mechanisms in crop biofortification by endophytes are improvement of nutrient absorption, direct synthesis and release of micronutrients, and induction of micronutrient synthesis in plants (Ku et al. 2019). The list of potential use of endophytes for human health also continues to grow with the advancements in science.

Conclusions

Excessive use of synthetic fertilizers and pesticides and changing environment has led to unfertile agricultural lands causing a major problem in feeding the growing population. The inevitable concern arising due to this is enhancing the crop productivity under shrinking land and minimization of chemical inputs. Hence, we have provided some critical insights about an emerging alternative of utilizing the plant endophytic microbiome for combating the concern. Endophytes are significantly influential and are providing us with the opportunity to overcome the global problem of agricultural productivity. Augmentation of indigenous and effective beneficial endophytes has the potential to bring consequential positive impacts on the current agriculture scenario by improving soil and yield quality. Endophytes have more potential than other rhizosphere microbes as they can be inoculated in the same plant species from which they are isolated and can easily colonize inside the plant body to provide sustainable crop productivity and food security under different environmental stresses. A consortium of endophytic microbes can be more effective as climate-resilient biofertilizers and biocontrol agents. In addition, the consortium can be a powerful approach for boosting plant growth and productivity along with the maintenance of the soil microbial community. The approach is environment friendly, ecologically sound, and socially acceptable. However, the studies on the effects of endophytic microbial consortium are very limited and should be explored further in combination with plant-growth-promoting microbes (PGPMs) for boosting the productivity in agricultural crops and improvement of soil health under different environmental conditions.

Acknowledgements The authors want to thank the Head of the Department, Institute of Environment and Sustainable Development, Banaras Hindu University. The authors especially are grateful to Science and Engineering Research Board (Ref. File No. EEQ/2017/000775) and the Government of India, for financial assistance to research endophytic microbes of chickpea. The authors are also thankful to IoE (6031) BHU, Varanasi for providing funds for research related to endophytes. MMR is thankful to University Grants Commission for providing financial assistance through NF-OBC (NFO-2018-19-OBC-BIH-68765).

Author contributions AM contributed to the preparation of the manuscript, its formatting and collection of data for writing and preparing figures. MMR, GKC and JKV contributed to creating figures and editing the manuscript. SB, GKC and SY contributed to the collection of data for preparing the tables. JPV contributed to the design, idea, final editing, and revision of the whole manuscript.

Declarations

Conflict of interest On behalf of all the authors, the corresponding author states that there is no conflict of interest.

Ethical approval This article does not contain any studies with animals performed by any of the authors.

References

Abdallah RA, Jabnoun-Khiareddine H, Nefzi A, Daami-Remadi M (2018) Evaluation of the growth-promoting potential of endophytic bacteria recovered from healthy tomato plants. J Hortic for 5:2. https://doi.org/10.4172/2376-0354.1000234

Afzal I, Shinwari ZK, Sikandar S, Shahzad S (2019) Plant beneficial endophytic bacteria: mechanisms, diversity, host range and genetic determinants. Microbiol Res 221:36–49. https://doi.org/10.1016/j.micres.2019.02.001

Ahsan MT, Saeed A, Mustafa T, Afzal M (2018) Augmentation with potential endophytes enhances phytostabilization of Cr in contaminated soil. Environ Sci Pollut Res 25(7):7021–7032. https://doi.org/10.1007/s11356-017-0987-x

Akinsanya MA, Goh JK, Lim SP, Ting AS (2015) Diversity, antimicrobial and antioxidant activities of culturable bacterial endophyte communities in *Aloe vera*. FEMS Microbiol Lett 362(23):fnv184. https://doi.org/10.1093/femsle/fnv184

Amaresan N, Jayakumar V, Kumar K, Thajuddin N (2012) Endophytic bacteria from tomato and chilli, their diversity and antagonistic potential against *Ralstonia solanacearum*. Arch Phytopathol 45:344–355. https://doi.org/10.1080/03235408.2011.587273

An H, Liu Y, Zhao X, Huang Q, Yuan S, Yang X, Dong J (2015) Characterization of cadmium-resistant endophytic fungi from *Salix variegata* Franch. in three Gorges Reservoir Region. China Microbiol Res 176:29–37. https://doi.org/10.1016/j.micres.2015.03.013

Barman DN, Haque MA, Islam SMA, Yun HD, Kim MK (2014a) Cloning and expression of *ophB* gene encoding organophosphorus hydrolase from endophytic *Pseudomonas* spp. BF1-3 degrades organophosphorus pesticide chlorpyrifos. Ecotoxicol Environ Saf 108:135–141. https://doi.org/10.1016/j.ecoenv.2014.06.023

Barman DN, Haque MA, Islam SMA, Yun HD, Kim MK (2014b) Cloning and expression of *ophB* gene encoding organophosphorus hydrolase from endophytic *Pseudomonas* sp. BF1-3 degrades organophosphorus pesticide chlorpyrifos. Ecotoxicol Environ Saf 108:135–141. https://doi.org/10.1016/j.ecoenv.2014.06.023

Bastias DA, Martínez-Ghersa MA, Ballaré CL, Gundel PE (2017) Epichloë fungal endophytes and plant defenses: not just alkaloids. Trends Plant Sci 22:939–948. https://doi.org/10.1016/j.tplants.2017.08.005

Bauer WD, Mathesius U (2004) Plant responses to bacterial quorum sensing signals. Curr Opin Plant Biol 7(4):429–433. https://doi.org/10.1016/j.pbi.2004.05.008

Becerra-Castro C, Prieto-Fernández Á, Kidd PS, Weyens N, Rodríguez-Garrido B, Touceda-González M, Acea MJ, Vangronsveld J (2013) Improving performance of *Cytisus striatus* on substrates contaminated with hexachlorocyclohexane (HCH) isomers using bacterial inoculants: developing a phytoremediation strategy. Plant Soil 362(1):247–260. https://doi.org/10.1007/s11104-012-1276-6

Behie SW, Bidochaka MJ (2013) Insects as a nitrogen source for plants. Insects 4:413–424. https://doi.org/10.3390/insects4030413

