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Review

Strategies to Enhance the Use of Endophytes as Bioinoculants in Agriculture

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Abstract: The findings on the strategies employed by endophytic microbes have provided salient information to the researchers on the need to maximally explore them as bio-input in agricultural biotechnology. Biotic and abiotic factors are known to influence microbial recruitments from external plant environments into plant tissues. Endophytic microbes exhibit mutualism or antagonism association with host plants. The beneficial types contribute to plant growth and soil health, directly or indirectly. Strategies to enhance the use of endophytic microbes are desirable in modern agriculture, such that these microbes can be applied individually or combined as bioinoculants with bioprospecting in crop breeding systems. Scant information is available on the strategies for shaping the endophytic microbiome; hence, the need to unravel microbial strategies for yield enhancement and pathogen suppressiveness have become imperative. Therefore, this review focuses on the endophytic microbiome, mechanisms, factors influencing endophyte recruitment, and strategies for possible exploration as bioinoculants.

Keywords: agricultural application; biodiversity; biostimulants; microbial recruitment; yield enhancement

1. Introduction

The envisioned sustainable development goals (SDGs) and food security can be achieved through agricultural intensification with the target of meeting world food demands [1]. However, the excessive use of chemical fertilizers to enhance soil nutrients and plant nutrition has led to several ecological and environmental problems, such as soil pollution, soil acidification, soil degradation, reduction of soil organic matter, nitrogen leaching, soil compaction, and loss of soil carbon, thus, making it unsustainable [2]. Therefore, there is a need to devise eco-friendly approaches by exploring plant-associated microbes as bioinoculants to improve agricultural productivity without the use of agrochemicals [3]. Furthermore, the methods to unlock seed endophytes as bioinoculants for improving soil health and crop production were evident from Mukherjee et al. [4], yet, establishing the efficacy of microbial bio-input towards commercialization needs further investigations.

Endophytic microbes contribute to plant growth by soil mineralization, induced systemic resistance, production of bioactive molecules, phytohormone synthesis, and resilience to drought stress [5]. The interdependence of microbes with host plants can mediate their recruitment with responsive feedback in the plant health management. Endophytic microbes can be engineered, although, their application as bioinoculants in modern agricultural systems is less explored. Nevertheless, the mechanisms employed by endophytic microbes have been documented in the literature [6–8]. Furthermore, the close interactions between the host plants and their associated microbes can enhance plant growth and health by increasing nutrient uptake and improving the plant's resistance to pathogens and stress [9].

Endophytic microbes contribute to the biochemical and physiological functions of plants by enhancing crop production, nutrient cycling, bioremediation, and energy storage [10]. Under certain conditions, microbial activities may be affected by low phytohormone synthesis, which is needed for plant nutrition. For instance, the bimodal and primordia effects of auxin production on root development in response to the force of gravity have been documented [11]. Auxins act as signal molecules that can mediate an interaction between microbes and plants [12]. The production of indole-3-acetic acid (IAA), which is involved in root imitation, cell enlargement, and division, has been reported by some endophytic microbes [13,14]. The ability of endophytic microbes to produce IAA is considered to be an important factor that drives cotyledon cell expansion, yield enhancement, root tip number, root length, and root surface area during seedling and plant growth [15]. Nevertheless, the IAA-producing potential of endophytic microbes for plant development may differ depending on their interactions [16]. Evidence from the literature has shown that most endophytic microbes can produce high concentrations of IAA with increasing root biomass, which can facilitate plant uptake of water and nutrients, which in turn can enhance their colonization [17–19]. Additionally, the regulatory mechanisms of cytokinins and gibberellin biosynthesis have been reported to positively or negatively influence root development and plant growth [20]. Cytokinin biosynthesis promotes cell division in plant roots and shoots and the growth of buds. It has been reported that this hormone is produced by some endophytic microbes in culture media [21]. Although, little information is available on the cytokinins production by endophytic microbes. A study by Bhore et al. [22] investigated the screening of cytokinin-like compounds from endophytic bacteria including *Acenitobacter calcoaceticus*, *Paenibacillus polymaxa* and *Pseudomonas resinovorans* isolated from the leaves of *Gynura procumbens*; thus, suggesting possible use as plant growth enhancers. Similarly, gibberellins also stimulate several plant metabolic functions, important for plant growth and development, which include seed germination, stem elongation, flowering, and fruit formation and senescence [23]. The discovery of gibberellins from endophytic microbes is less studied, as little is known about gibberellin production by microbial endophytes. However, endophytic bacteria including *Curtobacterium oceanosedimentum*, *C. luteum*, *Enterobacter ludwigii*, *E. tabaci*, *Bacillus cereus* and *Micrococcus yunnanensis* from rice plants [24] have been reported to produce gibberellins (GA1, GA4, GA7, GA8, GA9, and GA12) which contribute to plant growth and overall yield under drought and salinity stress. The amount of gibberellins produced by endophytic microbes can be measured in chemically defined media by capillary gas chromatography-mass spectrometry (CGC–MS). Dar et al. [25] reported the key role of abscisic acid (ABA) in boosting plant resilience to abiotic stress. ABA accumulation in soils mediates diverse aspects of the plant life cycle, including seed dormancy, germination, and adaptive responses to environmental stresses [26]. Diverse plant growth-promoting endophytic bacteria have been reported to produce ABA in a defined culture medium [27]. Limited information is available on the role of ABA in fungal metabolism, which may be of importance for establishing fungal-host interactions and virulence of fungal phytopathogens. Drought tolerance of plants can be linked to an increase in the concentration of ABA in the host plants [25]. Nevertheless, the production of ABA by endophytic microbes as a core mechanism of mitigating abiotic stressors has been rarely documented. However, endophytic microbes may boost plant resistance to abiotic stress through other important mechanisms. Other phytohormones, such as strigolactones and ethylene, have been reported to promote root hair and primary and adventitious root formation [28].

