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Streptomyces as endomicrobiome: Potential bioinoculants for agricultural sustainability

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ABSTRACT

The need for chemical-free farming methods is becoming more important due to the detrimental impacts of chemicals on human health and the environment. Finding innovative ways for the establishment of sustainable agricultural is crucial that may avoid the overuse of chemical fertilizers and pesticides as a means of increasing output. Microorganisms that promote plant development and act as biocontrol agents have become safe substitutes for chemical fertilizers in the agriculture sector. Endophytic microorganisms or microorganisms associated with plants, have become a vital and promising tool for sustainable agriculture. Endophytic *Streptomyces* act as the alternative for preventing disease-causing microorganisms and help to regulate plant growth. Bacteria belonging to the genus *Streptomyces* are well-known producers of secondary metabolites, which can be potentially utilized to replace chemical fertilizers and pesticides. The current status of endophytic *Streptomyces* in sustainable agriculture is employed as safe biocontrol and plant growth-promoting (PGP). This review emphasizes the biocontrol and PGP benefits of the endophytic *Streptomyces*. Additionally, their ability to enhance plant growth has been confirmed in a number of crops, thus encouraging the wide use of streptomycetes as biofertilizers to increase plant productivity.

1. INTRODUCTION

In the field of microbiology and plant biology, recent studies have a strong emphasis on plant-microbial interactions. Plant growth development depends highly on the extracellular enzymes produced by plant growth-promoting bacteria (PGPB). Microorganisms constantly interact and turn on the other organisms within their community [1].

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Plants and their closely related species are influenced by the presence of unicellular or multicellular organisms. Interactions between microorganisms and plants occur both internally (via the formation of plant microbial endospheres) and externally (surface of roots) [2]. Plants and microbes always maintain mutually beneficial symbiotic relationships with endophytes by providing some benefit to their living community [3,4]. Through the symbiotic relationship between plants and microorganisms, endophytes may act as a convenient substitute to replace the use of pesticides [5,6]. The excessive application of agrochemicals and insect control in modern agriculture based on organic principles is difficult to maintain and results in crop loss. Additionally, the current scenario has led to increased pathogens with pesticide or drug resistance and soil infertility [7].

Microorganisms that are endophytic, such as bacteria, fungi, and actinomycetes, inhabit the surface layer of plant tissues through symbiotic relationships. Actinomycetes are one of the prominent bacterial species, including the largest genera, *Streptomyces*. The production of secondary metabolites, including bioactive substances and antibiotics, is a standout characteristic of *Streptomyces* and guanine and cytosine content was high in the genome [8]. Hundreds of distinctive plant growth regulators, antibiotics, and bioactive components have been discovered in terrestrial microorganisms, particularly from the genus *Streptomyces*. The relationship between endophytes and plants is dominantly reported as commensalism. Various applications have been reported in the plant growth components extracted from the *Streptomyces* sp. [9,5]. The earlier studies revealed that endophytic *Streptomyces* notably increase the growth and tolerance in varieties of monocot and dicot plant species [10,11]. The upsides of the *Streptomyces* endophytes for biocontrol and promoting plant growth are illustrated in this review. Recent studies of *Streptomyces* endophytes on various crops for their biological pesticide, natural fertilizing ability, and plant growth stimulating factor were also discussed.

2. BIODIVERSITY OF ENDOPHYTIC *Streptomyces*

The composition of the cell envelope in *Streptomyces* was used to differ from other Gram-negative bacteria, and cell composition was used as the identification characteristic [12]. Plants extensively interact with the different ranges of microorganisms and acquire benefits through minerals and nutrition exchange [13,7]. The endophytes colonized the plant's roots and mainly contributed to nitrogen fixation and solubilization of mineral nutrients. The studies on the root-associated microbes, especially rhizobacteria, influence the morphology and physiology of the plants to prevent the pathogenic insect attack. Plant defense mechanisms will initiate and express salicylic acid, ethylene, and jasmonic acid. A plant's root releases metabolic signals such as alkaloids, flavonoids, terpenoids, and strigolactones that attract the microbial communities around the rhizosphere (Fig. 1). Endophytic *Streptomyces* influence the richness of soil with nutrients and significant growth with many components. In addition to the endophytes' phosphate solubilization ability, which produces the various enzymes that break the complex nutrients into simple minerals such as cellulase, chitinase, β-fructofuranosidase (invertase), lipase, keratinase, pectinase, protease, peroxidase, phytase, and xylanase. Antimicrobial peptides and biocontrol components are identified through the metabolic studies on endophytes *Streptomyces*. Microbial interactions revealed the unique features of endophytes beneficial for biocontrol and biofertilization in potatoes [14,15].

3. METHODS FOR ISOLATING ENDOPHYTIC *Streptomyces*

Isolation of endophytic *Streptomyces* is carried out in different plant parts, such as a different scale of primordium of meristem, leaf, and roots. The sequencing approach was made to screen the diversity of endophytes in the seed and needles of *Pinus monticola*. Isolation of endophytes is still challenging, and broad reviews were established to isolate *Streptomyces*. Endophytes are isolated from the plant tissue extract or ground tissues by inoculating in the *Streptomyces*-specific media. Different culture mediums were employed to isolate endophytic fungi from the roots and fruits of *Azadirachta indica* [48]. The study confirmed that the mycological agar medium yielded many isolates with species richness. *Streptomyces peucetius* were isolated using surface-sterilization methods and identified by morphological characteristics.

Earlier, biochemical and morphological characteristics were used to identify endophytes belonging to Actinomycetes. Molecular identification by ribosomal DNA (rDNA) sequence analysis is currently used to identify microorganisms. It reduced the biased judgments, and rDNA sequence data are robust in resolving endophytes' taxonomy (Table 1).

