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Meta-omics of endophytic microbes in agricultural biotechnology

Bartholomew Saanu Adeleke, Olubukola Oluranti Babalola *

Food Security and Safety Focus Area, Faculty of Natural and Agricultural Sciences, North-West University, Private Bag X2046, Mmabatho, 2735, South Africa

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ABSTRACT

Endophytic studies are becoming popular with the current advancement in microbial ecology. The internal tissue of the plant represents a discreet region for diverse endophytic microbes to flourish for plant nutrition through the uptake of essential nutrient (i.e. nitrogen, phosphorus, and potassium) synthesis of phytohormones, metabolic compounds, organic acids, siderophores, and hydrolytic enzymes. Nevertheless, these microbes are less explored than expected. The mechanisms of endophytic microbes that best explain their interactions with the host plant and other microbes can unravel their functional role in agricultural biotechnology based on gene specificity and competence under biotic and abiotic stress conditions. The establishment of microbial communities in plants contributes to plant health for yield enhancement. The dominant bacterial phyla, Proteobacteria, Firmicutes, Actinobacteria, Bacteroidetes, and Chloroflexi; and fungal phyla Ascomycota, Basidiomycota, and Zygomycota previously reported from sunflower, maize, rice, and wheat using meta-omics approaches form the basis of understanding the endophytic concept in the present and future studies. Meta-omics approaches create opportunities to unravel, explore and incorporate endophytic bioproducts in developing eco-friendly agriculture. Despite the established prospects of meta-omics approaches in agricultural biotechnology and industry, providing information on the reality of endophytic microbial bioproducts in assisting stress tolerance and disease control in plants is important with the view of combating current agricultural challenges for crop production. Hence, this review focuses on the endophytic bacteria and fungi, structural diversity, meta-omics approaches, and their agricultural, biotechnological, and industrial importance.

1. Introduction

The multifunctional agriculturally important microbes are found inhabiting the internal tissue of plants (Mukherjee et al., 2021; Song et al., 2019; Gupta et al., 2021). This review shall focus majorly on the endophytic microbes with potent endosymbiotic functional traits in enhancing plant nutrition, stress tolerance, and disease control in plants. Endophyte is two jointed Greek words, i.e., *endon* means within/inside/internal and *phyton* means plant. Some endophytic microbes with plant growth-promoting traits have been explored for various agricultural, industrial and biotechnological purposes (Bambharolia et al., 2020; Khan et al., 2020). The release or intrusion of endophytic microbes in and out of their host plants is facilitated by the structural dynamics through root hair development, tissue damage, cracks or injuries, and epidermal junctions. Root injury or wound contributes to the profuse release of exudates containing carbon and nitrogen-rich compounds to the root-soil environment by providing the required energy for microbial metabolic activities (Tsunoda and van Dam, 2017; Muresu et al., 2019; Mavrodi et al., 2021). Functionally, endophytic microbes contribute to

* Corresponding author.

E-mail address: olubukola.babalola@nwu.ac.za (O.O. Babalola).

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plant growth by enhancing crop yield, root development, stress tolerance, seed germination rate, plant height, leaf area, and other parameters, such as protein, mineral elements (nitrogen, phosphorus, potassium, etc.), and chlorophyll contents (Alkahtani et al., 2020; Khalil et al., 2021).

The close association of endophytic microbes within the plant tissues reveals their unique attributes compared to other microbes. Plant shields endophytes from internal or external abiotic factors, which influence their survival and productivity (Gomes et al., 2018). Findings have shown the adverse effect of abiotic factors, such as drought, cold, temperature, flooding, salinity, trace metals, and nutrient deficiency on plant growth in terms of increase in transpiration and metal accumulation, decrease in carbon(iv)oxide, reduction in soil fertility and moisture content, photosynthesis rate, and nitrogen fixation, accumulation of reactive oxygen species, disruption of hormone biosynthesis, and lowering of chlorophyll pigmentation (Bilal et al., 2021; Eid et al., 2021). Similarly, the adverse effect of biotic factors, such as pathogenic microbes (fungi, insects, nematodes, viruses, and bacteria) have been reported to cause biodiversity loss, disrupt transport system and hormone synthesis, reduce soil fertility, photosynthetic rate, plant biomass, accumulate reactive oxygen species, inhibit cell division, and host susceptibility to disease (Nadeem et al., 2014; Eid et al., 2021).

To mitigate the effect of stress in plants, one of such strategies relies on how host immunity and plant health can be improved upon exposure to stress. The endosymbiotic mechanisms of endophytes that assist in conferring abiotic stress tolerance are categorized into two; (i) activation of plant stress response systems after exposure to certain stressors, thus allowing the plant to escape or mitigate the impact of such stressors, and (ii) production of anti-stress agents by the beneficial endophytes. Unraveling the mechanism mediating these strategies may suggest their molecular basis and other bioinformatics-related tools for use in agriculture (Del Carmen Orozco-Mosqueda and Santoyo, 2021). The role of endophytic microbes in agricultural biotechnology to mitigate environmental stressors have provided excellent biological systems in the understanding of diverse mechanisms involved in plant growth and health (Mahgoub et al., 2021a). The potential of endophytic microbes to support plants against abiotic stress rely on the secretion of multiple bioactive and volatile compounds, such as phenolic compounds, exopolysaccharide, ethylene, organic acids, and siderophore (Alkahtani et al., 2020). The expression of oxidative genes and genes involved in secretion systems by some endophytic microbes underlined their potential in reducing abiotic stress in plants (Samaras et al., 2020; Gaeth et al., 2021). Mahgoub et al. (2021a) reported single or combined inoculation of endophytic *Bacillus thuringiensis* and *B. subtilis* to reduce the effect of salinity stress in broad bean.

Consequently, the secretion of antimicrobial compounds, induction of systemic resistance (ISR), and diverse secondary metabolites contribute to endophytic functions in plants against biotic stress. The biocontrol attributes of endophytes prevent pathogen invasion into the host cell. For example, the suppression of pathogenic fungi due to the secretion of secondary metabolites, such as hydrogen cyanide, pyoleutin, 2,4-diacetylphloroglucinol, pyrrolnitrin, and penzin-1-carboxylic acid by endophytic *Pseudomonas* species has been documented (Eid et al., 2021). The secondary metabolites production ability of endophytes can complement that of plants by increasing the derivable metabolites, especially in medicinal plants. Nevertheless, the diversity, quality, and quantity of secondary metabolites produced in the host plants can be altered due to the long term coevolution and coexistence of endophytes, which enabled them to establish unique cooperations based on the genomic and metabolic connections for the formation of crude metabolic products (Gond et al., 2021). Since microbial endophytes affect plant metabolism, their exploration as bioinoculants is expected to contribute to

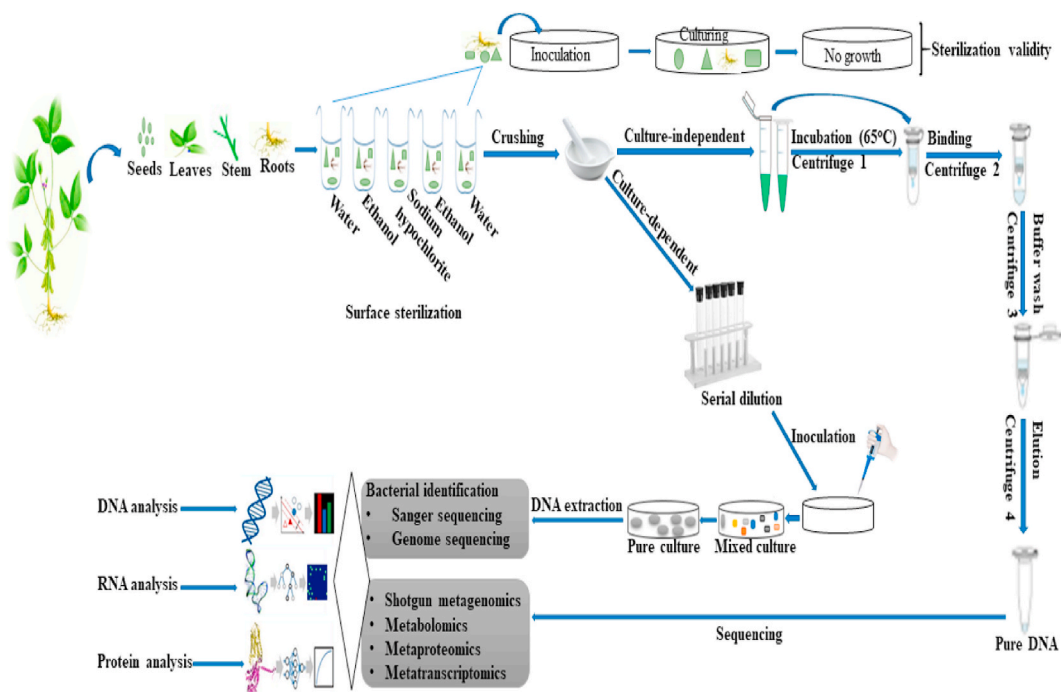


Fig. 1. Techniques involved in the isolation and identification of endophytic microbes.

crop quality and yield. Although, information on the metabolite synergy between plants and microbes is less documented, which required further studies.

Despite the diverse nature of endophytic microbes in plants and their effect on plant growth promotion; yet, few of them have been characterized, while some are yet to be cultured. Therefore, integrating various meta-omics methods in endophytic studies promises to provide a fast approach and opportunities in unraveling yet-to-be cultured endophytic microbes and their possible exploration in assisting stress tolerance and disease control in plants with the view of combating diverse agricultural problems and ensuring food safety. Hence, this review provides information on the diverse endophytic bacteria and fungi microbes, structural diversity, meta-omics approaches, and bioprospecting in sustainable crop production.

2. Sources and characterization of endophytic microbes

The source and identification of endophytic microbes from plant samples, such as root, leaves, stem, seeds, flower, and ovule, form the frontline approaches in determining their phenotypic and genetic features (Tariq et al., 2014; Herrera et al., 2020; Zhao et al., 2020). Based on the host specificity, plant organs and their location may influence the microbial population. Many findings validate higher endophytic microbial communities' belowground level, i.e., the root compared to the other parts of the plants (Kruasuwana and Thamchaipenet, 2016; Kuźniar et al., 2019; Cordero Elvia et al., 2021). After the sampling process and isolation of microbial endophytes from plant tissues, it is recommended to first cut the samples into sizes, and then surface sterilized by immersion in 70% ethanol and 3% sodium hypochlorite for 3 min (depending on the protocol), and finally rinsed with sterile distilled water to remove the disinfecting agents (Fig. 1). The essence of surface sterilization is to ensure the plant samples are free from epiphytic microbes and other surface contaminants. The level of sterility is usually confirmed by plating the last rinse of water on the appropriate microbiological media. Consequently, the surface-sterilized plant materials are then macerated with 15–20 mL of 0.85% saline solution inside mortar and pestle, vortexed, serially diluted, and pour plated for microbial isolation.

Due to media composition and growth conditions for culturing endophytic microbes, it is important to perform screening and optimization to ascertain the best cultural and growth conditions by following standard procedures (Banik et al., 2019; Ke et al., 2019). Identification of endophytic microbes can be achieved by (i) culturing, (ii) DNA extraction, (iii) polymerase chain reaction with specific primers for the amplification process, (iv) sequencing, and (v) comparison of the sequenced data with those available in the bioresource database. Furthermore, the taxonomic classification based on the phylogeny plot is obtained from the aligned sequence datasets using different phylogeny styles on molecular evolutionary genetics analysis (MEGA-X) online software.

3. Structural diversity of endophytic microbes in plants

The complex microbial interactions around plant environments have contributed to shaping the entire plant and soil microbiome; with their presence either beneficial or pathogenic (Goodwin, 2022). The beneficial microbes contribute immensely to crop yield enhancement, while the pathogenic types cause symptomatic disease conditions in plants (Compant et al., 2020). Plant-microbial networking and interactions; however, create a direct or indirect permissible route of infiltration through the soil-root interface to the stem and other parts of the plants, such as seeds, flowers, and leaves in an apoplastic manner (Babalola et al., 2020). The distribution of microbes in soils and various plant organs can be influenced by both biotic and abiotic factors, some of which include, soil profiling, agricultural practice, plant genotype, organ and tissue, seed cultivars, pathogens, erratic weather conditions, etc. (Centenaro et al., 2018; Etesami, 2018). Understanding the influence of these factors on the abundance and diversity of soil and plant microbiome will help reveal their lifestyle for soil health and plant benefits.

Due to the hyper-accumulation of organic matter belowground level, microbial density and abundance tend to show a significant difference in the belowground (root, soil, and sometimes bulk soil) compared to the aboveground (stems, shoot, seeds, and leaves) of the most economical crops (Cordero Elvia et al., 2021; Kelly et al., 2021), with few exceptions to non-vascular seedless plants that do not have true leaves, roots, and stems. Also, the age of plants greatly contributes to microbial diversity; such that, an increase in microbial diversity during growth stages of perennial plants across different seasons and soil nutrients influence their functions in contributing to the health status of plants (Zhang et al., 2022).

Diverse endophytic microbial communities in plants have been studied using cultured-dependent and culture-independent techniques (Pei et al., 2017; Kuźniar et al., 2019; Khalil et al., 2021). The *in vitro* cultural screening of diverse plant-growth-promoting endophytic microbes (PGPEM) with potential traits and application under greenhouse and field experimental conditions have been proven efficient (El Attar et al., 2019; Sánchez-Cruz et al., 2019; Alaylar, 2022). Nevertheless, there is a need for research intensification to maximally explore endophytic microbial bioresources in agricultural biotechnology.