Screening of endophytic microbes for plant growth-promoting traits and upon solely or combined inoculation under greenhouse conditions has proven to be efficient in improving crop yields [29]. Highlights on the importance of endophytic microbes in agriculture are evident in the literature [6,30]. Nevertheless, little information is available on the strategic approaches to harness endophytic microbes in crop breeding. Hence, employing diverse approaches in crop breeding systems by determining plant genotype and beneficial plant microbes may help to understand the endophytic lifestyles in crop production [31,32]. In

recent times, insights into the taxonomy and functional profiling of yet-to-be cultured endophytic microbes using next-generation sequencing (NGS) have been understudied and less emphasized; hence, further studies are required. Despite the efforts so far by many researchers, there is still a need to provide information on the diverse approaches and strategies employed by endophytic microbes in enhancing crop productivity. Also, the inconsistency and variability surrounding bioinoculant usage need to be properly managed by devising appropriate strategies for plant nutrition. Therefore, understanding this phenomenon may suggest a way to maximally explore endophytic microbes as bioinoculants in modern agriculture. Hence, this review discusses the endophytic microbiome, mechanisms, factors responsible for endophytic recruitment, and strategies for shaping the plant microbiome.

2. Endosphere Microbiome

All microorganisms that live in the tissues of plants are referred to as the endophytic microbiome. Hardoim et al. [33] recently redefined this terminology, which is being used in a variety of research and provides that endophytes and pathogenic invaders can be distinguished practically. Information gained in recent years has shown that symbiosis or pathogenicity of microbes could be influenced by different factors, which include the colonizing microbiota itself, the environment, and plant genotypes [34]. As a result, without comprehensive functional investigation, distinguishing the beneficial endophytes from the pathogenic types based on conventional molecular methods and phylogenetic markers might be difficult. As a result, Hardoim et al. [33] proposed that the word endophytes can be any group of microbes that colonize and complete their life cycle within the plant endosphere.

Diverse Endophytic Microbes Associated with Plants

The root–soil interface contains diverse microbial populations compared to other plant organs [35]. Findings have shown diverse microbial communities in plants [36,37]. For example, the bacteria phyla, including Verrucomicrobia, Acidobacteria, Planctomycetes, Proteobacteria, Bacteroidetes, and Actinobacteria, have been reported as the most identifiable bacterial taxa from the endosphere and rhizosphere of plants [33]. On the other hand, rhizosphere bacteria can infiltrate soil–root regions and become endophytes. Also, Acidobacteria, Proteobacteria, Actinobacteria, Planctomycetes, Chloroflexi, Bacteroidetes, Gemmatimonatedes, Verrucomicrobia, and Firmicutes have been reported in sunflower and grapevine roots [38,39]. Bacteroidetes, Proteobacteria, and Firmicutes have also been documented as prominent phyla inhabiting the roots of maize plants [40,41].

Diverse plant species may compose of different microbiota; however, developmental stages and plant genotypes have been reported to influence microbial community structures and functions in different ecological niches [42]. Usually, the observed changes in the microbial diversity belowground can be linked to the soil environment, soil history, and biotic and abiotic factors [34,40,43,44]. Deveau et al. [45] documented bacterial-fungal interactions, mechanisms, and challenges in ensuring safe ecosystems. A study by Fadiji et al. [46] showed that endophytic fungi and archaea in the roots of maize were affected by different farming practices. The authors further affirmed the dominant three archaeal phyla, namely Thaumarchaeota, Crenarchaeota, and Euryarchaeota, and two fungal phyla, Basidiomycota and Ascomycota, in organic farmlands compared to other sites.

Different farming practices have been employed in crop production with varied effects on plant microbial diversity. However, recent studies revealed that organic farming is now being embraced globally [47]. An organic farming system involves the combination of different practices to increase soil quality and reclaim soil nutrient loss with the view of ameliorating the effect of agrochemicals on the desirable soil microbiota [48]. This farming practice and other methods, such as cover cropping, manure, and compost amendments, need to be embraced to enhance soil nutrients and improve biodiversity and soil health [49,50]. Many studies unraveled the distinct attributes of organic and conventional

farming practices and their effects on microbial density in plant environments [47,48,51,52]. Maize plants cultivated under organic farming systems have been reported to harbor more endophytic microbial communities compared to inorganic fertilizer soils [46].

Consequently, a recent study by Harrison and Griffin [53] revealed differences in the assemblage of endophytic microbiomes inhabiting below- and aboveground tissues, which was attributed to the growth and habitat of the host plant. The study further revealed endophytic microbial richness in the stems of woody plants compared to the roots of graminoids, which harbored higher microbial communities [53]. Diverse assemblages of endophytic microbiomes have been investigated in the leaves' endosphere and their abundance often depends on extrinsic conditions, such as genotypes, microclimate and climate, and plant species [43,54]. Interestingly, maize seeds also predominantly harbored bacterial phyla, such as Actinobacteria, Proteobacteria, Bacteroidetes, and Firmicutes [55,56]. Molecular investigation of seed endophytes has also revealed similar taxa in the genus Setaria [57] and the family Brassicaceae [58].

So far, little research has been conducted on the potential roles and applications of seed-borne endophytes [59]. Extant research on seed endophytes focuses on the use of seed-related bacteria to boost host immunity, while some reports have revealed the biocontrol and phytoremediation ability of seed-borne endophytes [60,61]. Seed endophytes often employed a similar colonization pattern to those found in other plant components. On the other hand, certain endophytes are capable of living inside plant tissues under adverse conditions [62]. The phrase "competent endophytes" refers to microorganisms that efficiently colonize plant sections with the potential to stimulate physiological changes in plants based on the host selection [63]. The ecology and functions of seed bacterial endophytes are less studied. Several seed bacterial endophytes can influence the physiological and biochemical functions of plants by altering the phytohormones and ethylene levels of the host plants [64]. The inoculation of seeds with beneficial endophytic bacteria, known as EndoSeed^{TM}, has recently been established as a unique strategy to improve plant characteristics and related microorganisms in a well-defined manner. The inoculation of seeds with copious microbial strains before seed germination and fruiting is necessary to ascertain their potential use. Earlier studies on the plant growth-promoting bacterial species *P. phytofirmans*, as well as their inoculation into the flower, colonization during the development of embryos, penetration of the stigma and style, and finally, established settlement within the mature seeds, back up this theory [65].