4. MOLECULAR APPROACHES FOR CHARACTERIZATION

The identification and characterization of endophytes through metagenomic studies, molecular markers, molecular cloning, and gene

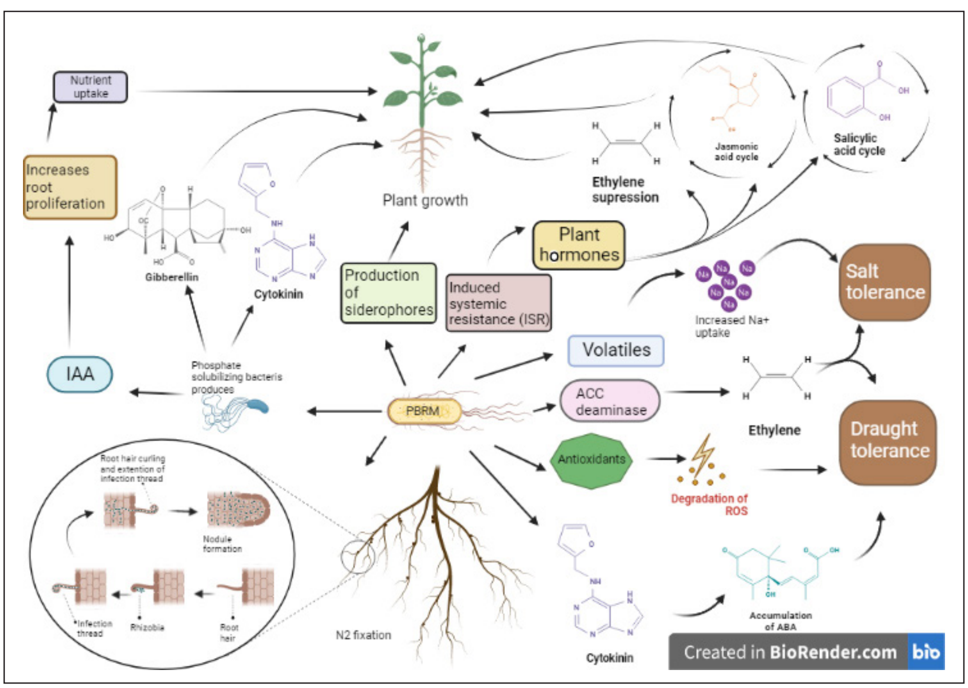

Figure 1. Interaction and tolerance of PGPMs to plant.

Table 1. Potential soil and plant root, tissue surface of the *Streptomyces* species.

S. No	*Streptomyces*	Source of isolation	References
1.	*S. coelicolor*	Soil	Bentley *et al.* [16]
2.	*S. xiamenensis*	Mangrove sediment	Xu *et al.* [17]
3.	*S. atrovirens*	Rhizosphere soil	Abdallah *et al.* [18]
4.	*S. griseoviridis*	Tomato plants	El-Tarabily [19]
5.	*S. lydicus*	Rhizosphere soil	Khamna *et al.* [20]
6.	*S. olivaceoviridis*	Soil	Verma *et al.* [21]
7.	*S. rimosus*	Medicinal plants	Lin and Xu [22]
8.	*S. rochei*	Rhizosphere soil	Tsavkelova *et al.* [23]
9.	*S. viridis*	Rhizosphere soil	Nascimento *et al.* [24]
10.	*S. igroscopicus*	Sand truffles	Goudjal *et al.* [25]
11.	*S. axinellae* sp. nov.	Sponge	Pimentel-Elardo *et al.* [26]
12.	*S. griseus*	Soil	Waksman [27]
13.	*S. chumphonensis*	Marine	Phongsopitanun *et al.* [28]
14.	*S. rochei*	Decomposed dung	Srivastava *et al.* [29]
15.	*S. fildesensis* sp. nov.	Antarctic soil	Li *et al.* [30]
16.	*S. scabies*	Potato scab	Lambert and Loria [31]
17.	*S. oryzae* sp. nov.	Stem of rice	Mingma *et al.* [32]
18.	*S. wadayamensis*	Citrus plant tissue	de Oliveira *et al.* [33]
19.	*S. kebangsaanensis* sp. nov.	Inner tissue of *porulaca aleracea*	Sarmin *et al.* [34]
20.	*S. phytohabitans* sp. nov.	Roots of *curcuma phaeocaulis*	Bian *et al.* [35]
21.	*Streptomyces* **sp.**	Sorghum stem	Patel and Archana [36]
22.	*Streptomyces* sp.	Wheat	Coombs and Franco [37]
23.	*Streptomyces sp.*	Clover	Franco-Correa *et al.* [38]
24.	*S. lydicus*	Pea	Tokala *et al.* [39]
25.	*Streptomyces* sp.	Mung bean	Rungin *et al.* [40]
26.	*Streptomyces* sp.	Soybean	Nimnoi *et al.* [41]
27.	*S. aurantiogriseus*	Rice	Harikrishnan *et al.* [42]
28.	*S. hygroscopicus*	Kidney beans	Igarashi *et al.* [43]
29.	*S. filipinensis, S. atrovirens*	Tomato	El-Tarabily [19]
30.	*S. spiralis*	Cucumber	El-Tarabily *et al.* [44]
31.	*Streptomyces* sp.	Chickpea	Gopalakrishnan *et al.* [45]
32.	*Streptomyces* sp.	Clover	Franco-Correa *et al.* [38]
33.	*Streptomyces* sp.	Chickpeas	Gopalakrishnan *et al.* [46]
34.	*Streptomyces* sp.	Veggie	Nimnoi *et al.* [41]
35.	*Streptomyces* sp.	Soil	Zhu *et al.* [47]

expression studies, are the current trends and advanced developments in molecular-level studies. The metagenomic approach is one way to find microorganisms from various environments that are difficult to isolate. A metagenomic system was used to characterize the uncultured endophytic microorganisms colonizing *Solanum tuberosum* L. contained the 1-aminocyclopropane-1-carboxylate deaminase gene (acdS) operon. It was concluded that metagenomic analysis could supplement polymerase chain reaction-based research and provide information on whole functional genes [49]. Denaturing gradient gel electrophoresis profiles of 16s rRNA gene fragments amplified from complete plants' DNA were used to detect non- culturable endophytic bacteria by comparing the profile with the bands obtained from the culturable endophytes from citrus plants [50]. The bacterial endophytes community of potato plants was investigated using automated ribosomal intergenic spacer analysis and pyrosequencing [12]. After being spooled and transferred to a screw-capped vial, the DNA was washed with 70% cold ethanol, allowed to air dry, and then suspended in TE buffer.