The member of bacteria phyla Acidobacteria, Actinobacteria, Bacteroidetes, Chloroflexi, Cyanobacteria, Firmicutes, Proteobacteria, Tenericutes, and Verrucomicrobia (Bulgarelli et al., 2015; Liu et al., 2022), and fungal phyla Ascomycota, Basidiomycota, Blastocladiomycota, Chtridiomycota, Cryptomycota, Entomophthoromycota, Glomeromycota, Monoblepharidomycota, Neocallimastigomycota, and Zygomycota have been identified in the rhizosphere and non-rhizosphere of wheat plants using culture-independent techniques (Gqozo et al., 2020). Adeleke et al. (2021a) reported dominant bacteria phyla, such as Firmicutes, Proteobacteria, Actinobacteria, Bacteroidetes, and Chloroflexi in sunflower growing under different agricultural systems with promising use in the present and future agriculture. A study by Nguyen et al. (2021) documented Ascomycota, Basidiomycota, Kickxellomycota, Mortierellomycota, and Mucoromycota as the most dominant endophytic fungal phyla in two Oak species.

An account of diverse bacteria genera, such as *Azoarcus*, *Corynebacterium*, *Dyadobacter*, *Filimonas*, *Lysinibacillus*, *Aspergillus*, *Schizosaccharomyces*, *Talaromyces*, *Filobasidiella*, *Ajellomyces*, *Coprinopsis*, *Gibberella*, *Metarhizium*, *Filobasidiella*, *Ustilago*, *Malassezia*, *Tilletia*, *Sordaria*, *Leptosphaeria*, *Phaeosphaeria*, *Sclerotinia*, and *Podospora* colonizing the endosphere of maize have been documented

(Lata et al., 2019; Fadiji et al., 2020b). Also in a recent study, Liu et al. (2022) reported dominant endophytic bacterial genera, *Rhizobacter*, *Terriglobus*, *Candidatus*, *Sphingomonas*, *Acidibacter*, *Methylobacterium*, *Rhodanobacter*, *Alistipes*, *Burkholderia*, *Pseudomonas*, *Klebsiella*, *Dongia*, *Haliangium*, *Faecalibacterium*, *Alloprevotella*, *Bradyrhizobium*, *Dokdonella*, *Lactobacillus*, and *Eubacterium* from the root, stem, and leaves of *Oryza meridionalis*. The varied abundance of diverse endophytic fungal genera has also been identified in the roots, branch, petiole, stem, twig, and leaf of two oak species, *Quercus mongolica* and *Q. serra* in Korea (Nguyen et al., 2021).

Based on the host specificity, few reports are known about endophytic microbes. Furthermore, few reports are available on the comparative analysis of beneficial endophytic bacteria and fungi from different environments, such as extreme, temperate, and arctic environments (Nissinen et al., 2012). Hence, designing research in this aspect will be interesting in future studies.

Compared to the endophytic bacterial and fungal studies, research on archaea is less documented. Nevertheless, recent approaches, using next-generation sequencing (shotgun metagenomics) have been employed in identifying archaea phyla belonging to the Crenarchaeota, Euryarchaeota, and Thaumarchaeota in the maize plant under different farming practices (Fadiji et al., 2020b), but rarely documented in some plants, such as sunflower, ginseng, millet, etc. Based on the less information on the endophytic archaea, this limits insights into the biotic and abiotic factors influencing their diversity and functions for possible exploration. Furthermore, the study of the endophytic virus is still contentious, as some viruses inhabiting plant tissue can be asymptomatic, unlike endophytic bacteria and fungi. Based on the asymptomatic attributes of some viruses in plants (i.e. non-pathogenic nature), they can be regarded as beneficial microbes (Gomes et al., 2003; Wilson, 1995). Although, a study by Enebe and Babalola (2020) reported viral family Myoviridae, Podoviridae, Siphoviridae, Asfarviridae, Circoviridae, Inoviridae, Microviridae, Phycodnaviridae, and Retroviridae from the maize root environment. However, studies on the endophytic virus are rarely documented in the literature. Even though some findings are evident on the varied microbial diversity from one plant to another (Table 1), there is still a need to further investigate their dominant role in the ecosystem.

According to the recent findings on the use of culture-dependent methods in the isolation of endophytic bacteria isolates; authors, Wang et al. (2021a) and Adeleke et al. (2021c) reported endophytic *Paenibacillus glycinis* and *Stenotrophomonas indicatrix* from the soybean and sunflower, respectively. Screening of different plant microbes with plant growth-promoting attributes, such as nitrogen

Table 1
Diverse endophytic microbial phylotypes and genera in plants.

Plant	Phyla/Genera	References
<i>Alkanna tinctoria</i>	Actinobacteria: <i>Tsukamurella</i> , <i>Pantibacter</i> , <i>Paenarthrobacter</i> , <i>Micromonospora</i> , <i>Lysinimonas</i> , <i>Conexibacter</i> , <i>Cellulomomas</i> , <i>Kocuria</i> ; Alphaproteobacteria: <i>Bradyrhizobium</i> , <i>Brevundimonas</i> , <i>Beijerinckia</i> , <i>Bosea</i> , <i>Labrys</i> , <i>Methylophila</i> , <i>Paracoccus</i> , <i>Shinella</i> , <i>Tardiphaga</i> , <i>Roseomonas</i> , <i>Inquilius</i> Bacteroidetes: <i>Pedobacter</i> , <i>Filimonas</i> , <i>Chitinophaga</i> , <i>Flavobacterium</i> , <i>Muciliginibacter</i> Firmicutes: <i>Bacillus</i> , <i>Staphylococcus</i> , <i>Cohnella</i> , <i>Domibacillus</i> , <i>Psychrobacillus</i> , <i>Tumebacillus</i> , <i>Brevibacterium</i> , <i>Brevibacillus</i> ; Gammaproteobacteria: <i>Luteibacter</i> , <i>Enhydrobacter</i> , <i>Acinetobacter</i> , <i>Xanthomonas</i> , <i>Stenotrophomonas</i> , <i>Pantoea</i> , <i>Lelliottia</i> , <i>Buttiauxella</i> Proteobacteria: <i>Shinella</i> , <i>Rhodobacter</i> , <i>Devosia</i> , <i>Bradyrhizobium</i> , <i>Agrobacterium</i> , <i>Nitrobacter</i> , <i>Geobacter</i> , <i>Pantoea</i> , <i>Citrobacter</i> , <i>Enterobacter</i> , <i>Microbacter</i> Planctomycetes: <i>Planctomyces</i> , <i>Gemmata</i> Actinobacteria: <i>Streptomyces</i> Bacteroidetes: <i>Flavobacterium</i>	Rat et al. (2021)
<i>Oryza sativa</i>	Actinobacteria: <i>Streptomyces</i> Bacteroidetes: <i>Flavobacterium</i> Actinobacteria: <i>Lechevalieria</i> , <i>Pseudomocardia</i> , <i>Streptomyces</i> , <i>Nonomuraea</i> , <i>Actinomadura</i> , <i>Rubrobacter</i> Firmicutes: <i>Bacillus</i> Planctomycetes: <i>Gemmata</i> Proteobacteria: <i>Pedomicrobium</i> , <i>Roseomonas</i> , <i>Reyranelia</i> , <i>Pseudomonas</i> Tenerricutes: <i>Asteroleplasma</i>	Singha et al. (2021)
<i>Citrus sinensis</i>	Actinobacteria: <i>Anthrobacter</i> , <i>Curtobacterium</i> , <i>Microbacterium</i> , <i>Mycobacterium</i> , <i>Streptomyces</i> Bacteroidetes: <i>Niastella</i> Firmicutes: <i>Bacillus</i> Proteobacteria: <i>Devosia</i> , <i>Enterobacter</i> , <i>Mezobacterium</i> , <i>Neorhizobium</i> , <i>Nophosphingobium</i> , <i>Pantoea</i> , <i>Phyllobacterium</i> , <i>Polaromonas</i> , <i>Pseudomonas</i> , <i>Ralstonia</i> , <i>Rhizobium</i> , <i>Spingomonas</i> , <i>Yersinia</i>	Yang and Ancona (2021)
<i>Beta vulgaris</i>	Actinobacteria: <i>Anthrobacter</i> , <i>Curtobacterium</i> , <i>Microbacterium</i> , <i>Mycobacterium</i> , <i>Streptomyces</i> Bacteroidetes: <i>Niastella</i> Firmicutes: <i>Bacillus</i> Proteobacteria: <i>Devosia</i> , <i>Enterobacter</i> , <i>Mezobacterium</i> , <i>Neorhizobium</i> , <i>Nophosphingobium</i> , <i>Pantoea</i> , <i>Phyllobacterium</i> , <i>Polaromonas</i> , <i>Pseudomonas</i> , <i>Ralstonia</i> , <i>Rhizobium</i> , <i>Spingomonas</i> , <i>Yersinia</i>	Okazaki et al. (2021)
<i>Thuidium cymbifolium</i> , <i>Cirriphyllum cirrosum</i> , <i>Tortella tortuosa</i> , <i>Tortula reflexa</i>	Proteobacteria: <i>Pseudomonas</i> , <i>Rugamonas</i> , <i>Massilia</i> Firmicutes: <i>Bacillus</i> , <i>Paenibacillus</i> Actinobacteria: <i>Rhodococcus</i> , <i>Arthrobacter</i> , <i>Clavibacter</i> , <i>Plantibacter</i> Bacteroidetes: <i>Pedobacter</i> , <i>Flavobacterium</i>	Lan et al. (2020)
<i>Phragmites australis</i> , <i>Chloris virgate</i>	Firmicutes: <i>Bacillus</i> , <i>Staphylococcus</i> Proteobacteria: <i>Beijerinckia</i> , <i>Pseudomonas</i> , <i>Serratia</i> , <i>Actinobacter</i> , <i>Acinetobacter</i> Actinobacteria: <i>Promicromonospora</i> , <i>Microbacterium</i>	Wu et al. (2021)
<i>Cardamine hupingshanensis</i>	Firmicutes: <i>Bacillus</i> , <i>Oceanobacillus</i> , <i>Terribacillus</i> , <i>Exiguobacterium</i> , <i>Lysinibacillus</i> , <i>Paenibacillus</i> Proteobacteria: <i>Brevundimonas</i> , <i>Ralstonia</i> , <i>Citrobacter</i> , <i>Acinetobacter</i> , <i>Pseudomonas</i>	Li et al. (2021)
<i>Noccaea caerulea</i>	Firmicutes: <i>Bacillus</i> , <i>Paenibacillus</i> Bacteroidetes: <i>Hymenobacter</i> Actinobacteria: <i>Rhodococcus</i> , <i>Microcococcus</i> , <i>Propionibacterium</i> , <i>Norcadia</i> , <i>Microbacterium</i> Proteobacteria: <i>Sphingomonas</i> , <i>Stenotrophomonas</i> , <i>Delftia</i> , <i>Variovorax</i> , <i>Enterobacter</i>	Durand et al. (2021)

fixation, siderophore, and indole-3-acetic acid production, extracellular enzyme biosynthesis, antibiotic production, zinc phosphate, and potassium solubilization have been investigated (Table 2).

The genomic information of endophytic microbes; however, can help predict their function in the ecosystem. The antibiosis mechanism, ISR, and phytohormone synthesis by endophytic microbes may suggest their use as bioinoculants on a commercial scale in developing eco-friendly agriculture (Lata et al., 2019). The genomic insights into endophytic microbes associated with many plants, that reveal their multifaceted biological functions in an ecosystem, have recently been documented (Knapp et al., 2018; Gorai et al., 2021; Wang et al., 2022). For example, the genomic analysis of *Enterobacter cloacae* Ghat1 and *Bradyrhizobium diazoefficiens* 113-2 revealing various genes involved in plant growth promotion have been recommended for further exploration in agriculture (Li et al., 2020a; Shastry et al., 2020).

A report by Adeleke et al. (2021c) revealed multiple functional genes involved in various microbial metabolic pathways from *S. indicatrix* isolated from sunflower roots. Similarly, the prediction of notable genes and a secondary metabolite (lovastatin), in the

Table 2
Summarized data on the type of endophytes, sources, and characterization.