The root zone's endophytic community produced all-encompassing multifunctional chemicals as nutrient sources with ease [66]. The majority of microorganisms discovered in the endosphere may have unique genes capable of enhancing plant growth [67]. However, culturing techniques have only helped in the isolation and identification of approximately 1% of the entire microbial community in the endosphere. As a result, more studies on microbial solation can effectively present them as a vital tool for agricultural productivity in the future [68]. Nitrogen fixation, phytohormone (gibberellins, auxin, cytokinins, etc.) production, phosphate solubilization, and production of biocontrol agents to suppress plant and soil pathogens are some of the mechanisms employed by endophytic microbes for growing and sustaining plant growth [6]. Additionally, the production of secondary metabolites, siderophores, antibiotics, hydrogen cyanide, and ammonia indirectly contribute to the plant resistance to biotic and abiotic stresses [69]. Furthermore, the induction of systemic resistance by endophytic microbes can play a major role in the plants' tolerance and survival under extreme environmental conditions [70]. Therefore, exploring these microbial worlds within the plant can be promising in agriculture to ensure food security and the production of industrial bioactive compounds.

3. Mechanism Involved in Shaping the Endophytic Microbiome for Nutrient Acquisition in Plants

Shaping the plant holobiont by modifying the endophytic microbiome is a new approach to enhance nutrient acquisition in soil and crop production. There are different

techniques for microbial inoculation into the host plants and these include inoculation into the soil and plant tissues, direct injection into the seeds, and atomization into the plant tissues [71]. The endophytic microbiome can be integrated indirectly by using soil amendments and certain substrates and directly by using microbial inoculants [72].

3.1. Inoculation into the Soil and Plant Tissues

Soil amendments entail the addition of organic and inorganic fertilizers to the soil to modulate plant-microbial interactions and increase productivity [72]. Biological components, such as fungi, microalgae, bacteria, cyanobacteria, lichens, and actinobacteria, can be incorporated into the plant holobiont. Since the microbiome associated with the root plays a pivotal role in plant growth, protection against biotic stress, enhancing nutrient acquisition, and tolerance to abiotic stresses [73], isolation, screening, and revisiting this microbiome will further reveal its possible use as a bioinoculant. Different microbial species can colonize plant roots. For example, Dubey et al. [66] and Babalola et al. [74] revealed potential root-associated endophytic microbes in enhancing soybean and sunflower yields. Soil inoculation with important microbial species can mediate nutrient biotransformation in the soil for plant nutrition [71]. In particular, co-inoculations of the bacterium *Pseudomonas libanensis* TR1 and the arbuscular mycorrhizal fungus *Claroideoglomus claroideum* BEG210 into the root region of sunflowers have been reported to enhance the growth of the plants under salt and metal stresses [75]. The development and tolerance to the soil-borne *Phytophthora capsici* of chili plants were accomplished when the roots of the plants were enriched with *Acinetobacter* sp. UQ202, *Bacillus amyloliquefaciens* and *B. velezensis* [76]. Also, *Agrobacterium* sp. 10C2 increased the nodule number and biomass of bean plants, including antioxidants, flavonoids, and phosphorus content of the pods of the legume [77]. Recent studies by Aleynova et al. [78] and Bielecka et al. [79] reported flavonoids and stilbene production by endophytes (e.g., quercetin and resveratrol), which mediate microbial functions in the host plants.

The activities of the root-associated microbiome can be influenced by incorporating soil amendments or adding and activating signal molecules, such as root exudates, that attract a certain group of microbes to the endo-rhizosphere region (Figure 1). Concerning this, studies have been conducted using certain exudates as substrates in the field [80–82].
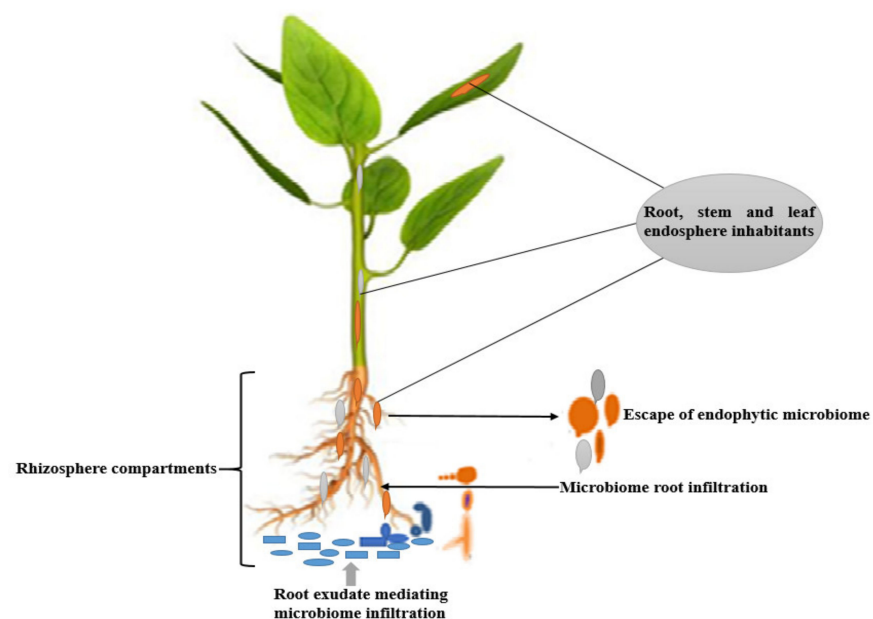

Figure 1. Plant roots showing root exudates attracting plant growth-promoting bacteria into the root tissues as endophytes and also expelling bacteria from the root tissues into the rhizosphere soil.

3.2. Direct Infection into the Seeds

Seed endophytes have also been reported to boost the germination and development of plants; such traits can be passed on to the generations down the line [65]. Inoculation of a tomato seedling rhizosphere with *Stenotrophomonas maltophilia* and *P. stutzeri* enhanced plant development. The inoculated microbes released dispersible substances (such as dimethyl disulfide) that were effective against the foliar pathogen *Botrytis cinerea* [83].

3.3. Atomization into Plant Tissues

Rhizobacteria, infiltrating plant tissues as endophytes, can be multiplied and transferred to the next generation of the plant. For instance, root exudates attract certain microbes into the rhizosphere [83–85] and the roots can serve as vital organs that filter beneficial microbes that penetrate the plant as endophytes [86]. However, plants eject bacteria into the rhizospheric soil [56], but the mechanisms of entrance and exit of the microbes from the plant holobiont need further research. Also, plant roots can directly attract microbes from their immediate environment for nutrient bioavailability [87]. The presence of these microbes within the plant endosphere and rhizosphere may display similar roles in the growth and development of plants (Table 1).

Table 1. Plant growth-promoting traits of some beneficial endophytic and rhizosphere microbes.