5. PLANT- *Streptomyces* INTERACTION

In plant and microbe interaction, specific sRNA responded to the up and down-regulation of the biotic and abiotic stresses and pathogens [51,52]. To analyze and tackle the ecosystem challenges in agriculture, it is obligatory to understand the gene regulation of sRNAs in plant response in endo-microbiome and biocontrol beneficial bacteria. Small regulatory RNAs are highly responsive to cellular functioning, such as oxidative stress response, quorum sensing, carbon starvation, and iron deficiency [53]. sRNA showed gene expression in transcriptional and post-transcriptional stages, and synthetic and functional processes were described [54]. The precise and targeted gene regulation makes plant sRNA distinctive and capable gene modulators. A better acknowledgment of sRNA can be exploited for its myriads of applications, from basic gene function study to targeted genes [55].

sRNA synthesis starts from the transcription of MIR genes by RNA polymerase II. It proceeds through the formation of precursor micro RNA duplexes before single-stranded miRNAs are inserted into the RNA-induced silencing complex (RISC). Following the RISC formation, argonaute (AGO) proteins guide the miRNAs strand to its target mRNA, and another strand of the duplex undergoes degradation [56]. Targeted identification of many miRNA-mRNA duplex modules in plant-microbe interactions, but very few studies have been functionally validated for the importance of agriculture and horticulture [57]. A few studies on microRNAs have been increased, including genome-wide profiling of sRNA and miRNA responses to drought, salt, cold, heat, systematic stress, and pathogenic microflora [51,52,58]. The specific impacted of miRNAs can play distinct roles across species or different crops. However, the advances in miRNAs mediated the regulation of genes related to plant-microbes' interactions, emphasizing the role of plant miRNAs in disease susceptible and resistance, which can be exploited for improved crop varieties.

6. *Streptomyces* AS PLANT GROWTH PROMOTERS

In general, actinobacteria may be beneficial to plant nutrition in terms of minerals. This is related to the ability to mobilize metals and fix nitrogen, as well as the uptake of mineral nutrients such as Fe, Zn, and Se. However, metagenomic investigations have not demonstrated the involvement of *Streptomycetes* in such advantageous procedures [59]. The taxonomic and phylogenetic makeup of these microbial communities is restricted to a few bacterial phyla, including actinobacteria, according to metagenomic studies of the bacterial microbiota in plants.

Emphasizing the role of *Streptomycetes* in the growth and health of plants. Through nutritional interactions and the composition of its root exudate (chemotaxis), the plant has a significant influence in influencing the growth of its root microbiome [60–62]. Flavonoids, strigolactones, and terpenoids are among the metabolic signals found in plant root exudates that have the power to influence the microbial communities in the rhizosphere. It is still unknown what cues draw *Streptomycetes* into the rhizosphere. *Streptomycetes* are able to penetrate roots and colonize root tissues and arteries. From there, they can be separated and purified in order to characterize their physiology and the interactions among microbes [37]. Actinobacteria, like *Streptomyces* species, act as nutrient enhancers and affect soil fertility by interacting with various minerals. They are known to produce a variety of enzymes, such as amylase, chitinase, cellulase, invertase, lipase, keratinase, peroxidase, pectinase, protease, phytase, and xylanase, which convert complicated nutrients into simpler mineral forms, in addition to siderophores and solubilizing phosphate. Their ability to cycle nutrients makes them excellent choices for natural fertilizers [63].

6.1. Nitrogen Fixation

One of the most crucial macronutrients for plant growth is nitrogen (N_2). The abundance of N_2 in the atmosphere is about 78% and is inaccessible to plants. Numerous plant growth promoting (PGP) microorganisms that are capable of freely or in symbiotic relationships with legumes carrying out biological nitrogen fixing have been identified [64]. The issue of biological N_2 fixing is crucial since the use of synthetic nitrogenous fertilizers has resulted in excessive water pollution and the eutrophication of rivers and lakes. Serious environmental issues arise from N_2 fertilizers leaching into the land, especially in water systems [65]. Inoculating seeds, seedlings, roots, or soil with N_2-fixing microbes promotes plant growth, enhances soil quality, and keeps the soil's N_2 content stable [66]. The endophytic N_2-fixing bacteria from both leguminous and nonleguminous crops have been thoroughly studied. Endophytic bacteria belong to various phyla including actinobacteria, bacteroidetes, firmicutes, and proteobacteria.

There have been reports of the major N_2-fixing endophytic bacteria from several host plants. There are many uses for N2-fixing endophytic bacteria in sustainable agriculture, including maintaining plant development, crop output, and soil health [67]. An investigation, [68] demonstrated that *Streptomyces galilaeus*, *S. avidinii*, *S. albogriseolus*, *S. albidoflavus*, *S. spororaveus*, and *S. cellulosae* have the ability to fix N_2, P-solubilization and production of ACC deaminase and siderophores. In addition, the *S. avidinii* and *S. cellulosae* increases seed germination of pepper, bean, and cucumber. In a similar investigation, inoculation of N_2 fixing *Streptomyces alfalfae* with multiple pant growth promoting attributes [produce indole acetic acid (IAA) and siderophore and have phosphate-solubilizing] can effectively promote the seed germination and growth of switch grass [69].

6.2. Phosphorous Solubilization

After nitrogen, phosphorus (P) is the second most crucial nutrient for plants. It can be found in soil as mineral salts or combined with organic matter. Despite being prevalent in soils in both organic and inorganic forms, its availability is limited because it is primarily found in insoluble forms. The average soil contains around 0.05% (*w/w*) of P, but due to poor solubility and soil fixation, only 0.1% of the total P is available for plant uptake [70]. Since phosphorus deficit is very common in agricultural soils globally, the majority of farmers frequently apply chemical fertilizers that dissolve into the soil to prevent cropping systems from experiencing P-limiting circumstances. When applied to either acidic or alkaline soils, the P often precipitates through the production of non-bioavailable compounds [71].