Bhagobaty RK, Joshi SR, Kumar R (2010) *Penicillium verruculosum* RS7PF: a root fungal endophyte associated with an ethno-medicinal plant of the indigenous tribes of Eastern India. Afr J Microbiol Res 4(9):766–770. https://doi.org/10.5897/AJMR.9000548

Bilal L, Asaf S, Hamayun M, Gul H, Iqbal A, Ullah I, Lee IJ, Hussain A (2018) Plant growth promoting endophytic fungi *Asprgillus fumigatus* TS1 and *Fusarium proliferatum* BRL1 produce gibberellins and regulates plant endogenous hormones. Symbiosis 76(2):117–127. https://doi.org/10.1007/s13199-018-0545-4

Brevik EC, Pereg L, Steffan JJ, Burgess LC (2018) Soil ecosystem services and human health. Curr Opin Environ Sci Health 5:87–92. https://doi.org/10.1016/j.coesh.2018.07.003

Brevik EC, Slaughter L, Singh BR, Steffan JJ, Collier D, Barnhart P, Pereira P (2020) Soil and human health: current status and future needs. Air, Soil Water Res 13:1–23. https://doi.org/10.1177/1178622120934441

Casas C, Omacini M, Montecchia MS, Correa OS (2011) Soil microbial community responses to the fungal endophyte *Neotyphodium* in Italian ryegrass. Plant Soil 340(1):347–355. https://doi.org/10.1007/s11104-010-0607-8

Chaparro JM, Sheflin AM, Manter DK, Vivanco JM (2012) Manipulating the soil microbiome to increase soil health and plant fertility. Biol Fertil Soils 48(5):489–499. https://doi.org/10.1007/s00374-012-0691-4

Chaudhary N, Choudhary KK, Agrawal SB, Agrawal M (2020) Pesticides usage, uptake and mode of action in plants with special emphasis on photosynthetic characteristics. Pesticides in crop production. Physiol Biochem Action. https://doi.org/10.1002/9781119432241.ch9

Chen Y, Ren CG, Yang B, Peng Y, Dai CC (2013) Priming effects of the endophytic fungus *Phomopsis liquidambari* on soil mineral N transformations. Microb Eco 65(1):161–170. https://doi.org/10.1007/s00248-012-0093-z

Chen QL, Ding J, Zhu D, Hu HW, Delgado-Baquerizo M, Ma YB, He JZ, Zhu YG (2020) Rare microbial taxa as the major drivers of ecosystem multifunctionality in long-term fertilized soils. Soil Biol Biochem 141:107686. https://doi.org/10.1016/j.soilbio.2019.107686

Chen X, Wicaksono WA, Berg G, Cernava T (2021) Bacterial communities in the plant phyllosphere harbour distinct responders to a broad-spectrum pesticide. Sci Total Environ 751:141799. https://doi.org/10.1016/j.scitotenv.2020.141799

Chouhan GK, Veram JP, Jaiswal DK, Mukherjee A, Singh S, Pereira APA, Liu H, Abd-Allah EF, Singh BK (2021) Phytomicrobiome for promoting sustainable agriculture and food security: opportunities, challenges, and solutions. Microbiol Res 248:126763. https://doi.org/10.1016/j.micres.2021.126763

Coba de la Peña T, Fedorova E, Pueyo JJ, Lucas MM (2017) The Symbiosome: legume and rhizobia co-evolution toward a nitrogen-fixing organelle? Front Plant Sci 8:2229. https://doi.org/10.3389/fpls.2017.02229

Conn VM, Walker AR, Franco CMM (2008) Endophytic actinobacteria induce defense pathways in Arabidopsis thaliana. Mol Plant Microbe Interact 21(2):208–218. https://doi.org/10.1094/MPMI-21-2-0208

De Silva NI, Brooks S, Lumyong S, Hyde KD (2019) Use of endophytes as biocontrol agents. Fungal Biol Rev 33(2):133–148. https://doi.org/10.1016/j.fbr.2018.10.001

Devi KA, Pandey G, Rawat AK, Sharma GD, Pandey P (2017) The endophytic symbiont-*Pseudomonas aeruginosa* stimulates the antioxidant activity and growth of *Achyranthes aspera* L. Front Microbiol 8:1897. https://doi.org/10.3389/fmicb.2017.01897

Devi NN, Prabakaran JJ (2014) Bioactive metabolites from an endophytic fungus *Penicillium* sp. isolated from Centella asiatica. Curr Res Environ Appl Mycol 4(1):34–43

Egamberdieva D, Wirth SJ, Shurigin VV, Hashem A, Abd-Allah EF (2017) Endophytic bacteria improve plant growth, symbiotic performance of chickpea (*Cicer arietinum* L.) and induce suppression of root rot caused by *Fusarium* solani under salt stress. Front Microbiol 8:1887. https://doi.org/10.3389/fmicb.2017.01887

Fadiji AE, Babalola OO (2020) Elucidating mechanisms of endophytes used in plant protection and other bioactivities with multifunctional prospects. Front Bioeng Biotechnol 8:467. https://doi.org/10.3389/fbioe.2020.00467

Franzluebbers AJ, Nazih N, Stuedemann JA, Fuhrmann JJ, Schomberg HH, Hartel PG (1999) Soil carbon and nitrogen pools under low-and high-endophyte-infected tall fescue. Soil Sci Soc Am J 63(6):1687–1694. https://doi.org/10.2136/sssaj1999.6361687x

Geetha A (2019) Phytotoxicity due to fungicides and herbicides and its impact in crop physiological factors. AkiNik Publications, New Delhi, India

Giménez-Moolhuyzen M, Blom JVD, Lorenzo-Mínguez P, Cabello T, Crisol Martínez E (2020) Photosynthesis inhibiting effects of pesticides on sweet pepper leaves. Insects 11(2):69. https://doi.org/10.3390/insects11020069

Gond SK, Bergen MS, Torres MS, White JF, Kharwar RN (2015b) Effect of bacterial endophyte on expression of defense genes in Indian popcorn against *Fusarium moniliforme*. Symbiosis 66(3):133–140. https://doi.org/10.1007/s13199-015-0348-9