Microbial Niche	Host Plant	Beneficial Traits	References
Endosphere	*Ceriops decandra*	Biocontrol activity	[88]
	Vicia faba, *Ephedra pachyclada*	Plant growth-promoting traits	[89,90]
	Capsicum annum	Salt stress tolerance	[14]
	Triticum aestivum	IAA, ammonia, HCN, an enzyme production	[91]
	Glycine max	Bioremediation of heavy metals	[92]
	Corchorus olitorius	Nitrogen fixation, 1-aminocyclopropane-1-carboxylate (ACC) deaminase activity, IAA, and siderophore production	[93]
	Oryza sativa	IAA, phosphate solubilization, siderophore, HCN, DNase activity	[94]
	Hordeum vulgare	IAA, phosphate and potassium solubilization, nitrogen fixation, siderophore, ACC deaminase activity	[95]
Rhizosphere	*Zea mays*	Salt stress tolerance	[96]
	Cucumis sativus	Biocontrol activity, mineral solubilization, siderophore and enzyme production, IAA and polyamine biosynthesis, ACC deaminase activity	[97]
	Ocimum basilicum	Plant growth-promoting traits	[98]
	Pinus sylvestris	Phosphate solubilization, siderophore production, and IAA synthesis	[99]
	Lolium perenne	Phytoremediation of environmental pollutants	[100]
	Crocus sativus	Plant growth-promoting traits and biocontrol potential	[101]
	Ziziphus lotus	Heavy metal tolerance	[102]

In a study carried out by Mitter et al. [65], the endophytic bacterium *Paraburkholderia phytofirmans* PsJN was introduced into plants' flowers by atomization, thus, modifying the seed microbial composition by vertical inheritance and the growth pattern of the plants. In the greenhouse and field experiments, it was observed that the seeds harboring this bacterium grew significantly better than in the control experiments (plants that were not inoculated or modified by the bacterium *P. phytofirmans* PsJN). The study also investigated the transformations in the seed endophytic microbiome upon inoculation with the bacterium and observed a significant difference in the specific microbial taxa. The different effects manifested as a sharp reduction and an increase in α-/γ-Proteobacteria and β-Proteobacteria populations, respectively. The challenge of atomization technology is that

it might be difficult for the inoculated microbe to be inherited up to the second generation. However, this novel technique appears promising for growth enhancement using the plant microbiome [65,71].

4. Factors Determining Microbial Diversity in the Endosphere

Microbial diversity in the endosphere can be influenced by several factors, such as plant, soil, endophytic species, and environmental factors. The survival of microorganisms in the endosphere relies on their ability to colonize and secrete specific metabolites [103]. Singha et al. [104] reported the influence of plant species on the microbial diversity of the endosphere of many plants. For example, the diversity of microbes in the endosphere of maize could be different from that found in rice, cowpea, or wheat. However, plants with phylogenetic similarities may have a different endophytic microbiome composition [105] and this could be linked to differences in the nutrient requirements of the plants since microorganisms survive well where there is a source of energy that contributes to their metabolic activities.

4.1. Plant Organ Factor

Similar endophytic microbes might not be found in the same plants due to specific organ locations, recruitment tendencies, and colonization potentialities [106]. Additionally, there could be differences in the endophytic diversities in different organs of the same plant due to the peculiarity and activities of each organ. For instance, the surface area, temperature, concentration of nutrients, and direct access to sunlight can be differentiated across the organs of the same plant. Mina et al. [107] reported a significant difference in the endophytes found in the twigs and leaves of two plants, *Cvs. Cobrançosa* and *Verdeal transmontana*, due to differences in their chemical or physical properties. Campisano et al. [108] stated that the population of endophytes in roots was generally more stable than that in the stem; thus, suggesting a possible stability and microbial population in the root environment than in the stem. Other plant factors that can affect the microbial endophyte composition include physicochemical properties, chemistry of the cuticle, type of antibiotics produced, and plant resistance to microbial invasions.

4.2. Plant Exudate Secretion

Endophytic microbes might be shaped as a result of the phytochemicals and different root exudates released at the different growth stages of plants [109]. For instance, an increase in rhizobial growth and biofilm formation at higher concentrations of organic acids (oxalic acid and citric acid) and amino acids (glycine, glutamine, and glutamate) induces rhizobial chemotaxis behavior and has been reported to cause a change in the rhizobial chemotaxis, growth, and biofilm formation at different exudate secretion levels [110]. The authors further suggested that alterations in the root exudate secretion can contribute to the activity of the endophytic fungus *Phomopsis liquidambaris*, which mediates the peanut-rhizobia nodulation enhancement. Some specific exudates, such as hormones and phytochemicals, are released when a plant is infected and this can affect the diversity of endophytic microbes. Plants release exudates as a defense mechanism or response to pathogen infections [111–113].

4.3. Soil Factor

Hou et al. [114] reported the effects of soil depth on the diversity of plant endophytes by observing a higher endophytic population in *H. leave* and *P. villosa* at a depth of 10–20 cm and 20–30 cm in the soil, respectively. Canopy soils can often serve as a pool for endophytes found in the soil–root regions due to the pH, carbon, nitrogen, moisture content, and temperature in this region, which favors their growth and survival compared to opened ground soils [115]. The growth of endophytes might also be higher in canopy soils as a result of a higher extracellular enzyme activity that takes place in the region [115].

4.4. Climatic Factor

The endophytic community in plants is affected by different climatic conditions. For instance, Oita et al. [116] evaluated the effects of temperature and humidity on the endophytic communities of different trees across Panama and discovered that endophytes were more abundant in wetter forests, thus, indicating a negative correlation of endophyte diversity and high temperature. Also, Campisano et al. [108] revealed a decrease in the endophytic phylum of Proteobacteria in grapevines at fixed temperatures, with the smallest population at high temperatures in greenhouse experiments.

4.5. Crop Species

Some plant species significantly affect the diversity of endophytes present in the plant. For instance, Hou, He, Li, Wang, and Zhao [114] sampled three plants, namely *Hedysarum leave*, *Artemisia* and *Psammochloa villosa* plants, and observed a higher diversity of dark septate endophytes in *P. villosa* compared to other plants. In addition, Rodríguez-Blanco et al. [117] inferred the differences observed in the endophytic community structures in rice and maize to the genetic composition of the crops. The plant's genetic makeup is also a major factor that influences the type and diversity of endophytic microbes in diverse ecological niches.