Endophytes	Sources	Characterization	References
Bacteria			
<i>Flavobacterium, Xanthomonas, Microbacterium</i>	<i>Oryza sativa</i>	Nitrogen fixation, enzyme, siderophore, solubilize phosphate	Walitang et al. (2017)
<i>Pantoea, Erwinia</i>	<i>Echeveria laui</i>	fix nitrogen, solubilize phosphate, produce exopolysaccharides/IAA and antibiosis	Emmer et al. (2021)
<i>Bacillus, Stenotrophomonas</i>	<i>Helianthus annuus</i>	IAA, siderophore, ammonia, solubilize phosphate	Adeleke et al. (2021c)
<i>Bacillus, Brevibacillus, Lysinibacillus, Pseudomonas, Enterobacteria, Microbacterium, Kocuria</i>	<i>Vigna radiata, Vigna unguiculata, Cajanus cajan</i>	Ammonia, hydrogen cyanide, IAA, organic acid, solubilize phosphate, siderophore	Bhutani et al. (2021)
<i>Bacillus, Paenibacillus, Lysinibacillus, Erwinia, Herbaspirillum, Micrococcus, Methylobacterium, Sphingomonas, Bosea, Aurantimonas</i>	<i>Camellia sinensis</i>	IAA, solubilize phosphate, siderophores, ACC deaminase, nitrogen fixation	Jia et al. (2021)
<i>Aneurinibacillus, Serratia, Bacillus, Cedecea, Kosakonia, Ensifer, Lactobacillus, Oxyntema</i>	<i>Rosmarinus officinalis</i>	IAA, solubilize phosphate, siderophores, enzymes, nitrogen fixation, HCN, ammonia, antimicrobial	Sharma et al. (2021)
<i>Bacillus spp., B. cereus, B. aerophilus, B. megaterium, B. flexus, B. subtilis, Pseudomonas simiae, P. brenneri, Pantoea agglomerans, Ewingella Americana</i>	<i>Brassica napus, Zea mays, Helianthus annuus, Oryza sativa, Anacardium othonianum, Solanum tuberosum</i>	Phytohormone, siderophore, induced systemic resistance	(Adeleke et al., 2021b; Bahmani et al., 2021; Faria et al., 2021; Kumar et al., 2021; Lipková et al., 2021a, 2021b; Rana et al., 2021)
<i>Achromobacter xylosoxidans, P. fluorescens, Pseudomonas migulae, Bacillus subtilis, Burkholderia phytofirmans</i>	<i>Catharanthus roseus, Brassica campestris, Cicer arietinum, Triticum aestivum, Pisum sativum</i>	ACC deaminase	(Karthikeyan et al., 2012; Abd- Ali et al., 2014; Naveed et al., 2014; Abd-Allah et al., 2018; Sofy et al., 2021)
<i>Bacillus spp., B. megaterium, B. subtilis, B. cereus, B. panacihumi B. licheniformis</i>	<i>Zea mays, Vigna radiate, Cajanus cajan</i>	Protease, lipase, esterase, amylase, cellulase, pectinase, protease	Toghueo and Boyom (2021)
<i>Bacillus, Burkholderia, Acinetobacter, Enterobacter, Rhizobium, Pantoea, Serratia, Stenotrophomonas, Paenibacillus</i>	<i>Anacardium othonianum</i>	IAA, phosphate solubilization, siderophore production, and biocontrol	Faria et al. (2021)
<i>Enterobacter, Paraburkholderia, Brevibacillus, Enterobacter</i>	<i>Aleo vera</i>	Phosphate solubilization, enzyme activity, ACC deaminase, siderophore, antibiosis	Silva et al. (2020)
Fungi			
<i>Nigrospora, Alternaria, Aspergillus</i>	<i>Bacopa monnieri</i>	IAA, solubilize phosphate, catalase, siderophore	Soni et al. (2021)
<i>Alternaria, Penicillium, Aspergillus</i>	<i>Ephedra pachyclada</i>	Ammonia, IAA, enzyme activity	Khalil et al. (2021)
<i>Gliocladium, Bipolaris, Fusarium, Mucor, Penicillium, Basidiobolus, Aspergillus</i>	<i>Oryza sativa</i>	IAA	Roy et al. (2021)
<i>Beauveria, Rhodotorula, Metschnikowia</i>	<i>Glycine max, Hordeum vulgare</i>	Metal removal	Ignatova et al. (2021)
<i>Trichoderma</i>	<i>Glycine max</i>	Biocontrol activity	Sallam et al. (2021)
<i>Aspergillus, Fusarium</i>	<i>Mimosa spp.</i>	Siderophore activity, phosphate solubilization, and secretion of indole acetic acid and gibberellins	Bilal et al. (2018)
<i>Penicillium, Fusarium, Aspergillus</i>	<i>Camellia sinensis</i>	IAA, mineral solubilization	Nath et al. (2015)
<i>Coprinellus, Pyrenochaeta, Pholiota, Helotiales, Alternaria</i>	<i>Dendrobium officinale</i>	Plant growth-promoting activity	Hou and Guo (2014)
<i>Purpureocillium lilacinum,</i>	<i>Ulex europaeus</i>	Phosphate solubilization, siderophore	Herrera et al. (2022)

Key: IAA – indole-3-acetic acid, HCN – hydrogen cyanide.

genome of endophytic bacterium, *Herbaspirillum seropedicae* Os34 and fungus, *Diaporthe ampelina* colonizing the endosphere of rice and Indian bdellium-tree, which provides a genomic understanding of microbial mechanisms in sustainable plant health has been documented (Bhargavi et al., 2018; Lata et al., 2019). Interestingly, the genomic insights into the endophytic microbial community structures, functions, and metabolic pathways can be further explained by employing meta-omics technologies as briefly described in the sections below.

4. Meta-omics of endophytic microbes

The molecular basis of endophytic bacterial and fungal diversity and their interactions with the host plants can best be explained using meta-omics approaches, such as metabolomics, metagenomics, metaproteomics, and metatranscriptomics (Fig. 2). Meta-omics have been employed in studying plant-associated bacteria and fungi capable of enhancing plant growth by stimulating phytohormones and host defense to environmental stresses (Urumbil and Anilkumar, 2021). In addition, this approach is promising in understanding the inherent bacterial and fungal functions, which suggest their potential use in sustaining plant growth under different environments. The qualitative screening for detecting multiple functional traits of endophytic bacteria and fungi relies on sampling design, DNA extraction, sequencing, and sequence data analysis.

For more than three decades, DNA sequencing and analysis of sequenced data using various bioinformatics tools to predict novel genes have yielded success in the understanding of genome profiling and functions of endophytic bacteria and fungi associated with the plant endosphere (Labonte et al., 2018).

Hundreds of millions of genome datasets have been deposited in the online genome libraries for reference. Research efforts on the comparative genome analysis of endophytic bacteria and fungi have yielded success in recent times. The detection of notable genes involved in phytohormone synthesis, secretion systems, siderophore production, phosphate metabolism and transport, surface attachment, biofilm production, etc., can mediate plant-bacteria interactions for plant growth (Nascimento et al., 2020; Adeleke et al., 2021c).

The research design focusing on the functional traits, which underline bacteria and fungi mechanisms for plant health sustainably may help predict their novel attributes and possible suggestions for future commercialization as bioinoculants in combating agricultural problems (Bhardwaj et al., 2014). Based on the advancement in endophytic studies, a few of the whole-genome sequence profiling of endophytic bacteria and fungi has been documented (Table 3). Furthermore, findings have shown the selection of three endophytic bacteria and two endophytic fungi from sunflower based on their plant growth-promoting traits (Waqas et al., 2015; Bashir et al., 2021), and ten endophytic bacteria from Tall fescue (Gaeth et al., 2021). Knowing fully well the potentialities of the diverse endophytic microbes is critical to elucidate by applying meta-omics approaches.

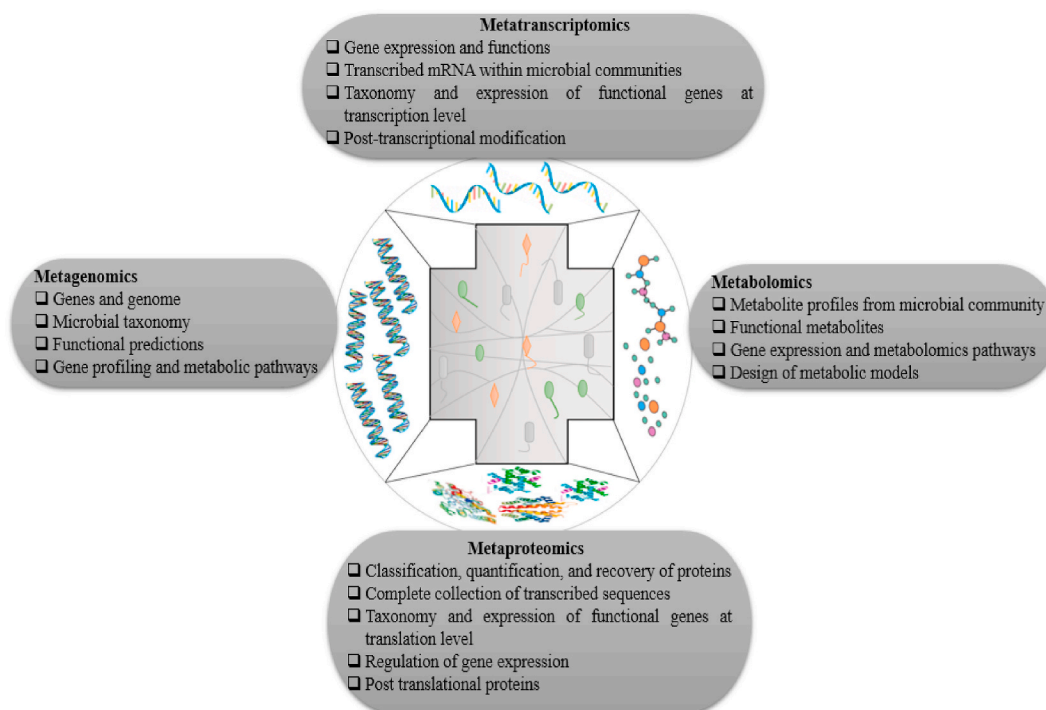


Fig. 2. The meta-omics of endophytic microbes and consortia in the root of the plant.

Table 3
Some examples of whole-genome sequence profiling of endophytic bacteria.

Microbial endophytes	Plant source	References
Bacteria		
<i>Stenotrophomonas indicatrix</i> BOVIS40, <i>S. maltophilia</i> JVB5, <i>Bacillus cereus</i> T4S	<i>Helianthus annuus</i>	(Adeleke et al., 2021b; Babalola et al., 2021)
<i>Bacillus paralicheniformis</i> KMS 80	<i>Oryza sativa</i>	Annapurna et al. (2018)
<i>Azospirillum</i> sp. B510		Kaneko et al. (2010)
<i>Herbaspirillum seropedicae</i> strain SmR1		Kaul et al. (2016)
<i>Stenotrophomonas maltophilia</i> RR-10		Zhu et al. (2012)
<i>Kosakonia oryzae</i> K0348		Meng et al. (2015)
<i>Mammaliicoccus vitulinus</i> RIT 801, <i>Citrobacter portucalensis</i> RIT 805, <i>Staphylococcus xylosus</i> RIT 806, <i>Priestiamegaterium</i> RIT 807, <i>Leclercia adecarboxylata</i> RIT 815	<i>Lolium arundinaceum</i>	Gaeth et al. (2021)
<i>Bradyrhizobium diazoefficiens</i> 113-2	<i>Glycine max</i>	Li et al. (2020a)
<i>Serratia plymuthica</i> AS9	<i>Brassica napus</i>	Neupane et al. (2012)
<i>Pantoea agglomerans</i> ANP8	<i>Medicago sativa</i>	Noori et al. (2021)
<i>Bacillus subtilis</i> Dcl1	<i>Curcuma longa</i>	Jayakumar et al. (2021)
<i>nterobacter cloacae</i> Ghats1	<i>Coscinium fenestratum</i>	Shastri et al. (2020)
<i>Pseudomonas aeruginosa</i> B18	<i>Saccharum officinarum</i>	Singh et al. (2021b)
<i>Gluconacetobacter diazotrophicus</i> Pal5		Bertalan et al. (2009)
<i>Klebsiella variicola</i> DX120E		Lin et al. (2015)
<i>Bacillus megaterium</i> TG1-E1	<i>Spartina anglica</i>	Vílchez et al. (2018)
<i>Bacillus flexus</i> KLBMP 4941	<i>Limonium sinense</i>	Wang et al. (2017)
<i>Burkholderia phytofirmans</i> PsJN	<i>Allium cepa</i>	Weilharther et al. (2011)
<i>Stenotrophomonas maltophilia</i> R551-3, <i>Pseudomonas putida</i> W619, <i>Serratia proteamaculans</i> 568	<i>Populus trichocarpa</i>	(Taghavi et al., 2010; Kaul et al., 2016)
<i>Pseudomonas fluorescens</i> PICF7	<i>Olea europaea</i>	Martínez-García et al. (2015)
<i>Raoultella terrigena</i> R1Gly	<i>Nicotiana tabacum</i>	Schicklberger et al. (2015)
Fungi		
<i>Diaporthe ampelina</i>	<i>Commiphora wightii</i>	Bhargavi et al. (2018)
<i>Penicillium aurantiogriseum</i> NRRL 62431	<i>Corylus avellana</i>	Yang et al. (2014)
<i>Aspergillus niger</i> CSR3	<i>Cannabis sativa</i>	(Lubna et al., 2018; Asaf et al., 2022)
<i>Cadophora</i> sp. DSE1049, <i>Periconia macropsinosa</i> DSE2036	<i>Festuca vaginata</i>	Knapp et al. (2018)
<i>Calcarisporium arbuscula</i> NRRL 3705	-	Cheng et al. (2020)
<i>Paraphaesphaeria sporulosa</i> 10515	<i>Festuca</i> spp.	Baroncelli et al. (2020)
<i>Sarocladium brachiariae</i>	<i>Brachiaria brizantha</i>	Yang et al. (2019)
<i>Pestalotiopsis fici</i>	<i>Camellia sinensis</i>	Wang et al. (2015)

4.1. Metagenomics

Metagenomics is one of the core aspects of genomic studies that reveal the genome i.e., DNA identity and integrity of endophytic microbes from plant samples (Handelsman, 2004). Metagenomics studies create diverse opportunities in unveiling the structural diversity and potential of yet-to-be cultured microbes from environmental samples (Krishnamoorthy et al., 2021). There are a lot of shortcomings surrounding the use of culture-dependent techniques in microbial isolation, as only a few microbes (<1%) can be recovered, thus limiting their exploration in agriculture. In recent times, information on the bacteria, fungi, and archaea dynamics and functions in the root endosphere has been revealed from metagenomics studies (Fadiji et al., 2020b; Durand et al., 2022; Samuel et al., 2022; Yuan et al., 2022). Wang et al. (2021c) and Liu et al. (2022) reported the use of next-generation sequencing in the study of diverse endophytic bacteria with notable functions from the root and seeds of rice. Diverse endophytic bacterial and fungal microbiota in the sprouts, roots, and stems of rice have also been studied (Wang et al., 2016).

