Actinobacteria Diversity Associated with Plant Growth Promotion

Subjects: Plant Sciences

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Abiotic stressors, such as drought, flooding, extreme temperature, soil salinity, and metal toxicity, are the most important factors limiting crop productivity. Plants use their innate biological systems to overcome these abiotic stresses caused by environmental and edaphic conditions. Microorganisms that live in and around plant systems have incredible metabolic abilities in mitigating abiotic stress. Recent advances in multi-omics methods, such as metagenomics, genomics, transcriptomics, and proteomics, have helped to understand how plants interact with microbes and their environment. These methods aid in the construction of various metabolic models of microbes and plants, resulting in a better knowledge of all metabolic exchanges engaged during interactions. Actinobacteria are ubiquitous and are excellent candidates for plant growth promotion because of their prevalence in soil, the rhizosphere, their capacity to colonize plant roots and surfaces, and their ability to produce various secondary metabolites. Mechanisms by which actinobacteria overcome abiotic stress include the production of osmolytes, plant hormones, and enzymes, maintaining osmotic balance, and enhancing nutrient availability. With these characteristics, actinobacteria members are the most promising candidates as microbial inoculants.

plants actinobacteria plant growth-promoting bacteria

1. Introduction

Abiotic stress is any environmental factor limiting plant growth and productivity [1]. It is brought on by environmental factors such as water, salt, light, temperature, and nutrients, which can significantly inhibit plant growth, yield, and survival [2]. It was estimated that environmental factors could reduce crop production by up to 70% [3]. Abiotic stress includes drought, flooding, temperature fluctuations, high soil salinity, and metal toxicity [4]. Plant responses to abiotic stress are both reversible and irreversible [5].

Drought stress is one of the most significant abiotic stresses that affect plant growth and development. Plants are drought-stressed when available water in the soil is reduced to critical levels and contributes to continuous water loss [6]. Reduction of leaf water potential, turgor pressure, stomatal closure, and cell development are all signs of drought stress in plants [7]. Numerous physiological and biochemical processes, including photosynthesis, chlorophyll synthesis, nutrient metabolism, ion uptake and translocation, respiration, and carbohydrate metabolism, are also reduced by drought stress [8]. In contrast to drought, excess water is another problem for plant growth and development [9]. Water stress causes a decrease in leaf water potential and stomatal opening, which leads to the downregulation of photosynthesis-related genes and decreased CO_2 availability [7][10]. Furthermore, temperature (high and low) strongly influences the metabolic activity of plants [11]. Cold-driven rigidification and heat-driven fluidization can cause membrane dysfunction, as exemplified by protein deactivation and ion leakage [12][13].

Soil salinity is another severe issue for plants, reducing crop yield worldwide [14]. Salt stress causes cellular dehydration, leading to osmotic stress and water removal from the cytoplasm, decreasing cytosolic and vacuolar volumes [6]. Osmotic stress causes various physiological changes, including membrane disruption, nutrient imbalance, impaired ability to detoxify reactive oxygen species, differences in antioxidant enzymes, decreasing photosynthetic activity and stomatal aperture, and accumulation of Na^+ and Cl^- ions in the tissues of plants [15]. Due to industrial waste and sewage disposal, heavy metals have long been accumulating in soils [16]. Plants exposed to heavy metals experience altered membrane permeability, enzyme inhibition, photosystem inactivation, and disturbances in mineral metabolism [17][18].

Plants have evolved various mechanisms to deal with abiotic stresses, one of which is the use of microbes, which is an effective, environmentally friendly, and economically viable method [19]. Microorganisms represent a natural soil microflora with high metabolic capacities for growth promotion and resistance to abiotic stresses [20]. Microbes may, directly and indirectly, contribute to plant growth and stress resistance by various mechanisms, including increased nutrient availability, prevention of diseases, nitrogen fixation, and production of hydrolytic enzymes and phytohormones [21][22][23][24]. Plants release numerous signals/clues that allow effective communication between plants and microorganisms [25]. Plants actively recruit their microorganisms from surrounding microbial reservoirs such as soil, rhizosphere, and phyllosphere [26]. The enrichment of microorganisms by the plant is not random, but rather a targeted process [22]. Several factors (such as geographic regions, soil abiotic factors, and climate conditions) may explain the dramatic variation in the correlation between microbial and plant diversity [27][28][29][30]. Even within the plant, different plant organs and plant stages are dominated by different microbes [31]. Some dominant bacterial phyla associated with plants are Acidobacteria, Verrucomicrobia, Bacteroidetes, Proteobacteria, Planctomycetes, and Actinobacteria [26][32].