5. Endophytic Microbial Recruitment in Agricultural Management

Plant–microbiome interactions can be modulated by plant species, plant genotype, plant immunity, signaling, plant-derived compounds, microbes, and biotic and abiotic factors. The highlights below are current insights into how some of these factors can facilitate microbial recruitment into the plant endosphere.

5.1. Plant Genotype

Differences in the microbial compositions of different genotypes by certain plant species have been reported [118–120]. Also, the genomic makeup of the plant host has been recognized as a critical component that determines the types of microbes that are recruited into the endosphere of plants [121]. For instance, cultivar-specific operational taxonomic units (OTUs) in three potato plants and the influence of a barley cultivar have revealed bacteria present in the root region of young potato and barley plants [118,122]. Peiffer et al. [123] showed that β-diversity and OTU richness were affected by maize plant genotypes, while Bulgarelli et al. [118] reported that the genotype of a particular plant contributed to the observed variation in the microbial composition of the plant. In addition, the impact of the genotype on the microbial community structure of wheat, oat, pea, and potato has been reported by some scientists [124,125]. Certain bacteria, such as *Acinetobacter*, *Chryseobacterium*, *Pseudomonas*, *Sphingobium* and *Stenotrophomonas,* have been reported to be more predominant in cultivars with low starch content than those with high starch content [125].

The microbial communities of genetically different wildtypes and transgenic plants were distinct in *Populus* [126]. Also, genomic variation within plant species can affect the microbial composition of the leaf endosphere [127]. Wagner et al. [128] performed a field experiment to reveal the diverse bacterial composition in the roots and leaves of *Boechera stricta* and further suggested that the plant genotype drives the leaf bacterial community composition with a varied root bacterial community across the sampling sites. The plant's choice of nutrients can also play an important role in the host specificity to certain groups of plant microbes [129]. However, whether these influential roles are hereditary, the microbial impact and the level interactions implemented in plant breeding are yet to be ascertained.

5.2. Plant Immunity and Signaling

The health status of plants can influence the types of microbes found in the plant endosphere. Plants use the following two kinds of defense mechanisms against pathogenic mi-

crobes: (i) pattern-triggered immunity (PTI) and (ii) damage-associated molecular pattern (DAMP). The PTI is elicited by conserved molecular structures, such as microbe-associated molecular patterns (MAMPs) and pathogen-associated molecular patterns (PAMPs), while the DAMP is associated with receptors localized in the plasma membrane [130]. It is not clear whether plants recognize beneficial microbes in the same way as they recognize pathogenic microbes. Upon attack by pathogens and herbivores, plants release phyto-hormones and volatile compounds that change the constituents of the plant root exu-dates [131,132]; thereby modifying the microbial community structure. *Arabidopsis thaliana* attacked by *P. syringae* showed an alteration in the expression of a malate transporter in the root due to the variation in malic acid production that enhanced the abundance of the beneficial *B. subtilis* [121,133]. Interactions between *Fusarium oxysporum* and cucumber roots led to an increase in the release of citric and fumaric acid and resulted in the production of biofilms by *B. amyloliquefaciens*. However, most scientists have focused on one-to-one plant microbial interactions, even though in a real-life situation, plants are prone to invasions by pests and microbial pathogens.

Plants adapt to different schemes to fight insects and pathogenic invasions, such as ac-tivation of immune responses, which cause alterations in the microbial composition of plant roots. Aphids activated the immune system of pepper plants after feeding on their leaves and attracted *B. subtilis* to the plants [134]. Enhanced JA signaling in *Medicago truncatula* can trigger better colonization by mycorrhizal fungi [135]. The endophytic microbes of the roots and the phyllosphere have been reported to change following a change in the JA signaling [136], while plants without jasmonate-mediated defense mechanisms showed more epiphytic microbes [137]. It is clear from the above-mentioned that plant defense mechanisms play a vital role in modulating bacterial community structures.

5.3. Plant-Derived Compounds

Diverse secondary metabolites released by plants include phenolics, alkaloids, and terpenoids [138]. Some of these metabolites are plant-specific, e.g., glucosinolates are produced by Brassicales [139]. It was reported that transgenic *Arabidopsis* releasing ex-ogenous glucosinolate showed different microbial groups in the root endosphere and rhizosphere [140]. Dastogeer et al. [106] highlighted the vital role of coumarins produced by the plant in determining the plant-associated microbial community. Authors proposed that certain coumarins can muster ferric iron and release reactive oxygen species, which selectively inhibit or kill some microbes and allow the proliferation of other beneficial ones. A special type of saponins, called avenacins, produced by oat plants (*Avena strigosa*), possesses antifungal properties and such that oat plants that did not produce avenacins attracted various fungal species in the roots [141,142], which were also more susceptible to pathogenic microbes [143]. However, a small difference was recently reported between the fungal communities of avenacin-producing and non-avenacin-producing oat plants. A profound influence of avenacins on Alveolates and Amoebozoa has been documented, but such influence has not been shown in bacterial communities [144]. This demonstrated that a little variation in the genotype of plants can trigger complex and unpredicted impacts on the recruitment and composition of plant microbial communities. These root-derived exudates might be specific to the host plant and can cause a change in the root-associated microbiome by selecting some specific microbes. Antimicrobial metabolites might selectively improve microbial growth by limiting the growth of other pathogenic microbes.

5.4. Plant Canopy Type

Plant canopy type can also affect the microbial composition of the endosphere. In particular, the bacterial population in sugar maple leaves directly correlated with the sugar canopy bacterial composition [145]. Microbial exodus via rain runoff might be a crucial factor responsible for the differences in the microbial composition of different plant canopy types [106]. Plant canopy structure affects the endophytic bacterial composition without influencing the rhizosphere bacterial community, which may suggest less impact from rain

runoff. There might be other factors, such as soil type or chemistry, responsible for the microbial differences [145].

6. Approaches and Strategies for Shaping Endophytic Microbes

The existing symbiotic interactions between microbes and host plants have offered a platform to investigate the nature and functions of endophytic microbes using various biotechnological tools [139]. More importantly, the strategies employed by endophytic microbes and how these microbes infiltrate plants for the possible derivation of chemical and biological products have necessitated the need for shaping the endosphere using various approaches, such as plant, microbiome, and meta-organisms [146].