Gond SK, Bergen MS, Torres MS, White JF (2015a) Endophytic *Bacillus* spp. produce antifungal lipopeptides and induce host defence gene expression in maize. Microbiol Res 172:79–87. https://doi.org/10.1016/j.micres.2014.11.004

Gouda S, Das G, Sen SK, Shin HS, Patra JK (2016) Endophytes: a treasure house of bioactive compounds of medicinal importance. Front Microbiol 7:1538. https://doi.org/10.3389/fmicb.2016.01538
Goudjal Y, Zamoum M, Sabaou N, Mathieu F, Zitouni A (2016) Potential of endophytic *Streptomyces* spp. for biocontrol of *Fusarium* root rot disease and growth promotion of tomato seedlings. Biocontrol Sci Technol 26(12):1691–1705. https://doi.org/10.1080/09583157.2016.1234584
Guo H, Luo S, Chen L, Xiao X, Xi Q, Wei W, Zeng G, Liu C, Wan Y, Chen J, He Y (2010) Bioremediation of heavy metals by growing hyperaccumulaor endophytic bacterium *Bacillus* sp. L14. Bioresour Technol 101(22):8599–8605. https://doi.org/10.1016/j.biortech.2010.06.085
Gupta A, Singh SK, Singh VK, Singh MK, Modi A, Zhimo VY, Singh AV, Kumar A (2020) Endophytic microbe approaches in bioremediation of organic pollutants. In: Kumar A, Singh VP (eds) Microbial endophytes. Woodhead Publishing, pp 157–174
Hamayun M, Hussain A, Iqbal A, Khan SA, Lee IJ (2018) Endophytic fungus *Aspergillus japonicus* mediates host plant growth under normal and heat stress conditions. BioMed Res Int 2018:7696831. https://doi.org/10.1155/2018/7696831
Hamayun M, Hussain A, Afzal Khan S, Iqbal A, Lee IJ (2019) *Aspergillus flavus* promoted the growth of soybean and sunflower seedlings at elevated temperature. BioMed Res Int 2019:1295457. https://doi.org/10.1155/2019/1295457
Hamonts K, Trivedi P, Garg A, Janitz C, Grinyer J, Holford P, Botha FC, Anderson IC, Singh BK (2018) Field study reveals core plant microbiota and relative importance of their drivers. Environ Microbiol 20:124–140. https://doi.org/10.1111/1462-2920.14031
Hardoim PR, Van Overbeek LS, Berg G, Pirttilä AM, Compant S, Campisano A, Döring M, Sessitsch A (2015) The hidden world within plants: ecological and evolutionary considerations for defining functioning of microbial endophytes. Microbiol Mol Biol Rev 79:293–320. https://doi.org/10.1128/MMBR.00050-14
Harrison JG, Griffin EA (2020) The diversity and distribution of endophytes across biomes, plant phylogeny, and host tissuesâ how far have we come and where do we go from here? Environ Microbiol 22(6):2107–2123. https://doi.org/10.1111/1462-2920.14968
Hassan SED (2017) Plant growth-promoting activities for bacterial and fungal endophytes isolated from medicinal plant of *Teucrium polium* L. J Adv Res 8(6):687–695. https://doi.org/10.1016/j.jare.2017.09.001
He W, Megharaj M, Wu CY, Subashchandrabose SR, Dai CC (2020) Endophyte-assisted phytoremediation: mechanisms and current application strategies for soil mixed pollutants. Crit Rev Biotechnol 40(1):31–45. https://doi.org/10.1080/07388551.2019.1675582
He C, Zeng Q, Chen Y, Chen C, Wang W, Hou J, Li X (2021) Colonization by dark septate endophytes improves the growth and rhizosphere soil microbiome of licorice plants under different water treatments. Appl Soil Ecol 166:103993. https://doi.org/10.1016/j.apsoil.2021.103993
Herrera SD, Grossi C, Zawoznik M, Groppa MD (2016) Wheat seeds harbour bacterial endophytes with potential as plant growth promoters and biocontrol agents of *Fusarium graminearum*. Microbiol Res 186:37–43. https://doi.org/10.1016/j.micres.2016.03.002
Hou WP, Wang JF, Nan ZB, Christensen MJ, Xia C, Chen T, Zhang ZX, Niu XL (2020) *Epichloë gansuensis* endophyte-infection alters soil enzymes activity and soil nutrients at different growth stages of *Achnatherum inebrians*. Plant Soil 455(1):227–240. https://doi.org/10.1007/s11104-020-04682-2