Phosphate-solubilizing microbes have solubilized insoluble P, providing an alternative to chemical phosphatic fertilizers and increasing P availability while reducing the need for chemical fertilizers [72]. Microbes produce enzymes like phosphonatases, C-P lyases, and phytases that facilitate the release of organic phosphates. The primary process of mineral phosphate solubilization involves the synthesis of acid phosphatases and organic acids (OAs) [73]. They release OAs such as propionic acid, succinic acid, lactic acid, and formic acid in order to dissolve the bonded P present in the soil. There is currently little information available on the phosphate-solubilizing actinomycetes [74].

In an investigation, [75] reported the isolation P-solubilizing *Streptomyces roseocinereus* with multiple PGP traits. Barley plants inoculated with *S. roseocinereus* enhance shoot and ear length as well as available phosphorus in ears and leaves and P and N contents in the soil. In another investigation, [76] evaluated the effect of rock phosphate solubilizing *S. bellus* and *S. saprophyticus* in promoting the growth of sugar beet in field conditions. Seeds inoculated with *S. bellus* stimulate root elongation and level of levels of soil-available phosphorus (P) and potassium. Inoculation with SS increased shoot and root elongation and enhanced chlorophyll levels in the plant leaves. In a report, [77] studied that P-Solubilizing and phytate degrading *Streptomyces* **s**p. stimulates the growth and P accumulation of maize.

6.3 Potassium Solubilization

Potassium (K) is regarded as a vital nutrient and a major component within all living cells. Naturally, soils have higher concentrations of K than any other nutrient; but plants are unable to absorb the majority of the K [78]. K is found in soil in a variety of forms, including water-soluble, exchangeable, non-exchangeable, and mineral forms. In most soils, 90%–98% of the total K is made up of unavailable mineral forms such as feldspar, orthoclase, and micas, which are relatively resistant to breakdown [79]. Plants with inadequate levels of K exhibit stunted roots, sluggish development, increased susceptibility to disease, delayed maturity, and eventually reduced agricultural yields. The soil loses its organic K content when chemical fertilizers are used on a regular basis. Applying biofertilizers may be the most effective way to improve the solubility of soil potassium in such circumstances [80].

Potassium-solubilizing microorganisms (KSMs) can reduce the need for chemical fertilizers and promote sustainable farming practices. Owing to the naturally occurring source of K in soil and the high cost of synthetic K fertilizers, the significance of KSM is growing every day. These KSMs have the potential to be a useful strategy for raising soil K availability, which is crucial for crop establishment in soils with low K levels [81]. KSMs can liberate K from soil/minerals into forms that plants can use, which would be a viable choice. Researchers are highlighting the possibilities of using KSMs as effective biofertilizers to increase agricultural productivity more and more [82]. A report [83] demonstrated the growth promotion and protection against root rot of sugar beet by two P and K solubilizing *Streptomyces* **s**p. under greenhouse conditions.

6.4. Zinc Solubilization

Zinc (Zn) is an important and key micronutrient required in trace amounts by agricultural crops for complete growth and development. It is a vital component of many different enzymatic processes, the metabolism of carbohydrates, the synthesis of proteins and auxin, and the integrity of plant cellular membranes [84]. According to reports, the most common micro-nutritional problem affecting food crops worldwide, including those in India, is Zn deficiency caused by inadequate soil solubility. Chemical fertilizers containing zinc should not be applied since they will convert to a form of zinc that is unavailable. Therefore, the isolation of Zn solubilizing bacteria (ZSB) having the ability to convert distinct unavailable forms of the Zn to available forms offers the most significant solution to fight Zn insufficiency [85]. The use of ZSB offers a low-cost, flexible approach to Zn biofortification and the most environmentally friendly way to revitalize sustainable agriculture.

ZSB residing within plant tissues or in the rhizospheric hub demonstrates their ability to solubilize Zn using a range of techniques. The best approach is the deposition of OAs, which causes the surrounding soil to become acidic [86]. This suggests that using microbes can help increase the amount of zinc in plants and improve crop quality, which sums up the function of microorganisms for a more environmentally friendly approach. By releasing OAs, siderophores, and other chelating substances, Zn-solubilizing bacteria function as organic bio-fortifiers that can solubilize the inaccessible form of zinc [87]. In an investigation, [88] revealed that the two *Streptomyces* strains have potential as Zn-solubilizers and can be suggested as bioinoculants to promote the growth and yield of soybeans. In another investigation, Z solubilizing *Streptomyces nanhaiensis* with other plant growth-promoting attributes increases the plant growth with increased leaf biomass and pigment production on millet crops [89].

6.5. Phytohormones Production

Plant growth and development are significantly regulated by phytohormones. The five classes of phytohormones identified by the traditional classification are auxins, gibberellins, cytokinins, ethylene, and abscisic acid. A variety of physiological processes in plants are regulated by phytohormones, such as fruit ripening, root formation, florescence, branching and tillering, and seed germination and quiescence [90]. They are recognized for having a significant effect on the metabolism of plants. They are also essential in stimulating the defense mechanisms that plants use to respond to stressors. Under stressful circumstances, exogenous phytohormone supplementation has been used to enhance growth and metabolism [91]. The phytohormones are produced by a variety of actinomycetes species when they are exposed to an appropriate precursor, like L-tryptophane [92].

Endophytes generate phytohormones that alter the morphology and physiology of plants and encourage plant growth. The biosynthesis and signaling pathways of phytohormones are important in regulating the development of plants during stress responses [93]. In a report, [94] demonstrated that IAA-producing *Streptomyces* sp. inoculation enhanced lateral root number, vegetative growth, fresh weight, chlorophyll content, and tolerance to abiotic stress in *Arabidopsis thaliana*. In another report, endophytic *Streptomyces* sp. promotes soybean plant growth and increases yield and seed quality through P-solubilization, siderophores, and phytohormones like IAA and antifungals under *in vitro* production [95].