6.1. Plant Strategies

Plant roots provide mechanical support for plant nutrient uptake and reduce water stress. The root-associated microbiomes can be engineered and explored as bioinoculants and upon inoculation to enhance plant growth under drought stress [147]. Root development due to IAA biosynthesis can structurally mediate host specificity by shaping the plant microbiome, which is crucial in plant adaptation under various environmental conditions [148]. The paradigm of plant–microbe interactions in the below ground level and exudate secretions, however, can trigger colonization and establishment of the desirable microbiota [149].

Plant genotype has been identified as one of the major factors influencing the diversity, survival, and functions of endophytic microbes [6]. For instance, reports have shown higher productivity in some wheat cultivars inoculated with *Herbaspirillum seropedicae* SmR1 in the absence of urea compared to wheat genotypes supplemented with urea with a less noticeable effect on the yield parameters [150]. This inferred that selecting desirable microbes as bioinoculants in crop breeding could be promising in enhancing crop productivity. The varied nutrient bioavailability in plant cultivars has shown differences in their microbial composition due to the plant genotype and alterations in the root architecture which cause a shift in the endosphere microbial communities [151]. Biotechnological approaches in the study of plant genomes and microbial interactions have shown how plant genomes can be manipulated to sustain beneficial microbiomes. Hence, modifications of the plant genome through genetic modifications to release exudates (chemoattractants) may enhance endosphere competence.

In plant-based strategies, diverse approaches for shaping the endophytic microbiome are employed, including plant breeding and genetic engineering [152]. Manipulation of a plant genome through different crop breeding for the selection of microbes of interest remains a fundamental approach to enhancing crop productivity to develop disease-and drought-resistant cultivars [153]. In recent times, research efforts in crop breeding have focused on the development of new plant varieties with high resistance to pathogens and adaptation to varied environmental conditions [154,155]. Liu, et al. [156] reported an endophytic bacterium, *Enterobacter* sp. E5, engineered by a surface plasmid display with ACC deaminase activity and a core function to reduce ethylene levels, which enhanced banana growth and plant resistance to pathogenic fungi, such as *Fusarium* wilt. The genetic modification of transgenic potatoes and the effects of antibacterial agents, cecropin/attacin, and T4 lysozyme produced by endophytic bacteria with pathogen-antagonistic potential compared to plant genotype, soil type, and pathogen infections has been reported as an effective strategy in the control of plant pathogens [157]. Nevertheless, further studies on how to assess genetically modified crops to obtain valuable information regarding their bioassay can be promising in the production of disease- and drought-resistant plant cultivars.

6.2. Microbial Strategies

To fully explore the culturable endophytic microbes, certain strategies need to be employed for functional measurements under various conditions. Many endophytic microbes may display dissimilar functions under different environmental conditions [158].

Research-based approaches to investigate the beneficial effects and adaptation of endophytic microbes in plants, however, can be used to measure the microbial biomass in the endosphere [159]. Diverse endophytic microbes, such as *Bacillus cereus*, *B. paralicheniformis*, *Pseudomonas aeruginosa*, *Enterobacter cloacae*, *Trichoderma asperellum*, *Epicoccum nigrum* and *Alternaria longipes*, with plant growth-promoting traits, ranging from induced systemic resistance, secretion systems, biological nitrogen fixation, quorum sensing, siderophore production, mineral solubilization to phytohormone synthesis, and antibiosis, have been reported to ensure sustainable plant growth and health [67,160–163]. Multiple antimicrobial agents and biosynthetic gene clusters, such as hydrogen cyanide, 2,4-DAPG, oligomycin, fengycin, iturin, and surfactin [164–166], as well as antifungal compounds, phenazine, pumilacidin, and pyrrolnitrin [167,168], produced by endophytic microbes with biocontrol activity against phytopathogens, have been investigated in greenhouse and field experiments. Also, inoculation of economic plants with endophytic microbiomes with secondary metabolite secretion potentials has been reported to reduce biotic and abiotic stresses in plants [169].

6.3. Meta-Organism Strategies

The synergy and interdependence of plants and microbes have contributed to plant growth in diverse ways, where the plants protect the microbes by making them secondary genomes and function as a holobiont or meta-organism [95,170]. To further explain the approaches and strategies for engineering host microbiomes for crop improvement and sustainable agriculture, the following recent literature reviews are recommended [146,152,171,172].

7. Next-Generation Sequencing (NGS) Technology in the Research of Endophytic Microbial Communities

The progression of the structure and functions of microbiomes remains a major topic in environmental microbiology [173]. Associations between plants and microorganisms can be influenced by several factors, such as the symbiont's genetic diversity, the way they are acquired from the environment, and the individual's ability to colonize hosts [174]. Large biological diversity exists among endophytes, with some plant species harboring over 100 different endophytic species [40]. Many attempts have been made to characterize endophytic microbial communities in maize plants using advanced molecular methods, but due to limiting factors, the results are often unreliable [47,175,176]. Characterization of endophytic microbial communities using conventional methods is often biased, as only less than 2% of the overall microbial populations can be identified [174,177].

Different NGS techniques have been used to unravel fungal endophytes in plants and these methods include the use of the following: denaturing gel gradient electrophoresis (DGGE), terminal restriction fragment length polymorphism (t-RFLP), pyrosequencing, internal transcribed spacer (ITS) sequencing, and Illumina amplicon sequencing [178]. The DGGE procedure was first carried out in 1993 by Muyzer [179] and the major mechanism behind this method is the attachment of a guanine- and cytosine-rich portion (G–C clamped region) in the amplified fragments. This method can be used to separate the PCR amplicon of a mixed microbial consortium using different melting points due to the differences in their amplicon sequencing; hence, giving opportunities for a comparison between microbial species [180]. Garbeva et al. [181] evaluated the microbial diversity in the root and stem of a potato (*Solanum tuberosum*) using the DGGE procedure and the culture-dependent method. The researchers discovered that the DGGE procedure was more efficient based on the discoverability of some organisms that cannot be readily isolated using the culture-dependent method. This reveals that the DGGE method can be more efficient compared to the culture-dependent method [181]. The DGGE procedure is simple and can be employed quickly in the visual profiling of microbial populations [182]. The drawbacks of this method include a restricted fragment size, a low resolution, which may take a long time to run from start to completion, and an overestimation of the sample population [176,180,183].