Regarding the complex nature of microbes in plants, they can be studied without culturing using a metagenome next-generation sequencing (mNGS) approach. In addition, Illumina and 454 pyrosequencing (Roche) have been employed to investigate diverse endophytic bacteria and fungi from sorghum and Oak plants (Maropola et al., 2015; Nguyen et al., 2021). Shotgun metagenome sequence analysis on various bioinformatics platforms, such as MG-RAST, and PiCRUST with the corresponding functional pipelines help unveil the taxonomy and putative functional genes involved in plant growth promotion (Hong et al., 2019; Toole et al., 2021). A study by Hara et al. (2019) reported diverse nitrogenase genes (*nifD*HK) from *Bradyrhizobium* isolated from sorghum roots.

Similarly, various functional genes involved in nitrogen metabolism, IAA and tryptophan biosynthesis, siderophore production, and phosphate solubilization has been reported by Fadiji et al. (2021) while investigating root-associated endophytic microbiome in maize plant using a shotgun approach. The metagenomic analysis of 1-aminocyclopropane-1-carboxylate (ACC) deaminase gene (*acdS*) operon in yet-to-be cultured endophytic bacteria isolated from *Solanum tuberosum* under a conventional farming system in Stotzing (Burgenland, Austria), which alleviate drought stress in plants has been reported (Nikolic et al., 2011). The frequent putative functional ACC deaminase, phosphate solubilization, 4-phytase, methanol utilization (*xoxF*), and N-metabolism-related genes in the *Panax ginseng* bacterial community has been detected and predicted by BLASTn and metagenomic analysis, respectively (Hong et al., 2019). The genes involved in bacteria attachment, pH regulation, osmotic stress, cold or heat shock, carbohydrate metabolism, and

secretion systems have also been investigated using the metagenomics approach (Liljeqvist et al., 2015).

4.2. Metatranscriptomics

Metatranscriptomics deals with the expression of all transcripts (i.e., mRNA) in microbial cells. This approach helps understand different genetic profiling of endophytic microbes in diverse environments (Starke et al., 2019). To successfully analyze metatranscriptome sequenced datasets, other protocols need to be followed, which include sampling, surface-sterilization, RNA extraction (using kits), mRNA enrichment, cDNA synthesis, metatranscriptomic library preparation, sequencing, sequence analysis, and data processing (Kaul et al., 2016). For a successful RNA extraction, it is recommended to know the details of the sample materials, time of collection, preparation, and storage conditions. Also, mRNA enrichment is required, as this forms one of the core aspects of metatranscriptomics.

The messenger ribonucleic acid (mRNA) sequencing analysis is a modern molecular technique employed in the transcriptome profiling of similar or dissimilar functions of endophytes (Gómez-Godínez et al., 2019). The induction of stress responses in plants can be controlled by complex molecules (proteins) and biological catalysts (enzymes). Stress induction has also been linked to the sigma factor RpoH1. Proteins serve as a precursor for the induction of multiple plant growth-promoting traits in endophytic microbes under stress conditions (Ranea et al., 2004). The ability of endophytic microbes to secrete ACC deaminase suggests their possible use in formulating bioinoculants for plant survival under stress conditions, such as drought, salinity, temperature, etc. (Dubey et al., 2020). Stress induction genes from endophytic microbes can serve as a catalytic switch for microRNA (miRNA), which modulate the low expression of notable genes involved in plant response to abiotic stress in wheat, rice, *Arabidopsis*, and *Medicago* (Trindade et al., 2010). The expression of miRNA169 and miRNA169c, which enhances stress response in tomato and rice plants have been documented by Zhang et al. (2011). Interestingly, Lima et al. (2011) and (Meena et al., 2017a) provided insights into the diverse miRNAs, which mediate metal stress in two different rice subspecies *indica* and *japonica* using the RT-PCR approach.

4.3. Metaproteomics

Aside from metagenomics, and metatranscriptomics; metaproteomics is another aspect of genomic studies that deal with the study of protein complement and gene expression from the endophytic microbial communities (Valenzuela et al., 2006). This technique has been employed in the classification and quantification of proteins from environmental microbes (Kaul et al., 2016). It also helps understand gene functions, transcription of DNA material to mRNA, and subsequent protein translation. Employing a metaproteomics approach in determining the protein structures and functions can help understand the molecular profiling and gene quantification of endophytic microbiomes under experimental conditions (Kaul et al., 2016). A study by Bao et al. (2014) reported diazotrophic methanotrophs and their localization in the root of rice using metaproteomic. The use of metaproteomics in environmental studies is increasing, as shotgun metaproteomics has unveiled microbial features in many plants (Gómez-Godínez et al., 2019). However, this concept is still in its infancy, as less information is available in the literature regarding protein expression of endophytic microbes in most economical crops. Hence, metaproteomic studies promise to unveil endophyte protein functions and genes involved in the metabolism of organic substrates.

Different bacteria proteins involved in amino acid, carbohydrate, and lipid metabolism have been reported in endophytic genera Proteobacteria, Bacteroidetes, Actinobacteria, and Firmicutes (Kaul et al., 2016). Application of metaproteomics, ranging from environmental studies, micro-microbe, soil-microbe, and plant-microbe interactions as reported in the previous studies, can be further intensified for more successes in agricultural biotechnology (Gómez-Godínez et al., 2019).

The endophytes' complexity, multiple functional genes, protein structure, and metabolic pathways as revealed by metaproteomics can serve as a model in understanding endophytic microbial functions. The genomic comparative assessment of endophytes inhabiting plants cultivated in water-limiting soils can help predict functional protein genes specific for bacteria or fungi (Kaul et al., 2016). Determining protein profiling of endophytic microbes in plants under stress and non-stress conditions can pinpoint specific enzyme-coding proteins responsible for stress mitigation in plants. The metaproteomics approach revealing diverse endophytic bacterium, *Gluconacetobacter diazotrophicus* in sugarcane cultivated under drought-prone soils has been documented (Lery et al., 2011). Interestingly, metaproteomics features, which include identification of proteins, enzymes involved in metabolic pathways, and osmotic balancing can further reveal microbial functions under drought stress.

4.4. Metabolomics

Aside from determining the diverse endophytic microbes, their functions, and pathways toward plant growth and health management, information on the diverse metabolic compounds which mediate microbial functions remains fundamental. Although, growing pathogen-free plants remains a priority to farmers; most times, plants are affected by pathogenic microbes with high resistance to commercial antibiotics. The discovery of novel metabolites involved in cellular functions and microbial networking can help derive alternative antibiotics from endophytic microbes through microbial metabolite profiling (Mahmood and Kataoka, 2020). Metabolomics is the aspect of science that deals with the study of metabolites in living cells. The metabolomics approach is an emerging field of science, and its use in endophytic research is limited. However, making information available in literature aim to advance research focus on endophytic microbes using metabolomics.

Cellular metabolism results in energy production for various biological functions, such as communication, reproduction, maintenance, protection, and repair (Alawiye and Babalola, 2021). Metabolites are biological molecules produced from the metabolic process for energy production in living cells. The metabolites secreted from the plant roots can serve as chemo-attractants, thus making the root zone a hotspot for microbial interactions with the plant root (Reinhold-Hurek et al., 2015). The prediction of microbial functions at the molecular level has been linked to metabolite synthesis. Before now, metabolomic has been extensively applied in

medicine (Wang et al., 2019), but less employed in determining functional traits in endophytic microbes. Nevertheless, the advancement in metabolomics, transcriptomics, metagenomics, and metaproteomics can serve as modern technologies to the plant breeders in understanding the overall activities of microbes in plants (Agtuca et al., 2020).

Application of metabolomics in crop production stands promising in determining metabolite composition in the plant at different developmental stages. Different microorganisms contain diverse metabolites and their analysis has been reported using capillary electrophoresis (CE-MS), liquid and gas chromatography with mass spectrometry (LC and GC-MS), and nuclear magnetic resonance spectroscopy (NMR) (Spina et al., 2021). Microbial metabolites contribute to plant growth and survival under harsh environmental conditions. According to Brader et al. (2014) and Asaf et al. (2022) whose findings focus on the metabolic potential of endophytic bacteria and fungi, the authors reported diverse functional secondary metabolites which cause a shift in microbial adaptation, lifestyle, and interactions in plants. Some identifiable metabolites from endophytic bacteria include sespenine (*Streptomyces* spp.), spoxazomicins (*Streptosporangium oxazolonicum*), siderophore (*Pseudomonas aeruginosa*), serobactin A (*Herbaspirillum seropedicae*), valienamine (*Burkholderia kirkii*), pavettamine (*Burkholderia* spp.), and coronatine (*Pseudomonas syringae*) (Brader et al., 2014); and endophytic fungi, which include, and lovastatin (*Diaporthe ampelina*), Taxol (*Penicillium aurantiogriseum* NRRL 62431, *Cladosporium cladosporioides* MD2, and *Aspergillus aculeatinus* Tax-6, BT-2), resveratrol, pterostilbene and piceatannol (*Alternaria* sp. MG1), huperzine A (*Shiraia* sp. Slf14, *Colletotrichum gloeosporioides* ES026, *C. gloeosporioides* Cg01, and *Penicillium polonicum* hy4) (Bhargavi et al., 2018; Bielecka et al., 2022).

Endophytic bacteria diversely produce secondary metabolites and this include; i) direct production of self-novel metabolites, e.g., rhizoxin produced by *Burkholderia rhioxinica* (Partida-Martinez and Hertweck, 2005), ii) induction of plant metabolite production, e.g., *Pseudonocardia* sp. strain YIM 63111 inducing artemisinin production in *Artemisia annua* (Li et al., 2012) and iii) enhancing the quality and quantity of metabolites secretion in the host plants, e.g., *Methylobacterium extorquens* enhancing the production of two furanoid compounds in strawberry (*Fragaria* spp.), which contribute to the fruit aroma (Verginer et al., 2010).

5. Plant health status and occurrence of potential human pathogenic microbes in the endosphere

The conventional approach of agricultural irrigation systems helps supply adequate water for plant growth and reduces fertilizer application (Cui et al., 2020). Conversely, irrigation by water contaminated with organic manure or animal waste can be a reservoir or route of pathogen transmission on farmlands (Becerra-Castro et al., 2015); hence, controlling plant microbial contamination remains critical. Therefore, it is important to ensure plant health status and crop safety to reduce the potential risk associated with the occurrence and distribution of potential pathogens in plants irrigated with polluted or contaminated wastewater. Studies have shown that soil amended with organic matter and irrigation with contaminated wastewater can increase the occurrence of potential opportunistic human pathogens in plants (Urta et al., 2019; Akanmu et al., 2021). Also, the long-term persistence of these waste materials in the soil can contribute to the strong affinity and attachment of microbial pathogens to the plant root surface, this aspect still requires further studies. Nevertheless, less information is available on the impact of agricultural practices in the distribution of potential plant pathogenic endophytic microbes and foodborne pathogen transmission.

The incidence of bacterial pathogens, *Klebsiella pneumoniae*, *Enterobacter*, and *Escherichia coli* from vegetable crops irrigated with contaminated wastewater has been documented (Ibenyassine et al., 2007). Gu et al. (2013) reported endophytic bacterial pathogens, *Salmonella enterica* serovar *Typhimorium* and *Salmonella* spp. from the internal tissue of tomatoes grown in organically amended soil. Also, a recent study by Cui et al. (2020) reported endophytic bacterial community structure and abundance of potential bacterial pathogens in the root endosphere of pepper using high throughput sequencing and real-time quantitative polymerase chain reaction (qPCR). Furthermore, the authors reported dominant root and fruit bacterial phyla, Actinobacteria, Bacteroidetes, Firmicutes, and

Table 4
Some examples of potential endophytic human pathogenic species from the root of plants.

Plant type	Endosphere and rhizosphere human pathogenic species	References
Tomato colonization	<i>Pseudomonas aeruginosa</i> , <i>Acinetobacter</i> sp., <i>Bacillus cereus</i> , <i>Staphylococcus saprophyticus</i>	Egamberdieva (2010)
Maize colonization	<i>Staphylococcus</i> spp., <i>Pseudomonas fulva</i> , <i>P. aeruginosa</i> , <i>P. mosselii</i> , <i>P. mendocina</i> , <i>Kosakonia cowanii</i> , <i>Enterobacter cloacae</i> , <i>Klebsiella pneumoniae</i> , <i>Bacillus cereus</i> <i>Pantoea agglomerans</i> , <i>Bdellovibrio</i> spp.	(Velázquez et al., 2016; Correa-Galeote et al., 2018; Fadji et al., 2020a)
Lettuce endosphere	<i>Salmonella enterica</i>	Klerks et al. (2007)
Cannabis colonization	<i>Salmonella enterica</i> , <i>Pseudomonas aeruginosa</i> , <i>Acinetobacter baumannii</i> , <i>Ralstonia pickettii</i> , <i>Escherichia coli</i> , <i>Stenotrophomonas maltophilia</i> , <i>Aspergillus</i> spp., <i>Penicillium</i> spp.	McKernan et al. (2016)
Pepper colonization	<i>Aeromonas hydrophila</i> , <i>Arcobacter butzleri</i> , <i>Bacillus cereus</i> , <i>Escherichia coli</i> , <i>Enterococcus faecium</i> , <i>Klebsiella pneumoniae</i>	Cui et al. (2020)
Rhizosphere of chickpea	<i>Actinomyces israelii</i> , <i>Rothia mucilaginosa</i> , <i>Porphyromonas endodontalis</i> , <i>Solobacterium moorei</i> , <i>Cutibacterium acnes</i> , <i>Alcaligenes faecalis</i> , <i>Mycobacterium celatum</i> , <i>Capnocytophaga ochracea</i> , <i>Collinsella aerofaciens</i> , <i>Paenibacillus lautus</i> , <i>Enterococcus</i> spp., <i>Roseomonas mucosa</i> , <i>Raoultella ornithinolytica</i> , <i>Proteus mirabilis</i> , <i>Coxiella burnetii</i> , <i>Prevotella</i> spp., <i>Staphylococcus</i> spp., <i>Elizabethkingia meningoseptica</i> , <i>Ruminococcus</i> spp., <i>Neisseria</i> spp., <i>Haemophilus parainfluenzae</i> , <i>Treponema</i> spp., <i>Mycoplasma genitalium</i> , <i>Leptospira noguchii</i> , <i>Halomonas meridian</i> , <i>Actinobacillus pleuropneumoniae</i> , <i>Aggregatibacter actinomycetemcomitans</i> , <i>Brachyspira hyodysenteriae</i>	Suyal et al. (2021)

Proteobacteria; and some endophytic bacterial pathogens, capable of causing disease in humans (Cui et al., 2020). The abundance of endophytic bacterial phyla, Gemmatimonadetes, Nitrospirae, Planctomycetes, Proteobacteria, TM6, Verrucomicrobia, and WS3 in the internal tissue of lettuce root irrigated with *Salmonella* contaminated water compared to the control (i.e. irrigation water containing no *Salmonella*) have been reported with more understanding about the long-term impact of reclaimed wastewater as a source of irrigation water on the leafy green vegetables associated microbes (Zhang et al., 2018).