Ikram M, Ali N, Jan G, Jan FG, Rahman IU, Iqbal A, Hamayun M (2018) IAA producing fungal endophyte Penicillium roqueforti Thom., enhances stress tolerance and nutrients uptake in wheat plants grown on heavy metal contaminated soils. PLoS ONE 13(11):0208150. https://doi.org/10.1371/journal.pone.0208150
Irizarry I, White JF (2017) Application of bacteria from non-cultivated plants to promote growth, alter root architecture and alleviate salt stress of cotton. J Appl Microbiol 122:1110–1120. https://doi.org/10.1111/jam.13414
Jan S, Singh R, Bhardwaj R et al (2020) Plant growth regulators: a sustainable approach to combat pesticide toxicity. 3 Biotech 10:466. https://doi.org/10.1007/s13205-020-02454-4
Janarthine S, Eganathan P (2012) Plant growth promoting of endophytic *Sporosarcina aquimarina* SjAM16103 isolated from the pneumatophores of *Avicennia marina* L. Int J Microbiol. https://doi.org/10.1155/2012/532060
Jannoura R, Joergensen RG, Bruns C (2014) Organic fertilizer effects on growth, crop yield, and soil microbial biomass indices in sole and intercropped peas and oats under organic farming conditions. Eur J Agron 52:259–270. https://doi.org/10.1016/j.eja.2013.09.001
Jasim B, Anisha C, Rohini S, Kurian JM, Jyothis M, Radhakrishnan EK (2014) Phenazine carboxylic acid production and rhizome protective effect of endophytic *Pseudomonas aeruginosa* isolated from Zingiber officinale. J Microbiol Biotechnol 30(5):1649–1654. https://doi.org/10.1007/s11274-013-1582-z
Johnston-Monje D, Lundberg DS, Lazarovits G, Reis VM, Raizada MN (2016) Bacterial populations in juvenile maize rhizospheres originate from both seed and soil. Plant Soil 405:337–355. https://doi.org/10.1007/s11104-016-2826-0
Kang W, Zhu X, Wang Y, Chen L, Duan Y (2018) Transcriptomic and metabolomic analyses reveal that bacteria promote plant defense during infection of soybean cyst nematode in soybean. BMC Plant Biol 18(1):1–14. https://doi.org/10.1186/s12870-018-1302-9
Karlen DL, Veum KS, Sudduth KA, Obrycki JF, Nunes MR (2019) Soil health assessment: past accomplishments, current activities, and future opportunities. Soil Tillage Res 195:104365. https://doi.org/10.1016/j.still.2019.104365
Kawasaki A, Donn S, Ryan PR, Mathesius U, Devilla R, Jones A, Watt M (2016) Microbiome and exudates of the root and rhizosphere of *Brachypodium distachyon*, a model for wheat. PloSOne 11(10):e0164533. https://doi.org/10.1371/journal.pone.0164533
Kemper KJ, Lal R (2017) Pay dirt! human health depends on soil health. Complement Ther Med 32:A1–A2. https://doi.org/10.1016/j.ctim.2017.04.005
Khalaf EM, Raizada MN (2018) Bacterial seed endophytes of domesticated cucurbits antagonize fungal and oomycete pathogens including powdery mildew. Front Microbiol 9:42. https://doi.org/10.3389/fmicb.2018.00042
Khan AL, Waqas M, Hussain J, Al-Harrasi A, Hamayun M, Lee IJ (2015a) Phytohormones enabled endophytic fungal symbiosis improve aluminum phytoextraction in tolerant *Solanum lycopersicum*: An examples of *Penicillium janthinellum* LK5 and comparison with exogenous GA3. J Hazard Mater 295:70–78. https://doi.org/10.1016/j.jhazmat.2015.04.008
Khan AR, Ullah I, Waqas M, Shahzad R, Hong SJ, Park GS, Jung BK, Lee IJ, Shin JH (2015b) Plant growth-promoting potential of endophytic fungi isolated from *Solanum nigrum* leaves. World J Microbiol Biotechnol 31(9):1461–1466. https://doi.org/10.1007/s11274-015-1888-0
Khan AR, Ullah I, Waqas M, Park GS, Khan AL, Hong SJ, Ullah R, Jung BK, Park CE, Ur-Rehman S, Lee IJ (2017a) Host plant growth promotion and cadmium detoxification in *Solanum nigrum*, mediated by endophytic fungi. Ecotox Environ Safe 136:180–188. https://doi.org/10.1016/j.ecoenv.2016.03.014
Khan AR, Waqas M, Ullah I, Khan AL, Khan MA, Lee IJ, Shin JH (2017b) Culturable endophytic fungal diversity in the cadmium hyperaccumulator *Solanum nigrum* L. and their role in