The t-RFLP is another method for profiling microbes. This method depends on the amplification of targeted DNA fragments using taxon-specific primers, then the characterization of the amplified DNA and digestion using a restriction enzyme, followed by the separation and detection of the labeled terminal fragments on a DNA sequencer [184]. This procedure was first carried out by Liu et al. [185]. In this method, the population of the diverse DNA fragments is used to estimate the number of strains present in the sample. The major advantage of this method is that it utilizes an automated sequencer, whose results are more reliable based on reproducibility [186]. Conversely, the drawback of this method is that it does not discover fungi at the species or strain level [184].

The pyrosequencing procedure, also known as the "sequence-by-synthesis" procedure, is a method that monitors DNA synthesis in real-time. This method was discovered by Hyman [187]. It involves the annealing of oligonucleotides to the template strand of a DNA to be sequenced by elongating the 3′ end with the information encoded in the template strand [188]. In this procedure, dNTPs are distributed into compartments that contain a DNA polymerase, primers, and a template DNA. When the polymerase introduces and adds the complementary dNTPs, inorganic pyrophosphate (PPi) is released [188]. Li et al. [189] successfully used this method to unravel the endophyte community in the *Dendrobium catenatum* and discovered different bacterial species, such as *Pseudomonas* spp. and *Burkholderia* spp. The major advantage associated with this method is that it is not laborious, quantitative, nor limited to measuring the status of methylation in a few CpG positions [190]. However, the pyrosequencing technique comes with some drawbacks which include complexity, duration, and high cost [191].

Internal transcribed spacer (ITS) sequencing is a technique employed for the identification of fungal species. This method has been previously used to evaluate fungal endophytes in plant species. For example, Jose et al. [192] reported the use of the ITS1 technique in the identification of endophytic fungi in *Wrightia pubescens* and *Cynometra ramiflora* L. plants. One of the advantages of the ITS region is that it can replicate two smaller segments on both sides with the 5.8S locus, which is useful in the case of replicating damage [193]. The disadvantage of the ITS technique is that it allows co-amplification of the fungal DNA, which could result in identification errors. Also, for samples that have degraded, it is usually difficult to recover the total ITS region and many copies of ITS can be present in the same microbial species, which could prevent the recovery of good sequencing data if the Sanger sequencing technique is used [194,195].

The Illumina amplicon sequencing is a procedure that is used to assess the genetic variations in specific regions in a genome and the in-depth sequencing of PCR products. Amplicon sequencing helps to identify and characterize different microorganisms from environmental samples. This method is majorly preferred due to its rapidness, cost-effectiveness, and high accuracy [196,197]. However, the problem of a low base diversity has made this method challenging [197]. Different methods for unraveling microbial endophytes come with their advantages and challenges; hence, the main aim of an experiment should be considered before selecting a method to use.

However, all these limitations can be overcome using high-throughput sequencing (HTS) techniques [178]. To evaluate the whole microbiome in a particular environment, two major types of HTS techniques can be used, namely shotgun metagenomics and meta-transcriptomics. The introduction of HTS techniques has enabled scientists to unravel and identify microbial communities inhabiting diverse plants [37,198]. Shotgun metagenomics is advantageous over other similar techniques, such as amplicon sequencing and other previous sequencing techniques, for the following two main reasons: (1) extensive sequencing of the entire metagenome, which enables the diversity, community structure, and functional evaluation of microbial communities in a given environment; and (2) if they existed in the database before, new functions can be allocated to the particular environment in which they were formally not recognized [199].

Hong et al. [200] first reported the use of the shotgun approach for assessing the structure and functions of the endophytic microbial community in *Panax*. The approach

gave a detailed taxonomic, functional, and metabolic profiling of the microbial community inhabiting *Panax*. Shotgun metagenomics has also been used for the first time to profile the effect of different farming practices on the endophytic microbial communities present in the root of maize plants [178,198]. The results showed that the maize plants cultivated on an organic farming site harbored more microbial communities compared to others cultivated on an inorganic site. Furthermore, the use of culture-independent approaches aims to assist in the understanding the effect of different biotic and abiotic factors on the diversity, abundance, and functions of endophytic microbiomes inhabiting economic plants, which are known to play a major role in the growth, development, and health of plants [201,202].

Consequently, NGS has been employed to unveil the endophytic bacterial community in *Aloe vera* plants, most importantly, by providing insights into the microbial colonization patterns in host tissues [177]. Metagenomic techniques coupled with in-silico analysis can help to provide details of the phylogenetic and functional attributes of the endophytic microbial community [203]. Delmotte et al. [204] and Rastogi et al. [205] reported the use of community proteogenomics for the identification of certain traits of bacteria present in *Arabidopsis* leaves. However, despite the usage of NGS techniques in the study of endophytes, the techniques have some barriers which need to be considered before employing them in plant microbes' research. The main barrier to these techniques is the presence of a high volume of sequences without homologs in public databases. To a large extent, metagenomic analysis of samples obtained from the same location may overcome this barrier [206].

Microarray-based methods are also used to profile the genome of endophytes, particularly with gene expression. A study carried out by Felitti et al. [207] revealed the potential of endophytic *Neotyphodium* and *Epichloe* cDNA microarrays for transcriptomic analysis. A microarray investigation of the gene expression of *Arabidopsis* tissue-associated *Pseudomonas* showed that the ET responsive genes were downregulated, while genes responsible for nodule development and hormone production in plants were upregulated [208]. Similarly, a dual genome Symbiosis Chip-based tool has been used to understand the plant–endophytic interactions and gene expression in both the host plants and endophytes [209]. In particular, the Symbiosis Chip-based tool was used to understand the synchronized differentiation during nodule development of *Sinorhizobium meliloti* and *Medicago truncatula* [209]. Also, a study on how to isolate and characterize bioactive metabolites from endophytic microorganisms has been conducted by various scientists [210,211]. Bacterial endophytes, particularly those associated with medicinal plants, are known to be the reservoirs of therapeutic compounds and other natural metabolites [5]; hence, they can be studied using different NGS techniques.

8. Future Prospects

Microbial dynamics within the plant compartments can mediate an endosphere competence in sustaining plant health. Although a lot of work has been done to unravel the diversity of endophytic microbes in different plants; yet, findings on the influence of exudate secretions on root-associated microbes are limited in microbial biotechnology. Hence, more research should be carried out to identify microbes capable of utilizing exudates as a source of energy needed for their metabolic activities and plant nutrition. Exudate secretions from plant roots may be influenced by biotic or abiotic factors, thus, limiting the extent of microbial recruitment for plant benefits. Hence, some organisms which do not directly utilize exudates but whose presence enhances plant growth promotion need to be explored.