Generally, the internal tissue of plants harbors both beneficial and pathogenic microbes. The beneficial microbes are more important due to the significant ecological services associated with them in plant growth promotion and health sustainability. Conversely, numerous pathogenic microbes, which negatively influence plant and human health status have also been found in the plant tissue and the surrounding environments (Tyler and Triplett, 2008). Some of these groups of endophytic microbes have emerged as opportunistic pathogens and their ability to cause diseases in humans has been linked to plant environment, mode of transmission, and genetic make-up (Banik, 2019). The different species of opportunistic pathogenic bacteria in the plant environment with a potential risk to humans are listed in Table 4, and more examples of potentially human pathogenic species in the plant environment can be found in the work of Berg et al. (2005). Compared to the endophytic bacteria, limited information is available on the potentially endophytic human pathogenic fungi. More emphasis is on endophytic bacteria human pathogens due to their occurrence and opportunistic nature. Hence, understanding the mechanism and approaches of shaping the endosphere microbiome can mediate their functions in terms of crop yield enhancement, plant health sustainability, and human safety (Poudel et al., 2019). Consequently, insights into the abundance and diversity of opportunistic human pathogenic bacteria in the endosphere can be the frontline approach in determining plant health status. Unraveling the plant-associated microbiome in organically amended soils with specific functions for disease suppressiveness can best be understood using omics techniques.

A study by Zhang et al. (2018) revealed the microbial community structure in the rhizosphere and root of lettuce irrigated with *Salmonella* contaminated water by comparing the variables based on harvest time, lettuce cultivar, and soil type. Authors reported that about 80% of the root-associated microbes originated from the rhizosphere; with a significant difference in the microbial communities found in the root compared to the rhizosphere (Zhang et al., 2018). The results imply that the lettuce root was less sensitive to the *Salmonella* inoculation through irrigation and the highly enriched microbes in the root originated from the rhizosphere.

The use of molecular markers and virulence genes for bacterial taxonomy can hypothetically validate the presence of soil-borne pathogens and the occurrence of opportunistic human pathogens into the plant endosphere through root tissue colonization. The phytopathogens can suppress the host defense mechanism and invasion of endophytic bacterial human pathogens. Hence, the suppressiveness of soil pathogens will be of an advantage in reducing the invasion of host plants by human pathogens (Mendes et al., 2013).

The occurrence of pathogenic bacterial genera, *Citrobacter*, *Salmonella*, *Klebsiella*, *Enterobacter*, and *Pantoea* has been reported in the endosphere of *Conzattia multiflora*, a leguminous crop grown in Mexico, which shows that the internal tissue of plants as an alternative host for pathogen survival can harbor enteric human pathogens (Wang et al., 2006).

Despite the occurrence of potential human pathogenic microbes in the plant endosphere; yet, how they infiltrate and colonize plant tissue is less understood. Depending on the plant species and pathogens involved, the colonization ability and number of human pathogens in the plant tissue can vary and be of great health and public concern, due to easy escape of surface sterilization or chemical treatment required for ensuring food safety.

Endophytic microbes are majorly found in abundance in the root region, where they enter the host plant (Dubey et al., 2021). Many findings have microscopically revealed the invasion of human pathogenic bacteria into the plant root at sites of lateral root emergence (Cooley et al., 2003; Kutter et al., 2006; Hirneisen et al., 2012). For instance, the invasion of *E. coli* O157: H7 and *Salmonella enterica* through the root injuries of lettuce and *Arabidopsis* have been observed microscopically (Tyler and Triplett, 2008). Similarly, the invasion of endophytic bacteria *Escherichia coli*, *Listeria monocytogenes*, *Serratia marcescens*, and *Klebsiella pneumoniae* in *Oryza sativa*, *Zea mays*, *Triticum aestivum*, *Medicago truncatula*, *M. sativa*, etc. through the plant root indicated their possible colonization and uptake into the food crops (Dong et al., 2003; Tyler and Triplett, 2008). The colonization of endophytic bacterium *S. typhimorium* and *Listeria* spp., a foodborne pathogen in barley root has been reported (Kutter et al., 2006).

Endophytic bacteria opportunistic human pathogens easily invade or colonize through root damage or cracks. The invasive and colonization of endophytic bacterium *Pseudomonas aeruginosa* PaBP35 in the shoots of black pepper and tomato seedlings by stem cuttings with high bacterial densities in the plant tissue have been investigated (Kumar et al., 2013). The observed high bacterial densities in the root and shoot of tomato seedlings inoculated with *Pseudomonas aeruginosa* PaBP35 compared to *P. aeruginosa* PA01; however, validate the level of host-specificity to endophytic bacterial colonization (Kumar et al., 2013). To sustain plant health status, there is a need to understand the nature and type of plant microbes, the occurrence of potential human pathogenic microbes in plants, and effective ways of controlling them.

6. Multi-functionalities of endophytic microbes in agriculture, biotechnology, and industry

To ensure sustainable agricultural food production, there is a need to devise long-lasting strategies to meet the current food demand for the growing population and proffer lasting solutions to hunger and food insecurity (Babalola, 2010). Harnessing copious microbial bioproducts and their application as growth stimulators stand promising in agricultural biotechnology as an alternative to agrochemicals in enhancing crop productivity (Zaidi et al., 2015; Romero-Perdomo et al., 2017). The effects of endophytic microbes on the host plants rely on their ability to grow, establish, colonize and assemble in the host plants via the development of cell organelles; for bacteria (flagella, pili, and fimbriae) and fungi (mycelia). Endophytic microbes, directly or indirectly sustain plant growth and health via stimulation of plant growth-promoting traits, such as nitrogen fixation, phosphate solubilization, siderophore and enzyme

production, phytohormone synthesis, ammonia and exopolysaccharide production, ACC deaminase activity, and ISR (Lally et al., 2017; Bhutani et al., 2021). Also, the role of endophytic microbes in plant stress tolerance, disease control, and nutrition cannot be overemphasized. Hence, the agricultural, biotechnological, and industrial importance of beneficial plant-associated microbes are discussed in the subsections below:

6.1. Endophytic microbes assist stress tolerance in plants

An increase in the human population demands more agricultural intensification for maximum crop production to ensure food security. Although, many factors hinder food production than expected. Abiotic stressors, such as high temperature, salinity, oxidative stress, drought, heavy metals, and climate change are common environmental conditions, which pose threats to crop productivity and degrade the environment (Omomowo and Babalola, 2021). More than 50% yield loss, cellular damage, and changes in the genotypic and phenotypic of plants can be linked to abiotic stress. It is therefore important to devise strategies that will enable the plant to adapt or cope with the effect of diverse environmental stress adaptors.

Endophytic bacteria and fungi adapt in different environments and confer abiotic stress tolerance in the host plants (Lata et al., 2018). Hence, exploring their bioproducts can be a promising strategy in averting challenges of low crop yield emanating from abiotic stress. Unraveling the biotechnological importance of endophytes can be of interest for improved plant stress tolerance and sustainable food production. Interestingly, the vast chemical compounds produced by endophytes immensely contribute to plant growth, adaptation, and survival in a complex stressed environment (Asaf et al., 2022). Plant inoculation with stress-tolerant endophytic microbes possessing growth hormone genes significantly enhances their growth and induces resistance to abiotic stressors (Spence and Bais, 2015).

6.1.1. Drought stress

Water forms an essential component in the living cell; basically for plant growth and other cellular responses. Water-limiting stress due to drought has been recognized as a major constraint influencing seed vigor and viability, plant performance, uptake of essential nutrients, and crop productivity (Hussain et al., 2018). Drought affects plant crops by prolonging seedling emergence and flowering, impairing cell division and functions, root elongation, promoting leaf senescence, reducing cell size, and yield parameters, retarding enzyme activity, inhibiting expression of stress response genes, and producing reactive oxygen species (Omomowo and Babalola, 2021).

Drought conditions subject plants to encounter some changes, which include the change in photosynthetic pigment, increase in ethylene biosynthesis, and alteration in the photosynthetic apparatus. Drought stress also accounts for the high accumulation of free radicals in plants, which alter membrane integrity and function, lipid peroxidation, superoxide ion formation, protein conformation, and finally cell death (Ojuederie et al., 2019). The impact of climate change is envisaged to increase problems of drought stress in future agriculture; hence, prevention of future occurrence is required.

In recent times, the impact of drought stress on the performance of some crops has been reported (Naveed et al., 2014), with a significant reduction in their yield. The exploration and biorational use of drought-stress tolerant endophytic microbes remain a fundamental approach in mitigating drought stress on plants to increase water potential, chlorophyll content, photosynthesis rate, and reduce yield and water loss. Endophytic microbes tend to display strong mechanisms for survival under water-limiting environments by forming a thick wall, accumulating osmolytes, enhancing electrolyte leakage, and synthesizing exopolysaccharides (Vurukonda et al., 2016). The drought-tolerance ability of endophytic microbes can be attributed to the expression of drought-tolerant genes, abundant solute in the plant tissue, and production of exopolysaccharides (EPS) (Igiehon et al., 2019). A study by Maqbool et al. (2021) reported a significant reduction and increase in water content, antioxidant activity, chlorophyll, and proline contents in maize inoculated by EPS-producing endophytic *Enterobacter cloacae* 2WC2 under drought stress. Similar findings have been documented on Fenugreek (*Trigonella foenum-graecum* L.) inoculated with arbuscular mycorrhizal fungi (AMF) (Irankhah et al., 2021).

The accumulation of compatible solutes, trehalose, betaine, proline, and glycine during drought stress contribute to bacteria functions by maintaining membrane integrity and protein structure (Mohammadi et al., 2019). A study by Srinivasan et al. (2022) reported the high level of specific metabolites (proline, trehalose, and pyroglutamic acid) production by endophytic bacteria *Arthrobacter agilis*, *Bacillus frigoritolerans*, and *Kocuria rosea*, which has been implicated in drought stress tolerance in bushy bean caper plant (*Zygophyllum dumosum*). An increase in salicylic acid and other metabolites in pepper (*Capsicum annuum* L.) inoculated with endophytic fungus *Penicillium resedanum* LK6 has also been reported in plant biomass recovery and stress mitigation (Khan et al., 2013). The co-inoculation of soybean with endophyte *Bacillus amyloliquefaciens* MN592674B and AMF *Rhizophagus irregularis*, *Sep-toglossom deserticola*, and *Acaulospora laevis* under drought stress has been reported to enhance plant growth and crop yield, metabolites biosynthesis (sugars, proteins, lipids, etc.), enzyme (glutathione-S-transferase) activity, and strengthened antioxidant and osmoprotectant (i.e. flavonoid, glycine betaine, and phenol contents) (Sheteiwiy et al., 2021). Furthermore, the authors affirmed changes in the stress hormones and adenosine triphosphate (ATP) content of an inoculated soybean.

6.1.2. Salinity stress

In the world today, salinity is regarded as one of the challenging conditions affecting crop productivity (Vaishnav et al., 2019). Salinity stress (SAS) adversely affects plant growth and reduces crop yield. The low water efficiency in the soil contributes to osmotic stress and high level of ions, which reduces microbial activity and uptake of essential nutrients from the soil for plant nutrition (Kumawat et al., 2021). The SAS in the soil usually occurs due to the presence of derivable toxic ions, such as nitrate (NO_3^-), calcium (Ca^{2+}), sodium (Na^+), chlorine (Cl^-), and potassium (K^+), which adversely affect microbial functions and plant growth (Omomowo and Babalola, 2021). Soil weathering or lesser rainfall contribute to the salt accumulation in the soil in form of electrically charged

ions. The adverse effect of SAS on crops is enormous, such that it causes nutrient imbalance, influence root nodulation, impair nitrogenase activity, increase soil solutes, reduce the soil water level and assimilation, seed germination, soil nitrogen pool, and crop yield (Mahgoub et al., 2021a). Furthermore, SAS damages crop health; reduces lipid peroxidation, and production of destructive ROS, which affects certain plant biomolecules.