7. INDUCED SYSTEMIC RESISTANCE IN PLANTS

Biologic stress can have a detrimental effect on a plant's growth, cellular development, inherent biological systems, and productivity. To counter these biotic stress conditions, endophytic microbes are essential to the plant environment. Furthermore, endophytic actinomycetes are naturally occurring symbionts of a number of plants that modify their defense mechanisms and systemic resistance in order to impart resistance to host plants in challenging environments [96]. Unlike synthetic drugs, these microorganisms can successfully manage many plant diseases by inducing systemic resistance (ISR) without posing any environmental harm. The ISR in host plants is triggered by endophytic colonization and operates through a variety of mechanisms to reduce further pathogen attack and disease progression [97]. The endophytic bacteria produce secondary metabolites that shield plants from phytopathogens, in addition to exo-enzyme secretion, which could be aiding plant colonization. Endophytes may accelerate the growth of the plant by phytohormone production and support plant growth under unfavorable biotic and abiotic stress [98].

In an investigation, [99] reported that endophytic *Streptomyces* sp. triggered systemic resistance in chickpeas under *Sclerotium rolfsii* stress. Another investigation, [100] revealed that *Streptomyces* strains promote plant growth and induce resistance against *Fusarium verticillioides* in maize plants. Chen *et al.* [101] reported that *Streptomyces chromofuscus* induces systemic resistance and activates plant defense responses against tomato yellow leaf curl virus **infection.** *Streptomyces chromofuscus* maintained relative chlorophyll contents by accelerating the expression of genes (*CLH1*, *HEMA1*, and *PORA*) associated with chlorophyll biogenesis.

8. BIOTECHNOLOGICAL APPLICATIONS IN AGRICULTURE

8.1. Biofertilizers

Researchers are becoming more interested in *Streptomyces* as a commercial biofertilizer. They can help with plant nutrition and growth by aiding in the biodegradation of diverse agricultural wastes and generating distinct enzymes in the soil [102]. Additionally, it has been discovered that actinobacteria generate plant growth hormones such as IAA [103], extending their possible uses in agriculture as biofertilizers [104]. A study revealed that the production of IAA, siderophores, and immobilized inorganic phosphate is produced by *Streptomyces* sp., *Streptomyces thinghirensis*, *Streptomyces* sp., and *Streptomyces tricolour* [105]. Actinobacteria inoculation has been demonstrated to increase plant production and growth in fields [106] as shown in maize greenhouse trials [107]. However, some actinobacteria species have poor capacity for plant development and growth limits their ability to support sustainable horticultural techniques. Because *Streptomyces* may increase the amount of phosphate available in soil, it has a significant advantage [108]. These bacteria produce phytase enzymes and a variety of phosphate-solubilizing acids, which can convert bound phosphate into an accessible form. However, the precise process of acid-mediated phosphate solubilization is yet unclear [109].

Recent studies have shown that biofertilizers containing strains of *bradyrhizobium* and *Streptomyces griseoflavus* encourage the growth of mung beans, soybeans, and cowpeas' roots and shoots. According to this study, these biofertilizers also boost plants nodulation, nitrogen fixation, phosphorus, and potassium uptake, which raise seed yields. According to a recent study, *Streptomyces* sp. can be used as biofertilizers in the form of biofilms that use perlite material as a carrier [110,111]. Further research revealed that the development and productivity of chickpea crops could be enhanced by the use of *Streptomyces* strains as biofertilizers. For sustainable farming techniques, it is essential to comprehend the potential of *Streptomyces* in agriculture encouraging outcomes in the management of disease, accelerated plant growth, and improved output [45].

In an investigation, three endophytic *Streptomyces* sp. strains were evaluated alone and in combination with *Azotobacter* in field trials with recommended fertilization rates in north-western Indian plains. Bioformulation of *Azotobacter* and *Streptomyces* improved the growth and yield of wheat plants [112]. In another investigation, [113] endophytic S*treptomyces* **s**p. that contained the crude IAA showed the maximum effect in promoting seed germination and root elongation of tomato plants. In a report, inoculation of wheat plants with endophytic *Streptomyces tuirus, S. levis*, and *S. radiopugnans* significantly enhanced the growth parameters such as seedling length and rootlets number compared to the uninoculated control [114]. Devi *et al.* [115] reported the PGP and biocontrol activity of endophytic *Streptomyces* sp. against early blight in *Solanum lycopersicum* seedlings**.**

8.2. Biocontrol Agents

Numerous bioactive compounds that are advantageous to soil and plants are produced by actinobacteria and they have the ability to serve as biocontrol agents [116]. Increasing the resistance of plants to biotic and abiotic stressors [117]. According to a study, several actinobacteria (*Actinomyces pactum*, *A.globisporus*, and *A. globisporus* subsp. *globisporus*) have the ability to break down fungal pathogens. A light-colored actinomycete called *Streptomyces griseoviridis* was isolated from *Sphagnum peat* and is an example of a biocontrol agent that lessens damage from different soil and seed infections [118,119]. According to a study, actinobacteria in soil produce antibiotics that are useful against plant diseases (Fig. 2). To combat plant diseases, *Streptomyces violaceusniger*, generates antibiotics including headache, gentamycin, and guanidylfingine. Actinobacteria have been shown in earlier research to improve plant development and efficiently treat plant ailments [117,119–121]. The main reason *Streptomyces*