enhancing phytoremediation. Environ Exp Bot 135:126–135. https://doi.org/10.1016/j.envexpbot.2016.03.005
Ku YS, Rehman HM, Lam HM (2019) Possible roles of rhizospheric and endophytic microbes to provide a safe and affordable means of crop biofortification. Agronomy 9(11):764. https://doi.org/10.3390/agronomy9110764
Kumar V, Jain L, Jain SK, Chaturvedi S, Kaushal P (2020) Bacterial endophytes of rice (*Oryza sativa* L.) and their potential for plant growth promotion and antagonistic activities. S Afr J Bot 134:50–63. https://doi.org/10.1016/j.sajb.2020.02.017
Kusari P, Kusari S, Lamshöft M, Sezgin S, Spiteller M, Kayser O (2014) Quorum quenching is an antivirulence strategy employed by endophytic bacteria. Appl Microbiol Biotechnol 98(16):7173–7183. https://doi.org/10.1007/s00253-014-5807-3
Lacercat-Didier L, Berthelot C, Foulon J, Errard A, Martino E, Chalot M, Blaudez D (2016) New mutualistic fungal endophytes isolated from poplar roots display high metal tolerance. Mycorrhiza 26(7):657–671. https://doi.org/10.1007/s00572-016-0699-y
Lally RD, Galbally P, Moreira AS, Spink J, Ryan D, Germaine KJ, Dowling DN (2017) Application of endophytic *Pseudomonas fluorescens* and a bacterial consortium to *Brassica napus* can increase plant height and biomass under greenhouse and field conditions. Front Plant Sci 8:2193. https://doi.org/10.3389/fpls.2017.02193
Li HY, Wei DQ, Shen M, Zhou ZP (2012) Endophytes and their role in phytoremediation. Fungal Divers 54(1):11–18. https://doi.org/10.1007/s13225-012-0165-x
Li Y, Wang Q, Wang L, He LY, Sheng XF (2016) Increased growth and root Cu accumulation of *Sorghum sudanense* by endophytic *Enterobacter* sp. K3–2: implications for *Sorghum sudanense* biomass production and phytostabilization. Ecotox Environ Safe 124:163–168. https://doi.org/10.1016/j.ecoenv.2015.10.012
Lin L, Wei C, Chen M, Wang H, Li Y, Li Y, Yang L, An Q (2015) Complete genome sequence of endophytic nitrogen-fixing *Klebsiella variicola* strain DX120E. Stand Genom Sci 10(1):1–7. https://doi.org/10.1186/s40793-015-0004-2
Liu J, Wang X, Pu H, Liu S, Kan J, Jin C (2017) Recent advances in endophytic exopolysaccharides: production, structural characterization, physiological role and biological activity. Carbohydr Polym 157:1113–1124. https://doi.org/10.1016/j.carbpol.2016.10.084
Liu H, Brettell LE, Qiu Z, Singh BK (2020) Microbiome-mediated stress resistance in plants. Trends Plant Sci. https://doi.org/10.1016/j.tplants.2020.03.014
Liu H, Li J, Carvalhais LC, Percy CD, Verma JP, Schenk PM, Singh BK (2021) Evidence for the plant recruitment of beneficial microbes to suppress soil borne pathogens. New Phytol 229:2873–2885. https://doi.org/10.1111/nph.17057
Liu D, Yan R, Fu Y, Wang X, Zhang J, Xiang W (2019) Antifungal, plant growth-promoting, and genomic properties of an endophytic actinobacterium *Streptomyces* sp. NEAU-S7GS2. Front Microbiol 10:2077. https://doi.org/10.3389/fmicb.2019.02077
Lopes RBM, de Oliveira Costa LE, Vanetti MCD, de Araújo EF, de Queiroz MV (2015) Endophytic bacteria isolated from common bean (*Phaseolus vulgaris*) exhibiting high variability showed antimicrobial activity and quorum sensing inhibition. Curr Microbiol 71(4):509–516. https://doi.org/10.1007/s00284-015-0879-6
Lubna S, Hamayun M, Gul H, Lee IJ, Hussain A (2018) *Aspergillus niger* CSR3 regulates plant endogenous hormones and secondary metabolites by producing gibberellins and indoleacetic acid. J Plant Interact 13(1):100–111. https://doi.org/10.1080/17429145.2018.1436199
Malinowski DP, Alloush GA, Belesky DP (2000) Leaf endophyte *Neotyphodium coenophialum* modifies mineral uptake in tall fescue. Plant Soil 227(1):115–126. https://doi.org/10.1023/A:1026518828237
Meagher RB (2000) Phytoremediation of toxic elemental and organic pollutants. Curr Opin Plant Biol 3(2):153–162. https://doi.org/10.1016/S1369-5266(99)00054-0
Mehmood A, Hussain A, Irshad M, Hamayun M, Iqbal A, Khan N (2019) *In vitro* production of IAA by endophytic fungus *Aspergillus awamori* and its growth promoting activities in *Zea mays*. Symbiosis 77(3):225–235. https://doi.org/10.1007/s13199-018-0583-y
Miller RM, Jastrow JD (2000) Mycorrhizal fungi influence soil structure. In: Kapulnik Y, Douds DD (eds) Arbuscular Mycorrhizas: physiology and function. Springer, Dordrecht
Mishra Y, Singh A, Batra A, Sharma M (2014) Understanding the biodiversity and biological applications of endophytic fungi: A review. J Microb Biochem Technol 8:4. https://doi.org/10.4172/1948-5948.S8-004
Monowar T, Rahman M, Bhore SJ, Raju G, Sathasivam KV (2019) Secondary metabolites profiling of Acinetobacter baumannii associated with chili (*Capsicum annuum* L.) leaves and concentration dependent antioxidant and prooxidant properties. BioMed Res Int 2019:6951927. https://doi.org/10.1155/2019/6951927
Mousa WK, Shearer CR, Limay-Rios V, Ettinger CL, Eisen JA, Raizada MN (2016) Root-hair endophyte stacking in finger millet creates a physicochemical barrier to trap the fungal pathogen *Fusarium graminearum*. Nature Microbiol 1:16167. https://doi.org/10.1038/nmicrobiol.2016.167
Mowafy AM, Fawzy MM, Gebreil A, Elsayed A (2021) Endophytic *Bacillus, Enterobacter*, and *Klebsiella* enhance the growth and yield of maize. Acta Agric Scand B Soil Plant Sci 71(4):1–10. https://doi.org/10.1080/09064710.2021.1880621
Mukherjee A, Gaurav AK, Singh S, Chouhan GK, Kumar A, Das S (2019) Role of potassium (K) solubilising microbes (KSM) in growth and induction of resistance against biotic and abiotic stress in plant: a book review. Climate Change Environ Sustain 7(2):212–214
Mukherjee A, Singh B, Verma JP (2020) Harnessing chickpea (*Cicer arietinum* L.) seed endophytes for enhancing plant growth attributes and bio-controlling against *Fusarium* sp. Microbiol Res. https://doi.org/10.1016/j.micres.2020.126469
Mukherjee A, Chouhan GK, Gaurav AK, Jaiswal DK, Verma JP (2021) Development of indigenous microbial consortium for biocontrol management. In: Verma JP, Macdonald C, Gupta V, Podile A (eds) New and future developments in microbial biotechnology and bioengineering phytomicrobiome for sustainable agriculture. Elsevier, Amsterdam, pp 91–110
Murphy BR, Doohan FM, Hodkinson TR (2014) Yield increase induced by the fungal root endophyte *Piriformospora indica* in barley grown at low temperature is nutrient limited. Symbiosis 62(1):29–39. https://doi.org/10.1007/s13199-014-0268-0
Muvea AM, Subramanian S, Maniania NK, Poehling HM, Ekesi S, Meyhöfer R (2018) Endophytic colonization of onions induces resistance against *Viruliferous thrips* and virus replication. Front Plant Sci 9:1785. https://doi.org/10.3389/fpls.2018.01785
Naab JB, Mahama GY, Yahaya I, Prasad PVV (2017) Conservation agriculture improves soil quality, crop yield, and incomes of smallholder farmers in North Western Ghana. Front Plant Sci 8:996. https://doi.org/10.3389/fpls.2017.00996
Nandy S, Das T, Tudu CK, Pandey DK, Dey A, Ray P (2020) Fungal endophytes: futuristic tool in recent research area of phytoremediation. S Afr J Bot 134:285–295. https://doi.org/10.1016/j.sajb.2020.02.015
Narisawa K (2017) The dark septate endophytic fungus Phialocephala fortinii is a potential decomposer of soil organic compounds and a promoter of *Asparagus officinalis* growth. Fungal Ecol 28:1–10. https://doi.org/10.1016/j.funeco.2017.04.001