Soil toxicity due to ion accumulation and osmotic stress; however, can affect the expression of genes involved in oxidative stress, stress resistance, and plant growth promotion in the genome of endophytic microbes (Geilfus, 2018). AMF as part of the plant ecosystem confers high salinity tolerance in the plant than bacteria, due to their sensitivity to a saline environment (Ghorchiani et al., 2018). How to manage salinity stress has been the major interest of agricultural scientists, environmentalists, and microbiologists. To this premise, different researchers have made reports on the role of PGPEM in alleviating the negative effect of salinity stress on plant growth (Abo-Kora, 2016; Kumawat et al., 2021; Noori et al., 2021). Furthermore, endophytic microbes induce salinity stress in plants through an indirect mechanism that regulates plant biochemical and physiological processes, ISR, and osmotic adjustment.

6.1.3. Temperature stress

Temperature stress remains a critical abiotic factor that needs to be controlled to ensure food security. Plants require optimum temperature for growth and higher productivity. Nevertheless, the growing of plants in the high or low temperate regions influences their survival and development, and if unchecked, it can cause plant death. An increase in environmental temperatures due to climate change affects plant cellular membrane, photosynthetic pigments, chlorophyll content, water level, metabolite secretion, and cell division (Wang et al., 2003). Similarly, cold or low temperatures can reduce the efficiency of enzymes needed to facilitate soil mineralization and nutrient uptake by plants. In addition, alteration of the cellular membrane, macromolecules interactions, and structural proteins can occur. Thus, at low or high temperatures, plant growth and metabolic activities are affected; by extension, with a negative effect on the seed vigor, emergence and germination rate, flowering, maturation, and harvesting period (Omomowo and Babalola, 2021).

Abiotic stress enhance fluidity (heat) or rigidity (cold), depending on the temperature conditions. Heat stress causes a change in plant response and phytohormone synthesis by increasing the amount of jasmonic acid and ethylene levels (Kumar and Verma, 2018). The plant developed diverse mechanisms of adaptation to subdue heat stress, with varied acclimatization patterns to either low or high temperatures. Production of heat-shock functional proteins and ROS-scavenging enzymes enables plants to adapt to heat and cold stress (Deng et al., 2018), with few exceptions. Therefore, it is important as a matter of urgency to devise a sustainable approach to mitigate temperature stress for sustainable crop production.

One of the promising approaches is to devise a suitable means for exploring endophytic microbes to mitigate the negative effects of temperature stress on plants (Kumar and Verma, 2018). The indirect mechanism and expression of heat or cold stress genes in the genome PGPEM enhance plant growth under heat stress. Based on the temperature requirements, microbes are grouped; either psychrophilic (i.e. growth at or below 15 °C) or psychrotrophic (grow above 15 °C) (Kumar and Verma, 2018). The expression of genes (*dnaJK*, *clpABPSX*, *groESL*, *hslU*, *hsp33*, *hsp70*, and *hspXG*) involved in temperature stress tolerance in the genome of endophytic *Stenotrophomonas indicatrix* BOVIS40 isolated from the root of sunflower has been reported to contribute to the photosynthetic rate, uptake of water and nutrient, resistance and survival of sunflower in temperate environments (Adeleke et al., 2021c). Similar findings by Nascimento et al. (2020) also revealed the survival of tomato plants inoculated with stress-resistant *Bacillus megaterium* STB1 under abiotic stressors.

The secretion of certain metabolites, such as trehalose and chaperone by endophytic microbes helps in the stabilization and conformation of cellular proteins, protects the microbial cell from thermal injury, and improves plant yield under heat stress (Kosar et al., 2020). Trehalose produced from endophytic fungi can safeguard protein from heat stress, thus preventing denaturation. The number of metabolites produced by the plant microbes relies on the type of endophytic microbes and abiotic stress. The successful colonization of temperature-tolerant endophytic microbes to plant tissue can immensely contribute to plant growth under different temperatures (Kumar and Verma, 2018). The thermostability effect of endophytic fungi, *Aspergillus* sp. SAP-3, *Aspergillus flavus* ACJ-2/ACJ-5, *Aspergillus* sp. LAS-4/SAP-6, and *Chaetomium* sp. LAS-6 on the 15 plant species has been reported to enhance fungal sporulation, and seedling growth under different temperature treatments (Sangamesh et al., 2018).

A study by Ali et al. (2018) reported the effect of heat-tolerant endophytic fungus, *Thermomyces* sp. CpE isolated from the root of *Cullen plicata* on cucumber plants grown in the field during the summer season in Egypt. The treated cucumber seeds with the spores of *Thermomyces* sp. CpE eliminates the heat stress on the cucumber seedlings by maintaining plant physiological and biochemical conditions compared to the untreated. Also, an account of the high accumulation of soluble proteins, saponins, flavonoids, total sugars, and antioxidants observed in the treated cucumber plants compared to the untreated plants suggests the biotechnological applications of this thermophilic heat-tolerant fungus in agriculture (Ali et al., 2018). Hence, the ability of heat-tolerant endophytic microbes for plant growth promotion and synthesis of metabolites under hyper-thermal conditions suggests their possible use as biofertilizers in developing safe and ecofriendly agriculture.

6.1.4. Heavy metals stress

The biotransformation process occurring below ground level due to the activity of endophytic microbes has assisted in reducing soil metal toxicity (Verma and Kuila, 2019). The excessive discharge of effluents and environmental wastes emanating from agriculture, human activities, and industry is alarming as a global threat to environmental conservation, soil and plant health (Kumar and Verma, 2018). Bioaccumulation of heavy metals (HVM) in agricultural soils can pose serious health issues to humans through the food value chain. The occurrence of HVM, such as chromium (Cr), cadmium (Cd), lead (Pb), copper (Cu), nickel (Ni), mercury (Hg), zinc (Zn), antimony (Sb), arsenic (As) in a metal stress environment influence the plant biochemical, metabolic, and physiological processes; thus

reducing soil nutrient pool, photosynthetic rate, nutrient assimilation, enzyme activity and enhancing the production of reactive oxygen species (Omomowo and Babalola, 2021). Also, HVM causes a reduction in crop yield, limiting seed viability and germination, and impairing root, shoot, and leaf formation in plants (Wang et al., 2020).

The removal of HVM from the soil by conventional means remains important to ameliorate their toxic effect on food crops for human safety and food security. The use of the conventional approach can be effective, but expensive; hence, there is a need to devise a cost-effective, reliable, and ecofriendly approach by exploring plant microbes (Kumar and Verma, 2018). In recent times, the use of plants microbes to remediate soils contaminated with HVM has been recognized as an emerging, innovative, promising, and sustainable technology that can easily be applied in diverse ways (Kuanar et al., 2022). The potential of endophytic microbes in the phytoremediation process can be a good indicator in alleviating heavy metal stress compared to the plant itself. For example, the inoculation of heavy metal-tolerant endophytic *Aspergillus welwitschiae* has been reported to efficiently tolerate metal stress up to 1200 µg/mL, enhanced phytohormones production (IAA - 54.83 µg/mL), phosphate solubilization, biosynthesis of metal stress-related metabolites, which assist the endophytic fungus in reclaiming As and Cr contaminated soil (Hussain et al., 2022). Furthermore, an increase in the root and shoot length, fresh and dry weight, antioxidants production, and enzyme activity in soybean inoculated with endophytic *A. welwitschiae* have been reported (Hussain et al., 2022). Similar findings on the metal resistance up to 1.0 mM in a growth medium containing glutathione-producing endophytic bacteria *Enterobacter ludwigii* SAK5 and *Exiguobacterium indicum* SA22 has been documented by Jan et al. (2019). Upon inoculation, a significant increase in the yield parameters (root and shoot length; root and shoot fresh weight) and photosynthetic pigment (chlorophyll) were observed compared to the treated un-inoculated rice. The study further revealed high metal accumulation in the roots of inoculated rice than the shoots; and significantly upregulated heavy metal stress genes (OsGST, OsMTP1, and OsPCS1) in the treated non-inoculated rice compared with treated inoculated rice, which suggests the activity of the endophytic strains SAK5 and SA22 in reducing heavy metal stress (Jan et al., 2019). In addition, authors reported high organic acids (abscisic acid and salicylic), increased proline level, and reduced sugar content in rice inoculated with strains SAK5 and SA22, thus revealing Ni and Cd stress inhibition by the endophytic bacteria (Jan et al., 2019).

The mechanism employed endophytic microbes in assisting bioremediation of soil contaminated with heavy metals from high toxicity to lesser toxicity is dependent on enzyme detoxification, volatilization, metal biotransformation, metal complexation, efflux, extracellular polymeric substance (EPS) sequestration, and impermeability to metals (Chug et al., 2021). Other mechanisms, such as ACC deaminase activity, IAA production, nitrogen fixation, phosphate solubilization, and siderophores contribute to the removal of heavy metals and promote plant growth (Faria et al., 2021). The manipulation of ethylene in plants and alteration in the amount of ACC production by endophytic microbes can reduce heavy metals tolerance in the plant environment (Jia et al., 2021).

A study by Zahoor et al. (2017) reported the biotransformation of Cr, Cu, Mn, Co, and Zn in soils by endophyte, *Mucor* sp. MHR-7, thus reducing metal accumulation for improved plant growth. The combined inoculation of endophytic fungi and bacteria in the removal of heavy metals on agricultural soils proves to be more effective than the single inoculation. To this premise, improvement in alfalfa yield and resistance tendency to Cd stress has been observed upon co-inoculation with the rhizobia and AMF compared to the single inoculation (Wang et al., 2021b). More also, the combined inoculation of alfalfa plants with siderophore-producing endophytic bacteria *Pseudomonas indica*, *P. fluorescence*, and *Sinorhizobium meliloti* at different Cd concentration mitigate Cd-induced oxidative stress and improve plant growth (Sepehri and Khatabi, 2021). The ability of these microbes to produce phytochelatin is also a major factor, which mediates microbe-metal affinity for efficient bioremediation. The siderophore-producing endophytes having metal chelating and resistance attributes assisted in phytoremediation, mineral solubilization, and nutrient acquisition for plant growth (Sepehri and Khatabi, 2021). More also, the expression of notable genes involved in the detoxification, uptake, and transportation of heavy metals can help reduce heavy metal stress in plants inoculated with PGPEM.

Furthermore, diverse endophytic microbes have assisted in the phytoremediation, and bioavailability of heavy metals in soluble forms for plant use through the synthesis of biosurfactants, organic acids (citric and gluconic acids), and siderophores, as well as, redox and biomethylation processes. A study performed by Bilal et al. (2021) on the synergistic effect of co-inoculation of endophytic fungi *Penicillium funiculosum* LHL06 and *Paecilomyces formosus* LHL10 enhanced yield parameters and reduced multi-metal stress in soybean. In their experiment, authors reported high carbohydrates, minerals, amino acids, and antioxidants contents and a decrease in the organic acids, heavy metals, and stress-response endogenous abscisic acid contents in the seeds of soybean under metal stress, upon a single and combined inoculation of strain LHL06 and LHL10 (Bilal et al., 2021).

6.2. The role of endophytic microbes in plant nutrition, growth, and yield improvement

The biotechnological approaches in understanding complex plant-microbe interactions are major interests of my researchers with emphasis on how endophytic microbes can be maximally harnessed to enhance soil nutrients for plant nutrition (Bargaz et al., 2018; Hayatsu et al., 2008). So far, the efforts in unraveling the importance of endophytes to avert nutrient deficiency in the soil through biofortification programs remain a feasible strategy for the nutritional enhancement of food crops under different agronomic practices. In recent times, agricultural biotechnology, which involves molecular breeding, gene editing, and manipulation; however, remains a promising strategy to ensure endosphere competence for easy biotransformation of soil nutrients (Ahmar et al., 2020).

Endophytic microbes play a major role in plant root development for nutrient absorption from the soil level. In a natural environment, the bioavailability and uptake of most essential soil nutrients, such as nitrogen, phosphorus, and potassium contribute to plant growth and yield (Banik et al., 2019). Several studies are evident on the role of endophytic microbes in the bioavailability, bioaccumulation, and accessibility of soil nutrients for plant nutrition (Ma et al., 2011; Russo et al., 2016; Batool et al., 2021). For instance, the use of diverse endophytic microbes as promising candidates for the uptake of nutrients in nutrient-limiting soils has contributed to the growth of many plants under challenging climates (Prieto et al., 2017; Hiruma et al., 2018; Ribeiro et al., 2018). PGPEM employed direct mechanisms in nutrient solubilization, phytohormone production, nitrogen fixation, siderophore

biosynthesis, and other indirect mechanisms in sustaining plant health (Faria et al., 2021). Besides these mechanisms, these microbes have the potential of reducing the effect of abiotic stress in plants (Ignatova et al., 2021).

With an emphasis on plant growth promotion by endophytic microbes, plant nutrition can be achieved basically in three ways; (i) increase in soil nutrient availability, (ii) restoring nutrients in the soil, and (iii) enhancing plant accessibility to soil nutrients. The role of endophytic microbes in the acquisition of phosphorus in the soil through the production of organic acids and phosphate-hydrolyzing enzymes for plant performance and improved crop yield have been recently reviewed (Bargaz et al., 2021; Etesami and Jeong, 2021). In addition, the endosymbiotic, mono-and-combined inoculation of bacteria and fungi to improve plant growth with unique quality traits for crop production has recently been documented (Noceto et al., 2021). Singh et al. (2019) reported an increase in plant growth and oil yield of *Mentha arvensis* co-inoculated with *Trichoderma harzianum* and *Brevibacterium halotolerans* under greenhouse and field experimental conditions. Hence, the exploration of endophytic microbes to improve nutrition profiling in plants has been recognized as a promising biofortification strategy in sustainable agriculture. Enhanced increase in the mineral uptake, chlorophyll content, crop yield, and peroxidase activity of tiger nut inoculated with endophytic strain YSD YN2 due to the expression of secondary metabolites and PGP genes have also suggested their biotechnological importance in crop breeding and as a suitable candidate for biofertilizer production (Wang et al., 2022). The synergistic effects of single and dual inoculation of endophytic *Bradyrhizobium* sp. (LSBR-3) and *Pseudomonas aeruginosa* (LSE-2) on the nutrient (nitrogen, phosphorus, and potassium) acquisition in soybean significantly increase in the plant height, number of seeds, number of pods, seed protein content, nodules formation, nodules dry and weight weights, shoot and root dry weight, chlorophyll content, enzyme activities, and total grain yield at the flowering stage compared to the vegetative stage (Kumawat et al., 2019). A study by Hashem et al. (2016) reported enhancement of Ca, Mg, N, P, and K contents, yield parameters, and phosphatase activities in *Acacia gerrardii* inoculated with endophytic *B. subtilis* and AMF under salt stress.