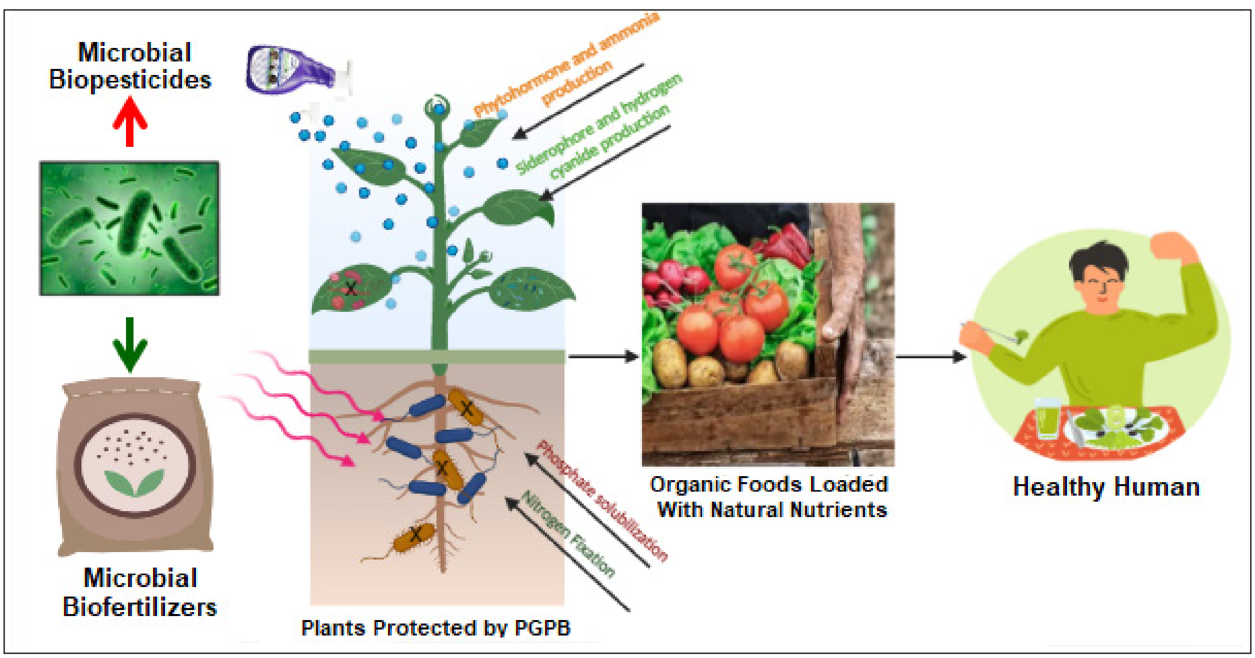

Figure 2. Effects of biopesticides/biocontrol agents.

strains are known for their ability to function as biocontrol agents they may produce strong volatile chemicals, metabolites, and antibiotics that have antipathogenic qualities [122].

A different investigation was conducted using chemicals released by strains of *Streptomyces coelicolor*, *S. violaceusniger*, and *S. violaceusniger*, including siderophore, chitinase, the antibiotic geldanamycin, and the antifungal nigericin. There were two strains of *Streptomyces* that showed biocontrol potential in this investigation by producing secondary active metabolites that inhibited the growth of harmful bacteria. The dangerous bacterial threat known as glumae, which causes panicle blight in rice plants and jeopardizes rice yields, was effectively controlled [123]. In a report, [124] demonstrated the induction of systemic resistance in *Solanum lycopersicum* **and** *Capsicum annum* seedlings against fusarium wilt by *Streptomyces* bioformulations. In another report, [125] revealed the formulation of bio-fungicides based on *Streptomyces caeruleatus* spores and efficacy against *Rhizoctonia solani* damping-off of tomato

Table 2. Bioformulations from endophytic *Streptomyces* and their potential effects.

Species	Host plant	Inoculated plant	Effect	Reference
Streptomyces asterosporus	*Solanum nigrum*	Tomato	Biocontrol of *Fusarium* root rot disease and growth promotion of seedlings	Goudjal *et al.* [132]
Streptomyces sp.	*Citrus jambhiri*	Tomato	PGP and biocontrol potentiality against early blight	Devi *et al.* [115]
Streptomyces sp.	Tomato	Tomato	Increasing root length, plant height, stem diameter and high biocontrol efficiency against tomato *Fusarium* wilt	Zheng *et al.* [133]
Streptomyces sp.	Pearl millet	Pearl millet	Protection against downy mildew and also promoted the vegetative and reproductive growth of the plant	Pushpalatha *et al.* [134]
Streptomyces sp.	Soybean	Soybean	Positively impacts growth, development, yield; and seed phytosanitary quality of plants under field conditions	Villafañe *et al.* [95]
Streptomyces parvulus	Green gram	Green gram	Improve the growth of green gram seedlings, showing enhanced shoot-, and root length and decreased incidence of *Fusarium* wilt disease symptoms	Kadaikunnan *et al.* [135]
Streptomyces caeruleatus	-	Tomato	Enhanced plant resistance to *Fusarium oxysporum* f. sp. *radicis lycopersici* root rot and promoted the growth of tomato seedlings	Zamoum *et al.* [136]
Streptomyces sp.	*Artemisia annua* L.	Arabidopsis	Enhanced plant disease resistance to pathogenic *Streptomyces scabies*	Lin *et al.* [137]
Streptomyces thermocarboxydus	Strawberry	Strawberry	Incidence rate of strawberry anthracnose was significantly reduced by treatment	Marian *et al.* [138]
Streptomyces sp.	Medicinal plant	Chilli	Antagonistic and PGP abilities	Passari *et al.* [139]
Streptomyces polychromogenes	Date palm	Date palm	Estimated disease severity indices in diseased seedlings were significantly reduced and conidial numbers of the pathogen significantly dropped	Alblooshi *et al.* [140]
Streptomyces coeruleoprunus	Date palm	Date palm	Estimated disease severity indices in diseased seedlings were significantly reduced and conidial numbers of the pathogen significantly dropped	Alblooshi *et al.* [140]
Streptomyces sp.	Moss	Wheat	Effectively suppressed the occurrence of wheat root rot caused by *Bipolaris sorokiniana*	Gao *et al.* [141]
Streptomyces sp.	Moss	Tomato	Effectively suppressed the occurrence of tomato bacterial wilt caused by *Ralstonia solanacearum*	Gao *et al.* [141]
Streptomyces physcomitrii **sp. nov.**	Moss	Tomato	Significantly reduced the disease severity of bacterial wilt on tomato seedlings	Zhuang *et al.* [142]
Streptomyces sp.	*Clerodendrum serratum*	Mung bean	Increased plant elongation and biomass, chlorophyll content, leaf area, leaf color and adventitious roots, and reduced the ethylene level under flooding conditions	Jaemsaeng *et al.* [143]
Streptomyces sp.	*Clerodendrum serratum* (L.)	Thai jasmine rice	Increased growth of rice and salt tolerance by reduction of ethylene via the action of 1-aminocyclopropane-1-carboxylate deaminase (ACCD) and further assists plants to scavenge ROS, balance ion content and osmotic pressure	Jaemsaeng *et al.* [144]

seedlings. In an investigation, [126] demonstrated the plant-growth promotion and biocontrol properties of three *Streptomyces* sp. to control bacterial rice pathogens. In a report, [127] revealed the insecticidal potential of endophytic *Streptomyces* sp. against *Zeugodacus cucurbitae*. In a similar report, [124] revealed that *Streptomyces* sp. bioformulations effectively controlled fusarium wilt in *Solanum lycopersicum and Capsicum annum seedlings*.