The harnessing of endophytic microbiomes as bioinoculants has future benefits in plant growth regulation and survival under drought stress [212]. However, the shelf life, storage condition (such as moisture, temperature, etc.), long-term potency of the carrier, and interference with the biological content can eventually reduce their efficacy. Hence, it is important to intensify the research to consider the long-term efficiency of bioformulations for plant growth improvement.

Insights into the plant endosphere and various factors underlining differences in microbial structures, functions, and metabolite syntheses can fundamentally mediate plant–microbe interactions for a stable ecosystem [6]. The compatibility of different microbes in different plants, environments, plant metabolites, and other biotic and abiotic factors need to be studied to unravel the efficiency of bioformulants under certain conditions and for commercialization to reduce labor loss. Hence, understanding the factors responsible for microbial modifications and functions is important before integrated crop breeding can be achieved. Consequently, devising approaches to ensure endosphere competence and engineering in modern agriculture can help maximize the potential of beneficial microbes in enhancing soil nutrients for plant nutrition. Of course, endophytes can be easily optimized with other substrates under various conditions to yield desirable biological products [213]. Manipulation of endophytic microbes through soil and plant inoculation can serve as a model for understanding their plant growth-promoting potential as bioinoculants, biostimulants, and biofertilizers. Today, different microbial bioinoculants from beneficial microbes are widely available in the market and commercialized, and their use has contributed to safe ecosystems and crop productivity [214].

After culturing, the bioprospecting of microbial inoculants upon application under greenhouse and field experiments often showed a significant difference in crop yield parameters, but the major challenge is the ability to adapt or survive and compete with soil microflora, colonize plant tissue, and persist under natural soil environments. These drawbacks to bioinoculant use can be linked to the inability to outcompete natural microflora, limited nutrient supplies, and environmental stressors [215]. However, the synergistic interactions between the resident microbes and inoculating microbes can underline the effectiveness of bioinoculants in forming strong networks in the endosphere regions for plant benefits. Hence, more research should be carried out to understand how endophytic microbes can be genetically modified and engineered. Furthermore, the research should be focused on endophytic microbes with dominant and functional genes involved in plant growth promotion.

Recent advancements in molecular biology and microbial genetics have provided a fascinating approach for shaping the endophytic microbes and based on their agricultural importance, genetic modifications can be guaranteed. NGS approaches have been employed by researchers in the analysis of endophytic microbial communities [39,216,217]. Aside from unraveling the relative abundance of microbial taxa, meta-omic techniques, such as metaproteomics and metagenomics, have provided information on the functional profiling of endophytic microbes in plants [218,219]. Also, the functional protein genes and microbial metabolites can best be explained by metabolomic and proteomic techniques. Fadiji et al. [220] reported profiling of microbial endophyte communities with functional genes in maize using a shotgun metagenomics approach; nevertheless, the authors recommended further studies using culture-dependent techniques to explore and recover identifiable microbes.

The prediction of notable plant growth-promoting genes and secondary metabolites from the endophytic bacterium *Stenotrophomonas* spp. from sunflowers has recently been reported using whole-genome sequencing [221,222]. Copious plant microbes with plant growth-promoting traits have been identified but engineering them for maximum exploration remains a challenge and needs further studies. The advancement in plant endosphere research following diverse approaches will help understand the potential of microbial endophytes in crop production sustainably. Furthermore, the efficient use of engineered endophytic microbes may face some challenges but with agricultural promises.

9. Conclusions

In conclusion, the plant endosphere remains a research focus by many researchers recently. So far, successes have been recorded in harnessing endophytic microbes as bio-input for improved agricultural productivity through diverse approaches and strategies, which include plant, microbial, and meta-organism strategies. The endophytic microbial

community forms a major biotic factor that determines plant growth under drought stress and their exploration in the formulation of bioinoculants and incorporation into crop breeding promise to contribute immensely to plant and soil health. Based on the diversity and functions of microbial endophytes in reclaiming nutrient and biodiversity loss in soil, this suggests their use in the present and future agriculture in producing low-input, cost-effective, safe, and environmentally friendly bioinoculants beyond their symbiotic action with the host plant alone. Furthermore, the biotechnological advancement in endophytic microbial research can help unravel their potential in integrated crop management and possible use with other organic amendments in enhancing soil health and promoting plant growth.

Despite the economic and biological potentials of microbial bioinoculants in modern agricultural systems, there are many limiting factors influencing their quality, efficacy, and successful use during production and after inoculation into the soil. The main contributing factors include large-scale production, formulation, storage, transport, and inoculation in the field. The variation in host specificity, media composition, growth conditions, reduced microbial viability, bioproduct registration, and regulation form major challenges confronting the efficient use of microbial bioinoculants. The challenges facing the use of microorganisms as bioinoculants include the following: (i) unimaginable gap between researchers and farmers, (ii) lack of awareness among farmers, (iii) poor channel of information dissemination to the farmers through the extension workers on the ecological importance of bio-input as opposed to the use of chemical input, (iv) lack of biological adjuvants as bio-careers, (v) erratic climatic conditions which alter microbial metabolism and functions under storage, (vi) inefficient storage facilities, and (vii) contamination with untargeted microbes. All those mentioned above can reduce microbial functions in natural environments upon inoculation. Therefore, the difficulties related to the large-scale production of inoculants need to be overcome to commercialize bio-products for a safer environment and maximum food production. Furthermore, understanding the complex association that occurs at the soil–root interface is essential since untargeted soil microbes can significantly influence the efficiency of the bioinoculants when inoculated into the soil. The inconsistency and variation of bioinoculant use from crop to crop, season to season, and place to place, which hamper agricultural productivity, still exist. The successful use of bioinoculants relies on researchers, industrialists, economists, and farmers. Therefore, farmers need to be educated and convinced of the biorational efficacy of bioinoculants and they need to be willing to purchase and apply bioinoculants instead of expensive chemical fertilizers. Conclusively, to further enhance farmers' confidence in using bio-inputs, improvements in the quality of biofertilizers, quality assessment, and regular training are most needed.

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