Furthermore, the biostimulation efficacy of endophytic microbes in enhancing nutrient recycling, crop yield, nutrient uptake, and improving crop quality underline their key functions in ensuring food security. Interestingly, the bioengineering of endophytes as a source of bioinoculants and their incorporation into an organic farming form the current research trend in ensuring a safe and sustainable ecosystem (Bhardwaj et al., 2014; Kour et al., 2020b). Today, some groups of nitrogen-fixing and phosphate-solubilizing microbes have been exploited as biofertilizers. To mention but few, bacterial genera, *Rhizobium*, *Thiobacillus*, *Azospirillum*, *Bacillus*, and *Azotobacter* have been employed in the production of known commercially available biofertilizers (BioPotash, Biosilica, Bio-N, Siron, Azonik, Get-Phos, Green Earth Reap N4, and MicroZ-109) and their efficient use have enhanced soil fertility and crop yields (Roriz et al., 2020).

Despite the known fact on the biofertilizers, their market value, globalization, and contributions of endophytic microbes as biostimulants are currently limited. Nevertheless, their maximum usage is thought of to reduce the harmful effect of agrochemicals and improve future crop production to meet food demand for the incessant world population sustainably. Additionally, more research into the role of endophytic microbes in plant nutrition, growth, and yield improvement still requires further studies.

6.3. Biotechnological and industrial application

Biotechnologically, endophytic bacteria can be explored and applied in crop production as bioinoculants to maximally enhance yield output and control phytopathogens (Maheshwari et al., 2019a). In medicine, the natural biological products from endophytic bacteria as a source of antioxidants, antibiotics, and enzymes in formulating biocontrol agents have been documented (Dong et al., 2018). The biotechnological advancement and molecular insights into endophytic studies have been a pointer with designs in reclaiming soil polluted with heavy metals. In industries, the relevance of endophytic bacteria has been profound in producing safe and cost-effective biological products (Lata et al., 2019). The geometric increase in the human population has caused havoc to the ecosystems, thus resulting in various health challenges (Timsina and Connor, 2001). One such example is the alarming antibiotic resistance by bacteria, which has been a significant concern in pharmaceutical industries. Research intensification in discovering potent antibiotics and bioproducts from endophytic bacteria can help find a lasting solution to antibiotic resistance. Although, research into endophytic bacteria in developing new antibiotics is underway. Therefore, it is fundamental to devise modern approaches to avert this shortfall in pharmaceutical industries.

6.4. Biological control of plant disease, and pharmaceutical potential of endophytic microbes

For more than a decade now, the use of endophytic microbes as biocontrol agents has been increasingly elucidated in agriculture, medicine, and industry (Berg et al., 2010; Li et al., 2012). Harnessing the endophytic bacteria and fungi with functional traits as a biological control agent against phytopathogens aims to protect and sustain plant health. The disease suppressiveness attributes of some endophytic microbes significantly reduce plant pathogenicity. Endophytic microbes employed diverse mechanisms in plant disease control through disruption of structural barriers, synthesis of bioactive metabolites, phytoalexin, and phenolic compounds, pathogen-related proteins, hydrolytic enzymes, and oligosaccharides (Orozco-Mosqueda et al., 2018). Endophytes capable of producing hydrogen cyanide, siderophores, eliciting ISR and antibiosis, competing for nutrients with the phytopathogens, parasitism, and predation can reduce disease severity in plants (Asghari et al., 2020). The ISR and antibiosis are known to be common mechanisms employed by plant microbes. For example, ISR by endophytic *Bacillus* sp. 2P2 against collar rot pathogen *Sclerotium rolfsii* in tomato has been documented (Sahu et al., 2019). Screening of endophytes for hydrogen cyanide production, which exerts lethal effects on plant pathogens has also been reported *in vitro* (Egamberdieva et al., 2022). A study by Lanteigne et al. (2012) reported the biocontrol activity of *Pseudomonas* sp. LBUM300 against the bacterial canker of tomato caused due to hydrogen cyanide and DAPG production.

The biocontrol activity of endophytic fungus, *Trichoderma harzianum* against *Rhizoctonia solani* and *Pythium aphanidermatum* has been reported to reduce the severity of rhizome rot and leaf blight diseases in turmeric in turmeric (*Curcuma longa* L.) (Vinayarani and Prakash, 2018). The biocontrol mechanisms of endophytic fungi can be attributed to their competition for nutrients, mycoparasitism,

enzyme (chitinase), metabolite, and antibiotic production. The antifungal activity of *Epicoccum* spp. and *Pleosporales* spp., *Xylaria feejeensis*, have assisted in the control of *Alternaria solani*, *Botrytis cinerea*, and *Fusarium oxysporum*, the causative agent of early blight, gray mold, and *Fusarium* wilt disease in *Solanum lycopersicum*, *Baccharis linearis*, and *Echinopsis chiloensis* (Brooks et al., 2022; Castro et al., 2022).

Screening of novel BCAs from endophytic microbes using diverse approaches has yielded success in recent studies (Li et al., 2020b; Nifakos et al., 2021; Bilański and Kowalski, 2022). The insecticidal attributes of endophytic fungi have been reported with potential effects in the control of diverse herbivorous insects in the host plants (Kaur et al., 2018). The insecticidal activity of endophytic fungus *Phomopsis oblong* colonizing the endosphere of elm plant against *Physocnemum brevilineum* beetle was first reported by Webber and Gibbs (1984). Today, several other studies have documented the toxic insecticidal compounds produced by endophytic fungi against plant pests (EL-Lebody et al., 2021; Singh et al., 2021a; Araújo et al., 2022). Other insect repellent compounds, such as naphthalene, and other volatile compounds (VoC) produced by novel endophytic fungi *Muscodor vitigenus*, *Hypocrea lixii* and *Beauveria bassiana* of *Paullinia paullinioides*, and *Phaseolus vulgaris*, which stimulate plant defense against sawfly, *Cephus cinctus*, pea leafminer, and fall armyworm has been reported (Daisy et al., 2002; Chebet et al., 2021).

Enzyme production potential is also another key attribute of endophytes in plant growth promotion (Toghueo and Boyom, 2021). Microbial enzymes participate in the hydrolytic activity by disrupting the pathogen cell wall and suppressing plant invasion by pathogenic fungi (Zaferanloo et al., 2013). The biotechnological application of enzymes from endophytic microbes has been profound in diverse fields, such as agriculture, molecular biology, pharmaceutical, detergent and textile, and medical (Castro et al., 2014).

Table 5
Biological activity of secondary metabolites produced endophytic microbes.

Endophytes	Plant source	Metabolites	Activity	References
Endophytic bacteria				
<i>Streptomyces</i> sp. NRRL 30566	<i>Grevillea pteridifolia</i>	Kakadumycin A, echinomycin	Antibacterial	Castillo et al. (2003)
<i>Aeromicrobium ponti</i>	<i>Vochysia divergens</i>	1-Acetyl-beta-carboline, 3-(hydroxyacetyl)-indole brevianamide F	Antibacterial	Singh and Dubey (2018)
<i>Bacillus velezensis</i> Bvel1	<i>Olea europaea</i>	oxydifficidin, Iturin A2, bacillibactin, surfactin-C13/-C15, azelaic acid, L-dihydroantcapsin	Antifungal	Nifakos et al. (2021)
<i>Streptomyces</i> spp., <i>Streptomyces</i> spp., <i>Bacillus atrophaeus</i> B. <i>mojavensis</i>	<i>Allium tuberosum</i> , <i>Aucuba japonica</i> , <i>Glycyrrhiza uralensis</i>	6-Prenylindole, cedarmycin A, B, phthalic acid	Antifungal	(Sasaki et al., 2001; Gos et al., 2017; Mohamad et al., 2018)
<i>Ktyococcus schroeteri</i> , <i>Streptomyces</i> spp., <i>Paenibacillus polymyxa</i> , <i>Burkholderia</i> spp., <i>Agrobacterium</i> spp.	<i>Ephedra foliata</i> , <i>Lychnophora ericoides</i> , <i>Boesenbergia rotunda</i> , <i>Ephedra foliate</i>	Camptothecin, 50-Dimethoxyisoflavone, fisetin, daunorubicin, ginsenoside Rg3, ginsenoside Rh2	Anticancer	(Conti et al., 2016; Fu, 2019; Yan et al., 2019; Ghiasvand et al., 2020)
<i>Streptomyces</i> spp	<i>Bruguiera gymnorhiza</i>	Xiamycin, trichodones A-C, halobacilin	Antiviral	Ding et al. (2010)
<i>Guignardia mangiferae</i>	<i>Gelsemium elegans</i>	Guignarderemorphilanes A-E, grignard lactone A	Anti-inflammatory	Liu et al. (2015)
<i>Microbacterium Burkholderia</i>	<i>Coptis teeta</i>	Berberine	Antitumor	Liu et al. (2020)
<i>B. thuringiensis</i> AK08	<i>Solanum lycopersicum</i> L.	Cholest-5-en-3-ol (3.beta.)-carbonochloridate	Anti-insect	Maulidia et al. (2020)
<i>Streptomyces</i> sp. NRRL 30566	<i>Grevillea pteridifolia</i>	Kakadumycin A, echinomycin	Anti-parasitic	Castillo et al. (2003)
Endophytic fungi				
<i>Arthrimum</i> sp. MFLUCC16-1053	<i>Zingiber cassumunar</i>	βcyclocitral, 3E-cembrene A, laurenan-2-one, sclareol, 2Z, 6E-farnesol, cembrene, β-isocomene, γ-curcumene	Antibacterial	Pansanit and Pripdeevech (2018)
<i>Aspergillus fumigatus</i>	<i>Albizia lucidior</i>	Ergosterol, ergosterol peroxide, helvolic acid, pseurotin A, monomethyl sulochrin, isosclerone, monomethyl sulochrin-4-sulphate, chaetominine, ciprofloxacin	Antibacterial	Hussein et al. (2022)
<i>Eupenicillium</i> sp. LG41	<i>Xanthium sibiricum</i>	Eupenicisirensin A/B, (2S)-butylitaconic acid, (2S)-hexylitaconic acid, xanthomegnin, viridicatumtoxin	Antibacterial	Li et al. (2014)
<i>Alternaria</i> sp. MHE 68	<i>Pelargonium sidoides</i>	Linoleic acid (9,12-octadecadienoic acid (Z,Z)), cyclodecasiloxane	Antibacterial	Manganyi et al. (2019)
<i>Arthrimum</i> sp. MFLUCC16-1053	<i>Zingiber cassumunar</i>	βcyclocitral, 3E-cembrene A, laurenan-2-one, sclareol, 2Z,6E-farnesol, cembrene, β-isocomene and γ-curcumene	Antibacterial	Pansanit and Pripdeevech (2018)
<i>Botryosphaeria dothidea</i> KJ-1	<i>Melia azedarach</i> L.	Pycnophorin	Antibacterial	Xiao et al. (2014)
<i>Fusarium</i> sp.	<i>Opuntia dillenii</i>	Equisetin	Antibacterial	Ratnaweera et al. (2015)
<i>Botryosphaeria dothidea</i> KJ-1	<i>Melia azedarach</i> L.	Stemphyperylenol	Antifungal	Xiao et al. (2014)
<i>Cladosporium</i> sp.	<i>Quercus variabilis</i>	Brefeldin A	Antifungal	Wang et al. (2007)
<i>Nigrospora</i> sp. LLGLM003	<i>Moringa oleifera</i> Lam.	Griseofulvin, dechlorogriseofulvin, 8-dihydroramulosin, mellein	Antifungal	Zhao et al. (2012)
<i>Xylaria</i> spp.	<i>Abies holophylla</i>	Griseofulvin	Antifungal	Park et al. (2005)
<i>Pestalotiopsis microspora</i>	<i>Terminalia morobensis</i>	Isopestacin	Antioxidant	Strobel et al. (2002)
<i>Cephalosporium</i> sp., IFB-E001	<i>Trachelospermum jasminoides</i>	Graphislactone A	Antioxidant	Song et al. (2005)

Enzymes contribute to microbial colonization, biodegradation, and biotransformation of natural organic compounds and the production of pharmaceutical products for sustainable healthy living by humans.