Nettles R, Watkins J, Ricks K, Boyer M, Licht M, Atwood LW, Peoples M, Smith RG, Mortensen DA, Koide RT (2016) Influence of pesticide seed treatments on rhizosphere fungal and bacterial communities and leaf fungal endophyte communities in maize and soybean. Appl Soil Ecol 102:61–69. https://doi.org/10.1016/j.apsoil.2016.02.008

Nicoletti R, Fiorentino A (2015) Plant bioactive metabolites and drugs produced by endophytic fungi of *Spermatophyta*. Agriculture 5:918–970. https://doi.org/10.3390/agriculture5040918

Ongena M, Jacques P (2008) *Bacillus lipopeptides*: versatile weapons for plant disease biocontrol. Trends Microbiol 16(3):115–125. https://doi.org/10.1016/j.tim.2007.12.009

Oses-Pedraza R, Torres-Díaz C, Lavín P, Retamales-Molina P, Atala C, Gallardo-Cerda J, Acuña-Rodríguez IS, Molina-Montenegro MA (2020) Root endophytic *Penicillium* promotes growth of Antarctic vascular plants by enhancing nitrogen mineralization. Extremophiles 24(5):721–732. https://doi.org/10.1007/s00792-020-01189-7

Otieno N, Lally RD, Kiwanuka S, Lloyd A, Ryan D, Germaine KJ, Dowling DN (2015) Plant growth promotion induced by phosphate solubilizing endophytic *Pseudomonas* isolates. Front Microbiol 6:745. https://doi.org/10.3389/fmicb.2015.00745

Patel JK, Madaan S, Archana G (2018) Antibiotic producing endophytic *Streptomyces* spp. colonize above-ground plant parts and promote shoot growth in multiple healthy and pathogen-challenged cereal crops. Microbiol Res 215:36–45. https://doi.org/10.1016/j.micres.2018.06.003

Pawlowski K, Demchenko KN (2012) The diversity of actinorhizal symbiosis. Protoplasma 249:967–979. https://doi.org/10.1007/s00709-012-0388-4

Pham VT, Rediers H, Ghequire MG, Nguyen HH, De Mot R, Vanderleyden J, Spaepen S (2017) The plant growth-promoting effect of the nitrogen-fixing endophyte *Pseudomonas stutzeri*A15. Arch Microbiol 199(3):513–517. https://doi.org/10.1007/s00203-016-1332-3

Pietro-Souza W, de Campos PF, Mello IS, Stachack FF, Terezo AJ, da Cunha CN, White JF, Li H, Soares MA (2020) Mercury resistance and bioremediation mediated by endophytic fungi. Chemosphere 240:124874. https://doi.org/10.1016/j.chemosphere.2019.124874

Pilon Smits EAH, De Souza MP, Hong G, Amini A, Bravo RC, Payabyab ST, Terry N (1999) Selenium volatilization and accumulation by twenty aquatic plant species. J Environ Qual 28(3):1011–1018. https://doi.org/10.2134/jeq1999.00472425002800030035x

Pirhadi M, Enayatizamir N, Motamedi H, Sorkheh K (2018) Impact of soil salinity on diversity and community of sugarcane endophytic plant growth promoting bacteria (*Saccharum officinarum* L. Var. CP48). Appl Ecol Environ 16:725–739

Priyanka S, Krishnamoorthy AS, Latha P, Kalaiselvi T (2019) Exploration of bacterial endophytes in cucumber (*Cucumis sativus* L.). Madras Agri J 106(4–6):406–414

Puente ME, Li CY, Bashan Y (2009) Endophytic bacteria in cacti seeds can improve the development of cactus seedlings. Environ Exp Bot 66(3):402–408. https://doi.org/10.1016/j.envexpbot.2009.04.007

Puri A, Padda KP, Chanway CP (2020) In vitro and in vivo analyses of plant-growth-promoting potential of bacteria naturally associated with spruce trees growing on nutrient-poor soils. Appl Soil Ecol 149:103538. https://doi.org/10.1016/j.apsoil.2020.103538

Radhakrishnan R, Khan AL, Kang SM, Lee IJ (2015) A comparative study of phosphate solubilization and the host plant growth promotion ability of *Fusarium verticillioides* RK01 and Humicola sp. KNU01 under salt stress. Ann Microbiol 65(1):585–593. https://doi.org/10.1007/s13213-014-0894-z

Rajkumar M, Ae N, Prasad MNV, Freitas H (2010) Potential of siderophore-producing bacteria for improving heavy metal phytoextraction. Trends Biotechnol 28(3):142–149. https://doi.org/10.1016/j.tibtech.2009.12.002

Rodriguez RJ, Woodward C, Kim YO, Redman RS (2009) Habitat-adapted symbiosis as a defense against abiotic and biotic stresses. In: White JF, Torres MS (eds) Defensive mutualism in microbial symbiosis. CRC Press, Boca Raton, FL, pp 335–346

Rosenblueth M, Martínez-Romero E (2006) Bacterial endophytes and their interactions with hosts. Mol Plant Microbe Interact 19(8):827–837. https://doi.org/10.1094/MPMI-19-0827

Sandhya V, Shrivastava M, Ali SZ, Prasad VS (2017) Endophytes from maize with plant growth promotion and biocontrol activity under drought stress. Russ Agric Sci 43(1):22–34. https://doi.org/10.3103/S1068367417010165

Santoyo G, Moreno-Hagelsieb G, del Carmen O-M, Glick BR (2016) Plant growth-promoting bacterial endophytes. Microbiol Res 183:92–99. https://doi.org/10.1016/j.micres.2015.11.008

Schulz B, Boyle C (2006) What are endophytes? In: Schulz BJE, Boyle CJC, Sieber TN (eds) Microbial root endophytes, Springer, Berlin, pp 1–13. https://doi.org/10.1007/3-540-33526-9_1

Shahid M, Ahmed B, Khan MS (2018) Evaluation of microbiological management strategy of herbicide toxicity to green gram plants. Biocatal Agric Biotechnol 14:96–108. https://doi.org/10.1016/j.bcab.2018.02.009

Shahrtash M, Brown SP (2021) A path forward: promoting microbial-based methods in the control of invasive plant species. Plants 10(5):943. https://doi.org/10.3390/plants10050943