8.3. Breakdown of Pesticides

Since native *Streptomycetes* are well adapted to live in soil and sediment habitats, using them for bioremediation in pesticide-contaminated environments shows to be a potential approach. The potential metabolic variety, mycelial growth habitat, fast growth rates, semi-selective substrate colonization, and genetic manipulation of *Streptomyces* strains are their main advantages. *Streptomyces* may develop into spores, which aid in their persistence and dissemination, they can last lengthy periods of time in soil with low nutrient concentrations and water availability [128]. These benefits have led to the investigation of several *Streptomyces* strains as viable candidates for bioremediation of contaminated settings using several chemical pesticide families, such as ureas, organochlorines, organophosphates, pyrethroids, and chloroacetanilides [128–130]. Microorganisms called *Streptomyces* have proven to be highly effective in removing or converting several pollutants at once. It was discovered that lindane and Cr(VI) could be effectively removed from soil polluted with both chemicals by both pure and mixed cultures of *Streptomyces* strains. In order to lower pesticide concentrations in various environmental matrices and stop their infiltration into the environment, thus lowering human exposure, *Streptomyces* degradation of pesticides has been thoroughly investigated in biotechnological process development [131] (Table 2).

9. BOOSTING THE COMPOSTING PROCESS

In order to speed up the rate at which trash breaks down and raise the quality of compost at the end, microbial inoculation techniques introduce capable microorganisms to the compost mixture. These microorganisms can be grown in culture mixtures including soil, manure, and straw, or they can be separated from microbial communities under certain selection pressures [145]. A single strain of effective microorganisms or a combination of them can be used as the inoculums [146] and seasoned compost samples [147]. Researchers are currently investigating the use of mixed inoculants, which is a collection of microorganisms that cooperate with one another [148–150]. Microbial inoculants increase mesophilic and thermophilic bacterial populations, which enhances temperature profile and ammonia emissions. Additionally, it speeds up the process of composting by increasing enzymatic activity and reducing the first lag time of biological processes. When generating compost with a higher nutritional value, microbial inoculation procedures can effectively reduce the discharge of odorous emissions, particularly volatile organic compounds [151,152]. Single or multi-stage applications of microbial inoculums can be made at different points in the composting process. The various stages of inoculum addition show a significant impact on the physicochemical parameters of the composting process [153].

9.1. Impact on the Composting Process

Naturally existing bacteria that live in the soil are called *Streptomyces*. They are a great option to utilize as additions for solid waste composting because of their well-known ability to produce a wide variety of enzymes [145]. These microorganisms can hasten the decomposition of organic matter and encourage a composting process. The capacity of *Streptomyces* strains to withstand extreme temperatures and other environmental factors is one of their main benefits when used in composting. They improve the condition of the soil and encourage the growth of other beneficial microorganisms by releasing vital nutrients into it as they break down complicated organic compounds [116].

Moreover, *Streptomyces* are efficient in decomposing a variety of organic items, such as plant debris, animal faces, and food leftovers. Because they can lessen waste volume and encourage more environmentally friendly waste management techniques, they are a great option for use in solid waste composting. Apart from their advantages in composting, *Streptomyces* can also aid in odor reduction and inhibit the formation of hazardous pathogens in a composting setting [154]. This can make the work environment safer and more comfortable for individuals who are doing the composting process. All things considered, adding *Streptomyces* to solid waste composting can have a variety of advantages, such as improved soil quality and a more sustainable waste management approach through more efficient composting [155].

Numerous studies have looked into the application of different microbes as additives in composting issues. There has not been much research on *Streptomyces* bacteria in this field. The effects of microbial inoculation on the effectiveness and quality of composting have been the subject of numerous studies. A sign of high-quality compost is a reduction in the amount of time the breakdown process takes because of microbial activity [156]. For instance, when lignocellulose degradation was investigated, it was discovered that actinobacteria inoculation sped up the synthesis of enzymes including lignin peroxidase, xylanase, and CMCase, which raised the rates at which organic matter degraded [157].

9.2. Inoculation Techniques for Improving Soil and Crops health

As an alternative to traditional chemical fertilizers, the use of beneficial microorganisms to improve soil and crop productivity has attracted a lot of interest in recent years [116]. These beneficial microbes have been shown to be crucial for maintaining healthy soil and promoting plant growth. On the other hand, little is known about the use of compost enhanced with *Streptomyces* on crops and soil. The application of *Streptomyces*-enriched compost to soil or crops has not yet been the subject of any research. Nonetheless, there is research on the utilization of manure enhanced with beneficial microbes that might also be used for composting [158]. Suggests several applications of manure supplemented with microorganisms based on the type of manure. One technique is to directly inoculate soil before planting or during cultivation with various preparations for efficient microorganisms (EMs). Fustigation is an additional technique in which EM formulations are irrigated into the soil using manure at ratios of 1:1,000 to 1:5,000 [159].

Using manure-based goods may have an adverse effect on the environment, therefore it is crucial to think about that and use the right management techniques to reduce any hazards. Even if these techniques might work in some situations, more investigation is required to ascertain their repeatability and dependability in various circumstances. Composting and crop rotation are two alternative strategies that can improve soil health and lessen the need for commercial fertilizers. All things considered, a variety of soil management strategies, such as the application of compost enhanced with EM, can support resilient and sustainable agriculture. Farmers and growers can maximize soil health and productivity while minimizing environmental impact by carefully weighing the advantages and disadvantages of various practices.

9.3. Inoculation in Composting: Obstacles and Suggestions

The Moroccan government introduced the Green Morocco Plan (GMP 2008-2020) as a national initiative to modernize and enhance the sustainability of the agriculture sector. The use of compost as a natural soil supplement and the promotion of organic agriculture are the main tenets [160]. The Moroccan government has passed laws to support this project, encouraging farmers to utilize sustainable techniques and to increase the use of compost in agriculture. In order to encourage the use of organic inputs like compost, Morocco passed the Organic Agriculture Regulation, which governs organic production and commercialization. The National Compost Strategy was also introduced by the government with the objective of expanding the use of compost in agriculture and creating a nationwide network of composting facilities [161].