The continuous exploration of novel bioactive and therapeutic agents from medicinal plants and the associated endophytic microbes is advancing based on their pharmaceutical importance in treating human diseases (Salehi et al., 2019). The functional properties of these compounds include cytotoxic, antimicrobial, antibiotic, antidiabetic, antiarthritic, anticancer, nematocidal, antioxidants, antitumor, immunosuppressants, anti-tuberculosis, aphicide, and topoisomerase inhibitors (Gouda et al., 2016). The natural extraction or production of these compounds by endophytic microbes can be achieved through microbial fermentation or biotransformation. However, biotransformation process has been considered most advantageous due to fewer catalysis processes involved in obtaining desirable products compared to the fermentation with several catalytic steps. In recent times, several novel metabolites from endophytic fungi with anticancer, and antineoplastic have received much attention. For example, the first promising endophytic fungus, *Taxomyces andreanae* isolated from the inner bark of pacific yew, *Taxus brevifolia* produced a Taxol anticancer compound (Stierle et al., 1995). A recent update on the anticancer-derived compounds from endophytic fungi can be found in a recently published review article by Hridoy et al. (2022). Some antimicrobial compounds from endophytic bacteria and fungi include ambuic acid, munumbicin A, B, C, and D, phomodione, phomoenamide, 3-O-methylalaternin, isopestacin, and altersolanol A (Devi et al., 2012; Ruma et al., 2013).

Nowadays, antibiotic resistance is a major problem that needs urgent attention in sustaining both human and plant health; as the resistance of human and plant pathogens to most antibiotics and other chemicals is currently being experienced. The discovery and exploration of novel antimicrobials from endophytes can be the best alternative. Currently, the pharmaceutical potential, such as antimicrobial, anti-parasitic, antioxidants, and antidiabetic activity of some endophytic microbes are evident with some examples listed in Table 5. For more information on the biocontrol activity of endophytic microbes, the following articles and books are recommended (Das et al., 2022; Hridoy et al., 2022; Mamangkey et al., 2022; Paschapur et al., 2021).

7. Beneficial plant traits

7.1. Nitrogen fixation

Biofertilization and soil amendment with nitrogen-fixing endophytic microbes have emerged as alternatives to nitrogen fertilizer use on farmlands without posing threats to the ecosystem (Romero-Perdomo et al., 2017). Reports by Akanmu et al. (2021) documented the biorational use of nitrogen-fixing plant microbes in plant disease management as the most efficient approach in sustaining plant health. Diverse nitrogen-fixing endophytic microbes associated with rice, *Arabidopsis*, sugarcane, and maize endosphere have been reported to contribute to the nitrogen pool in the soil for plant nutrition (Rana et al., 2021; Tian et al., 2022). The incessant use of chemical nitrogen fertilizers in crop production has been a major concern in the past and current agricultural system (Kour et al., 2020b).

Due to the persistence of chemical residues in the food value chain and negative impacts on the ecosystem, such as loss of biodiversity, soil degradation, and acidification, there is a need to devise an ecofriendly approach in reclaiming soil nutrients by inoculating with agriculturally important endophytic microbes (Burragnoni and Jeon, 2021). For example, bioinoculants derived from these microbes, however, are economical to be used as an alternative in developing eco-friendly agriculture sustainably (Bhardwaj et al., 2014).

In recent times, the use of nitrogen-fixing endophytic bacteria as bioinoculants in nutrient-limiting soils has pointed out the need to improve crop yield through agricultural intensification (Bhutani et al., 2021). A study by Lata et al. (2019) argued that the nitrogen-fixing potential of endophytic microbes needs to be more focused due to their close interaction within the plant endosphere, ability to fix nitrogen, and reduction in oxygen pressure in the plant compared to the rhizosphere microbes. The endomycorrhizal association with the plant root can increase soil nitrogen levels and boost crop production. The nitrogen-fixing bacteria and AMF inoculation of Chickpea under drought have been reported to increase the grain yield and protein content, thus suggesting their future use as bioinoculants (Oliveira et al., 2017).

7.2. Mineral solubilization

The solubilization of mineral elements, such as phosphate and potassium in the soil contributed to plant yield in terms of quality and quantity (You et al., 2020). Nevertheless, most soil mineral elements are sometimes low due to their immobilized and insoluble nature, which rendered them inaccessible and unavailable for plant use (Meena et al., 2017b). Hence, there is a need for phosphorus availability in phosphorus-limiting soils to enhance crop yield and agricultural productivity. Phosphorus is needed by plants for various metabolic activities (protein synthesis), tillering, early flowering, and root development (Yuan et al., 2015). To this premise, screening of phosphate-solubilizing endophytic microbes is important to determine their metabolic activities through the release of organic acids (carboxyl and hydroxyl groups), which contributed to the conversion of phosphates into soluble form via the chelation of bound phosphate (Wang et al., 2014). The most identifiable endophytic microbes are phosphate solubilizers. Notably, findings have validated the phosphate-solubilizing potential of diverse endophytic bacteria isolated from the sunflower, rice, maize, sorghum, and wheat through *in vitro* plate assays (Mareque et al., 2015; Majeed et al., 2018; Perini et al., 2020; Lipková et al., 2021a; Lu et al., 2021). Also, some endophytic fungi, such as *Acremonium* sp. (ENF 31) and *Penicillium simplicissimum* (ENF 22) isolated from maize and rice are known to be phosphate solubilizers (Potshangbam et al., 2017).

Endophytic bacteria employed enzyme biosynthesis (phytases, C-P lyase, and nonspecific phosphatases) in the solubilization of immobilized phosphate in the soil. An account of organic acid production and complexolysis, exchange reactions, and acidolysis by endophytic bacteria which enhances phosphate solubilization in soil have been documented (Stella and Halimi, 2015). Examples of

organic acid include lactate, acetate, tartarate, oxalate, ketogluconate, citrate, glycolate, gluconate, and succinate (Lata et al., 2019). The production of organic acid by endophytic microbes relies on substrate utilization potential to solubilize phosphate. Supplementation of phosphate production medium with sugars, such as galactose, sucrose, or glucose as a carbon source enhances phosphate activity of endophytic microbes (Yadav, 2018; Ye et al., 2019).

Diverse potassium solubilizing endophytic bacteria genera have been identified by many researchers (Yuan et al., 2015; Baghel et al., 2020; Kour et al., 2020a). A finding by Verma et al. (2015) reported potassium solubilizing endophytic bacterium, *Bacillus amyloliquefaciens* IARI-HHS2-30 isolated from wheat. The insoluble form of potassium in the soil includes mica, orthoclase, illite, muscovite, feldspar, and biotite. Muthuraja and Muthukumar (2021) reported *Aspergillus terreus* KSF-07, *A. niger* KSF 55, and *A. violaceofuscus* KSF-69 from maize plant, with strain KSF-69 exhibiting high potassium solubilization from mica and potassium aluminum silicate, thus suggesting strain KSF-69 as an alternative to potassium fertilizers in ameliorating potassium deficiency and pave the way for sustainable agriculture.

The role of endophytic microbes in the biotransformation of potassium in the soil cannot be overemphasized; thus suggesting their possible exploration in agricultural biotechnology to enhance potassium availability in the soil for plant nutrition (Unno et al., 2015; Muthuraja and Muthukumar, 2021). Lata et al. (2019) validated the use of potassium fertilizer in boosting potassium levels in agricultural soils. The limited use of potassium fertilizer by farmers can be linked to the cost of purchase compared to nitrogen or potassium fertilizers, and exploration of endophytic microbes in the formulation of potassium fertilizers can help minimize the high cost of chemical fertilizer input in agriculture.

7.3. Phytohormone's biosynthesis

Endophytic microbes produce phytohormones, such as indole-3-acetic acid (IAA), gibberellins, and cytokinins with different functions in plants (Chen et al., 2017; Muthuraja and Muthukumar, 2021). IAA functions in plant root development, mediate cell division, differentiation and extension, and fruit ripening. These attributes support plant root architecture, which enhances nutrient and water absorption from the soil for plant metabolism (Maheshwari et al., 2019a). The functions of IAA-producing endophytic microbes rely on their close interactions with the host plants. So, the cooperation between endophytic microbes and the host plants can contribute to plant growth and microbial survival in an ec niche. Findings on the IAA production under *in vitro* studies by copious endophytes have revealed their potentialities in plant growth promotion (Latif Khan et al., 2016; Gao et al., 2021; Muthuraja and Muthukumar, 2021). For instance, Reetha et al. (2014) demonstrated IAA screening of *Pseudomonas fluorescens* and *Bacillus subtilis* in a culture medium. Similarly, optimization of process parameters for IAA production in a culture medium supplemented with tryptophan by plant growth-promoting endophytic bacteria has been reported (Apine and Jadhav, 2011; Bharucha et al., 2013; Widawati, 2020). Different IAA concentration (mg/L) by endophytic fungi isolated from a medicinal plant, liquorice (*Glycyrrhiza glabra* L.) has also been reported by Arora et al. (2019).

Cytokinins are also a phytohormone produced by diverse endophytic microbes needed for plant growth (Wani et al., 2016). The early seed germination, apical dominance, activation of dormant buds, chlorophyll biosynthesis, induction of chloroplast proteins, early leaf development, and nucleic acids has been linked to the cytokinins biosynthesis by the plant endophytes (Wani et al., 2016). The induction of drought stress in plants influences plant growth and crop yield due to high ethylene production. Some identifiable endophytic microbes reduced ethylene levels in plants by producing ACC deaminase enzymes. Production of ACC deaminase by endophytic microbes contributes to plant immune responses against stress adaptors and maintains ethylene levels in the plant without growth impairments (Dubey et al., 2021). Also, ethylene serves as a tool, which modulates bacteria surface attachment. Furthermore, ethylene stimulates multiple functions in plants under different environmental conditions. For instance, aside from modulating plant growth, ethylene has been regarded as a stress hormone (Danish et al., 2020). The increase of ethylene levels in plants under drought stress, high temperature, salinity, low humidity, metal toxicity, pathogenicity, and waterlogging negatively influence plant performance (Zafar-ul-Hye et al., 2019). Some examples of ACC deaminase-producing plant growth-promoting endophytic microbes; bacteria include *Bacillus amyloliquefaciens*, *Agrobacterium fabrum*, *Pseudomonas fluorescens*, and *Chromobacter xylosoxidans* (Karthikeyan et al., 2012; Ali et al., 2014; Zafar-ul-Hye et al., 2019; Maheshwari et al., 2020) and fungi, which include *Trichoderma* DEMENTK3A0, *T. asperellum* MAP1, *T. asperellum* T203, (Viterbo et al., 2010; Jaroszuk-Ścisł et al., 2019; Rauf et al., 2021).

7.4. Siderophore biosynthesis

Some endophytic microbes produce siderophores, which mediate the transport of complex iron molecules by specific proteins. Siderophore biosynthesis has been implicated in plant growth promotion by direct or indirect mechanisms (Maheshwari et al., 2019b; Sánchez-Cruz et al., 2019). Siderophore production has been investigated using radiolabelled ferric siderophores as a source of iron (Pourbabaee et al., 2018). This method reveals plant ability to take up the labeled iron by a vast number of endophytic bacteria, such as *Pseudomonas*, *Enterobacter*, and *Sporothrodurans* (Pourbabaee et al., 2018). Similarly, notable endophytic fungi, *Penicillium chrysogenum* CAL1, *Aspergillus sydowii* CAR12, and *Aspergillus terreus* isolated from *Cymbidium aloifolium* have been screened for siderophore production in a recent study by (Chowdappa et al., 2020), with the future recommendation of harnessing strain CAL1 due to high siderophore production and antimicrobial properties in boosting plant resistance to pathogenic microbes.

8. Conclusion and future prospects

The need to boost agricultural food production through soil enrichment became important with a research focus on endophytic microbes in ensuring sustainable agriculture. The establishment of microbial communities in plants relies on the presence of attachment cell organelles and the synthesis of secondary metabolites. Due to the environmental threats posed by chemical fertilizer

usage, alternative and promising approaches need to be embraced in growing economically viable cereals, legumes, and oilseed crops. Singular or combined use of endophytic microbes as bioinoculants can ameliorate the effect of abiotic stress on the plant and maintain endosphere competence. The *in vitro* screening of endophytic microbes for plant growth-promoting attributes, such as nitrogen fixation, ACC deaminase activity, siderophore production, and phosphate solubilization have been investigated with success in the greenhouse and field experiment trials.

The study of the endophytic microbiome still needs to be intensified, to unravel their novel genes and provide information on their mechanisms of interactions with the host plants in alleviating abiotic stress. So far, understanding endophytic microbial lifestyle and functions in plants remain critical in recent times. According to the findings of Dubey et al. (2020), it was reported that approximately 2% of endophytic bacteria had been studied from terrestrial plants, while information regarding aquatic plants is still lacking. To maximally explore endophytic bioresources, there is a need for bioformulation and biofertilization as an organic amendment to sustain plant and soil health. Plant inoculation is faced with many challenges; hence, the need to understand how endophytes colonize, transmit, and interact with plants molecularly became important.

To date, little information is available on the database regarding metagenome data, while metabolomics data is less documented on endophytic microbes. Nevertheless, endophytic microbes remain a reservoir of novel biological and chemical compounds important in agriculture, medicine, and industry. Hence, understanding the genome attributes of endophytic microbes will help understand their mechanisms of interactions and metabolism for plant nutrition.

Furthermore, modern biotechnological approaches in endophytic research can be a gateway in averting shortfall in the pharmaceutical industry due to an increase in antibiotic resistance by some human and plant pathogens, which make them difficult to control. Derivable antimicrobial agents from endophytic microbes can be the best alternative in future medicine in treating diabetes, cancer, tumor, and other related diseases. Nevertheless, research findings in achieving this scientific phenomenon are still underway. Hence, it is recommended that more research should be focused on endophytes associated with medicinal plants, as the antimicrobial attributes of these plants can easily be mirrored on the associated microbes for the future development of pharmaceutical products.

Declarations of interest

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Authors' contribution

BSA and OOB had the idea of the review article and suggested the review topic. BSA performed the literature search and wrote the first draft. BSA revised and formatted the manuscript. OOB made substantial and technical contributions to the structure of the various manuscript drafts. Both authors read and approved the final manuscript.

Declaration of competing interest

None.

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