Sharma A, Kumar V, Handa N, Bali S, Kaur R, Khanna K, Thukral AK, Bhardwaj R (2018) Potential of endophytic bacteria in heavy metal and pesticide detoxifcation. In: Egamberdieva D, Ahmad P (eds) Plant microbiome: stress response. Microorganisms for Sustainability. Springer Belin, pp 307–336

Shentu X, Zhan X, Ma Z, Yu X, Zhang C (2014) Antifungal activity of metabolites of the endophytic fungus *Trichoderma brevicompactum* from garlic. Braz J Microbiol 45(1):248–254. https://doi.org/10.1590/S1517-83822014005000036

Shi Y, Xie H, Cao L, Zhang R, Xu Z, Wang Z, Deng Z (2017) Effects of Cd-and Pb-resistant endophytic fungi on growth and phytoextraction of *Brassica napus* in metal-contaminated soils. Environ Sci Pollut Res 24(1):417–426. https://doi.org/10.1007/s11356-016-7693-y

Shi Y, Lou K, Li C (2011) Growth promotion effects of the endophyte *Acinetobacter johnsonii* strain 3–1 on sugar beet. Symbiosis 54(3):159–166. https://doi.org/10.1007/s13199-011-0139-x

Shrivastava G, Ownley BH, Augé RM et al (2015) Colonization by arbuscular mycorrhizal and endophytic fungi enhanced terpene production in tomato plants and their defense against a herbivorous insect. Symbiosis 65:65–74. https://doi.org/10.1007/s13199-015-0319-1

Siciliano SD, Fortin N, Mihoc A, Wisse G, Labelle S, Beaumier D, Greer CW (2001) Selection of specific endophytic bacterial genotypes by plants in response to soil contamination. Appl Environ Microbiol 67(6):2469–2475. https://doi.org/10.1128/AEM.67.6.2469-2475.2001

Singh SP, Gaur R (2017) Endophytic *Streptomyces* spp. underscore induction of defense regulatory genes and confers resistance against *Sclerotium rolfsii* in chickpea. Biol Control 104:44–56. https://doi.org/10.1016/j.biocontrol.2016.10.011

Singh A, Sharma S, Singh B (2017a) Effect of germination time and temperature on the functionality and protein solubility of sorghum flour. J Cereal Sci 76:131–139. https://doi.org/10.1016/j.jcs.2017.06.003

Singh D, Rajawat MVS, Kaushik R, Prasanna R, Saxena AK (2017b) Beneficial role of endophytes in biofortification of Zn in wheat genotypes varying in nutrient use efficiency grown in soils sufficient and deficient in Zn. Plant Soil 416(1):107–116. https://doi.org/10.1007/s11104-017-3189-x

Singh BK, Trivedi P, Singh S, Macdonald CA, Verma JP (2018) Emerging Microbiome technologies for sustainable increase in farm productivity and environmental security. Microbiol Aust 39(1):17–23. https://doi.org/10.1071/MA18006

Singh R, Dubey AK (2015) Endophytic actinomycetes as emerging source for therapeutic compounds. Indo Global J Pharm Sci. 5:106–116

Song C, Zhu F, Carrión VJ, Cordovez V (2020) Beyond plant microbiome composition: exploiting microbial functions and plant traits via integrated approaches. Front Bioeng Biotechnol 8:896. https://doi.org/10.3389/fbioe.2020.00896

Sun Y, Cheng Z, Glick BR (2009) The presence of a 1-aminocyclopropane-1-carboxylate (ACC) deaminase deletion mutation alters the physiology of the endophytic plant growth-promoting bacterium *Burkholderia phytofirmans* PsJN. FEMS Microbiol Lett 296(1):131–136. https://doi.org/10.1111/j.1574-6968.2009.01625.x

Sun K, Cao W, Hu LY, Fu WQ, Gong JH, Kang N, Dai CC (2019) Symbiotic fungal endophyte *Phomopsis liquidambari*-rice system promotes nitrogen transformation by influencing belowground straw decomposition in paddy soil. J Appli Microbiol 126(1):191–203. https://doi.org/10.1111/jam.14111

Surono, Narisawa K (2017) The dark septate endophytic fungus *Phialocephala fortinii* is a potential decomposer of soil organic compounds and a promoter of *Asparagus officinalis* growth. Fungal Ecol 28:1–10. https://doi.org/10.1016/j.funeco.2017.04.001

Taulé C, Castillo A, Villar S, Olivares F, Battistoni F (2016) Endophytic colonization of sugarcane (*Saccharum officinarum*) by the novel diazotrophs *Shinella* sp. UYSO24 and *Enterobacter* sp. UYSO10. Plant Soil 403(1):403–418. https://doi.org/10.1007/s11104-016-2813-5

Tong J, Miaowen C, Juhui J, Jinxian L, Baofeng C (2017) Endophytic fungi and soil microbial community characteristics over different years of phytoremediation in a copper tailings dam of Shanxi, China. Sci Total Environ 574:881–888. https://doi.org/10.1016/j.scitotenv.2016.09.161

Trivedi G, Patel P, Saraf M (2020a) Synergistic effect of endophytic selenobacteria on biofortification and growth of *Glycine max* under drought stress. S Afr J Bot 134:27–35. https://doi.org/10.1016/j.sajb.2019.10.001

Trivedi P, Leach JE, Tringe SG, Sa T, Singh BK (2020b) Plant–microbiome interactions: from community assembly to plant health. Nat Rev Microbiol 18(11):607–621. https://doi.org/10.1038/s41579-020-0412-1

Ullah A, Farooq M, Hussain M (2020) Improving the productivity, profitability and grain quality of kabuli chickpea with co-application of zinc and endophyte bacteria Enterobacter sp MN17. Arch Agron Soil Sci 66(7):897–912. https://doi.org/10.1080/03650340.2019.1644501

Uzma F, Konappa NM, Chowdappa S (2016) Diversity and extracellular enzyme activities of fungal endophytes isolated from medicinal plants of Western Ghats, Karnataka. Egypt J Basic Appl Sci 3(4):335–342. https://doi.org/10.1016/j.ejbas.2016.08.007