The plan calls for actions including offering financial incentives and technical support to farmers who use compost-based farming methods, encouraging the advancement of composting technology research and development, and standardizing and certifying compost to raise its caliber and uniformity. Nonetheless, the government is still firmly committed to encouraging sustainable farming and lowering reliance on artificial inputs. A strong composting sector is thought to be essential to reaching these objectives. Notwithstanding these efforts, there have been a number of obstacles to the execution of these requirements, such as the high cost of organic inputs and the absence of infrastructure for the manufacturing and transport of compost among farms. However, in order to overcome these obstacles, the Moroccan government is implementing compost-based agriculture techniques in an effort to create a network of composting facilities and encourage the application of compost as an affordable and sustainable substitute for synthetic fertilizers [162].

The goals of the Moroccan Kingdom are to promote equitable and sustainable economic growth, lessen greenhouse gas emissions, and enhance soil health. Our study focuses on enhancing the composting process by using microorganisms like *Streptomyces* in the framework of the Moroccan government's efforts to promote sustainable agriculture with compost. Utilizing *Streptomyces* bacteria in composting is a novel waste treatment method that may have advantages. However, in order to create a technology that is both affordable and environmentally sustainable, a number of issues must be resolved [163], and determining the proper method and dosage of *Streptomyces* inoculation for the best composting is a significant problem. It needs research to understand the actions of *Streptomyces* bacteria during composting in order to choose the most appropriate inoculants, considering their stability, adaptability, physiological makeup, and functionality.

Furthermore, there are not many extensive studies on the use of *Streptomyces* bacteria in composting, and further research is required to validate the advantages shown in smaller-scale studies. Developing commercially feasible technological processes for the manufacture of *Streptomyces* inoculants is also essential. This includes making use of low-cost materials for inoculant propagation, such as plant-based substrates or agro-waste. Finding the right procedure is one of the biggest challenges. Finally, research into predicting and optimizing the composting process using engineering processing techniques is required to guarantee the composting sustainability process without sacrificing the final product's quality [164]. Our objective is to enhance sustainable agriculture and lessen its negative impact on the environment in Morocco and other regions by creating more effective and efficient composting techniques.

10. FUTURE PROSPECTS

In current agriculture practices, biocontrol agents and biofertilizers mostly contain plant growth-promoting microbes (PGPMs) as the sole ingredient. Plant growth promoting rhizobacteria colonized around the rhizosphere of plants induces a positive impact on the host, such as increased plant growth and improved defense against disease-causing pathogens (Fig. 2). The predominant bacterial genera in microbial-based biofertilizers and biocontrol agents are *Arthrobacter*, *Alcaligenes, Azospirillum*, *Azotobacter*, *Bacillus*, *Burkholderia, Enterobacter*, *Klebsiella*, *Pseudomonas*, *Rhizobium*, *Serratia,* and *Streptomyces* [165]. Microbial-controlling agents are the ultimate replacement for harmful pesticides. These sliving entities, such as microorganisms, provide eco-friendly nonchemical methods for maintaining free of the plant disease [166,167].

The biocontrol of endophytes results in cell wall lyses, iron depletion in the rhizosphere, and increased microbe resistance with the rhizosphere. Endophytes antibiotic-producing mechanism increased the host defense to control microbial diseases, with the potential of antimicrobial enzymes (β1,3-glucanases, chitinases, proteases, and lipases). The biosynthesis of siderophores with low molecular weight helps to chelate the iron content in rhizospheric soil, which blocks the invasion of pathogenic organisms [167,168]. Microbial inoculants increased agricultural promised sustainability, decreased crop loss by diseases, and enhanced the uptake of nutrients. Organic biocontrol microbes built the tolerance for the plants to grow under any conditions. These biopesticides formulation are cost-effective and harmless to the ecosystem when applied to crops [169–171]. The biopesticides improve the performance and yield of the crop. Localizing the bacterial inoculum in the soil will change the temperature and humidity. Soil microbiome interactions with plants improved the yield and productivity of the crop (Table 1).

11. CONCLUSIONS

This review focused on endophytic *Streptomyces*, the significant contribution ability of these microorganisms to promote plant growth, and their bioactive compounds beneficial to pharmaceuticals, environmental, agricultural, and industrial sectors. The use of eco-friendly microorganisms that reduce pest populations and enhance plant growth forms the foundation of this promise. A potential answer for a more sustainable agricultural future is using consortiums that are developed from two or more compatible strains, biopesticides, or biofertilizers in exemplary formulations. The studies mentioned in this review lend credence to the idea that developing new formulations with cooperative microbes may help improve plant protection and growth in various crops. These studies also emphasize the need for more research on this topic, with an emphasis on endophytic *Streptomyces*, which have only recently been used as inoculants to improve pristine ecosystems in agricultural soil, agricultural output, and food security.

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13. CONFLICT OF INTEREST

The authors report no financial or any other conflicts of interest in this work.

14. CONSENT FOR PUBLICATION

All authors agreed and given their consent for publication.

15. AUTHOR'S CONTRIBUTIONS

All authors made substantial contributions to conception and design, acquisition of data, or analysis and interpretation of data; took part in drafting the article or revising it critically for important intellectual content; agreed to submit to the current journal; gave final approval of the version to be published; and agree to be accountable for all aspects of the work. All the authors are eligible to be an author as per the international committee of medical journal editors (ICMJE) requirements/guidelines.

16. ETHICAL APPROVALS

This study does not involve experiments on animals or human subjects.

17. DATA AVAILABILITY

All the data is available with the authors and shall be provided upon request.

18. PUBLISHER'S NOTE

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19. USE OF ARTIFICIAL INTELLIGENCE (AI)-ASSISTED TECHNOLOGY

The authors declares that they have not used artificial intelligence (AI)-tools for writing and editing of the manuscript, and no images were manipulated using AI.

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