Verma JP (2018) Functional importance of the plant microbiome: implications for agriculture, forestry and bioenergy: a book review. J Clean Prod 178:877–879. https://doi.org/10.1016/j.jclepro.2018.01.043

Verma JP, Jaiswal DK, Sagar R (2014) Pesticide relevance and their microbial degradation: a-state-of-art. Rev Environ Sci Biotechnol 13:429–466. https://doi.org/10.1007/s11157-014-9341-7

Verma JP, Jaiswal DK, Singh S, Kumar A, Prakash S, Curá JA (2017) Consequence of phosphate solubilising microbes in sustainable agriculture as efficient microbial consortium: a review. Climate Change Environ Sustain 5:1–19. https://doi.org/10.5958/2320-642x.2017.00001.1

Von Bodman SB, Bauer WD, Coplin DL (2003) Quorum sensing in plant-pathogenic bacteria. Annu Review Phytopathol 41(1):455–482. https://doi.org/10.1146/annurev.phyto.41.052002.095652

Waller F, Achatz B, Baltruschat H, Fodor J, Becker K, Fischer M et al (2005) The endophytic fungus *Piriformospora indica* reprograms barley to salt-stress tolerance, disease resistance, and higher yield. Proc Natl Acad Sci 102(38):13386–13391. https://doi.org/10.1073/pnas.0504423102

Wang Y, Dai CC (2011) Endophytes: a potential resource for biosynthesis, biotransformation, and biodegradation. Ann Microbiol 61(2):207–215. https://doi.org/10.1007/s13213-010-0120-6

Wang Y, Li H, Zhao W, He X, Chen J, Geng X, Xiao M (2010) Induction of toluene degradation and growth promotion in corn and wheat by horizontal gene transfer within endophytic bacteria. Soil Biol Biochem 42(7):1051–1057. https://doi.org/10.1016/j.soilbio.2010.03.002

Wang L, Lin H, Dong Y, Li B, He Y (2020a) Effects of endophytes inoculation on rhizosphere and endosphere microecology of Indian mustard (*Brassica juncea*) grown in vanadium-contaminated soil and its enhancement on phytoremediation. Chemosphere 240:124891. https://doi.org/10.1016/j.chemosphere.2019.124891

Wang Z, Yu ZX, Solanki MK, Yang LT, Xing YX, Dong DF, Li YR (2020b) Diversity of sugarcane root-associated endophytic *Bacillus* and their activities in enhancing plant growth. J Appl Microbiol 128(3):814–827. https://doi.org/10.1111/jam.14512

Wani ZA, Ashraf N, Mohiuddin T, Riyaz-Ul-Hassan S (2015) Plant-endophyte symbiosis, an ecological perspective. Appl Microbiol Biotech 99(7):2955–2965. https://doi.org/10.1007/s00253-015-6487-3

Waqas M, Khan AL, Hamayun M, Shahzad R, Kang SM, Kim JG, Lee IJ (2015) Endophytic fungi promote plant growth and mitigate the adverse effects of stem rot: an example of *Penicillium citrinum* and *Aspergillus terreus*. J Plant Interact 10(1):280–287. https://doi.org/10.1080/17429145.2015.1079743

White JG, Kingsley KL, Verma SK, Kowalski K (2018) Rhizophagy cycle: an oxidative process in plants for nutrient extraction from symbiotic microbes. Microorganisms 6:95. https://doi.org/10.3390/microorganisms6030095

White JF, Kingsley KL, Zhang Q, Verma R, Obi N, Dvinskikh S, Elmore MT, Verma SK, Gond SK, Kowalski KP (2019) Review: Endophytic microbes and their potential applications in crop management. Pest Manag Sci 75:2558–2565. https://doi.org/10.1002/ps.5527

WHO (1996) Permissible limits of heavy metals in soil and plants. (Geneva: World Health Organization), Switzerland

Wilson D (1995) Endophyte: the evolution of a term, and clarification of its use and definition. Oikos 73:274–276. https://doi.org/10.2307/3545919

Win PM, Matsumura E, Fukuda K (2021) Effects of pesticides on the diversity of endophytic fungi in tea plants. Microb Ecol. https://doi.org/10.1007/s00248-020-01675-7

Xie XG, Zhao YY, Yang Y, Lu F, Dai CC (2020) Endophytic fungus alleviates soil sickness in peanut crops by improving the carbon metabolism and rhizosphere bacterial diversity. Microb Ecol. https://doi.org/10.1007/s00248-020-01555-0

Yao Q, Huang M, Bu Z, Zeng J, Wang X, Liu Z, Ma J, Zhang K, Liu X, Zhu Y (2020) Identification and characterization of a novel bacterial carbohydrate esterase from the bacterium *Pantoea ananatis* Sd-1 with potential for degradation of lignocellulose and pesticides. Biotechnol Lett 42(8):1479–1488. https://doi.org/10.1007/s10529-020-02855-8

Zhang P, Zhou PP, Yu LJ (2009) An endophytic taxol-producing fungus from *Taxus media*, *Cladosporium cladosporioides* MD2. Curr Microbiol 59:227–232. https://doi.org/10.1007/s00284-008-9270-1

Zhang L, Zhong J, Liu H, Xin K, Chen C, Li Q, Wei Y, Wang Y, Chen F, Shen X (2017) Complete genome sequence of the drought resistance-promoting endophyte *Klebsiella* sp. LTGPAF-6F. J Biotechnol 246:36–39. https://doi.org/10.1016/j.jbiotec.2017.02.008

Zhao L, Xu Y, Lai X (2018) Antagonistic endophytic bacteria associated with nodules of soybean (*Glycine max* L.) and plant growth-promoting properties. Brazilian J Microbiol 49(2):269–278. https://doi.org/10.1016/j.bjm.2017.06.007

Zhou LS, Tang K, Guo SX (2018) The plant growth-promoting fungus (PGPF) Alternaria sp. A13 markedly enhances *Salvia miltiorrhiza* root growth and active ingredient accumulation under greenhouse and field conditions. Int J Mol Sci 19(1):270. https://doi.org/10.3390/ijms19010270