Actinobacteria are Gram-positive bacteria common in soil conditions and constitute one of the largest bacterial phyla [33]. Actinobacteria exhibit a variety of characteristics that are similar to fungi [34]. The first hierarchal phylogenetic clustering of members of the Actinobacteria was provided by Stackebrandt et al. [35]. Actinobacterial taxonomy has evolved throughout time, with the most recent roadmap dividing the phylum into six classes, 46 orders, and 79 families, with 16 new orders and 10 new families [36]. Actinobacteria can form complex structures such as spores, spore chains, sporangia, and sporangiospores [33]. The growth of substrate mycelium, the position of the spore, the quantity of spores, the surface structures of the spore, the form of the sporangia, and whether or not the sporangiospore has flagella are all key morphological aspects of actinobacteria classification [37]. Actinobacteria have a wide range of morphologies, including rod shape (*Acidiferrimicrobium*) [38], coccoid (*Micrococcus*) [39], rod-coccoid (*Arthrobacter*) [40], and bent rods (*Sinomonas*) [41] forms, as well as fragmenting hyphal forms (*Nocardia*) and forms with permanently differentiated branched mycelia (e.g., *Streptomyces* and *Frankia*). Some develop elongated filaments on the substrate but no true mycelium (*Rhodococci*) [33][42], whereas some do not produce mycelia at all (*Corynebacterium*) [43], while some distinguished by the production of branched substrate hyphae that break up into flagellated motile elements (*Oerskovia*) [33][44]. Many actinobacterial members can invade plant roots and surfaces [45]. Furthermore, they can produce extracellular compounds that allow them to outcompete phytopathogens and act as plant growth regulators.

2. Actinobacteria Diversity Associated with Plants and Plant Growth Promotion

The rhizosphere is the soil zone surrounding plant roots that influence the biological and chemical properties of the soil [46]. Bacterial concentrations in the rhizosphere are about 10–1000 times greater than in bulk soil [47]. The rhizosphere is in direct contact with the plant roots and is actively nourished by a complex mixture of carbon/nutrient sources given by the plant, such as amino acids, sugars, and other nutrients [48].

Actinobacteria are dominant in the rhizosphere, and their contributions to soil systems have a significant economic influence [49]. They are considered rhizosphere competent because they can use plant nutrients found in the rhizosphere and stimulate plant development following inoculation [50]. Various rhizospheric actinobacterial members, with their plant growth promotion (PGP), nutrient cycling, anti-phytopathogenic activity, and ability to thrive in harsh conditions, have been reported for a wide range of plants. Among various actinobacterial members, *Streptomyces* are commonly found in soil and can colonize the rhizosphere and root tissues with PGP activity [51]. For example, *Streptomyces* sp. isolated from wheat rhizosphere showed PGP activities, namely, phosphate solubilization, production of indole-3-acetic acid (IAA), siderophore, phytase, and chitinase, as well as utilization of sugars in the rhizosphere [50]. *Streptomyces lydicus* WYEC108, that colonized and sporulated within the nodule's surface cell layers of pea root, influenced nodulation by increasing the average size of the nodules, improving the vigor of bacteroids within the nodules by enhancing nodular iron and possibly other soil nutrient assimilation [52]. The impact of *Streptomyces* spp. isolated from the rhizosphere on five legumes (soybean, kidney bean, chickpea, lentil, and pea) demonstrated that soil microbial populations were boosted, while soil nutrients and organic matter content were also increased [53]. Soil enrichment with *Streptomyces* sp. boosted photosynthesis, which subsequently increased legume production. *Streptomyces* sp. also boosted nitrogen availability in soil, legume tissue, and seeds, which activated critical nitrogen metabolizing enzymes such as glutamine synthetase, glutamate synthetase, and nitrate reductase. In addition to higher amounts of nitrogen-containing amino acids in actinobacterial-treated legume seeds, significant quantities of sugar, organic acids, and fatty acids, as well as antioxidant phenolics, minerals, and vitamins were also observed [53]. Members of the genus *Streptomyces* and a few *Kitasatospora* were predominantly isolated from the yam rhizosphere and promoted the growth of *Arabidopsis* seedlings [54]. All of them produced IAA and siderophores, half exhibited tricalcium phosphate-solubilizing activity, and 20% harbored 1-aminocyclopropane-1-carboxylic acid (ACC) deaminase activity. Not only *Streptomyces* spp., but other actinobacterial members have also been reported from the rhizosphere as having PGP activity. For example, a multiple growth-promoting *Tsukamurella tyrosinosolvens* (isolated from the rhizosphere soil of tea plants) was reported to secrete various organic acids, such as lactic acid, maleic acid, and oxalic acid; solubilize phosphate and produce IAA and siderophore to enhance plant growth [55].

The actinobacterial strains also showed PGP activity in field trials. *Streptomyces corchorusii* UCR3-16 isolated from rice rhizosphere was tested for PGP activity in field trials utilizing a talcum-based powder formulation [56]. *S.*

corchorusii UCR3-16 significantly improved shoot length, shoot and root weight, total grain yield, and grain weight in rice. The sheath blight disease in rice leaves was also dramatically decreased by the talcum formulation [56]. Similarly, *Streptomyces* sp. CAI-8 isolated from rhizosphere soils of chickpeas under field conditions showed an increment in nodule numbers, root weight, stover yield, and grain yield [57]. Antifungal activity of *Streptomyces* spp. VV/R1 and VV/R4 isolated from the rhizosphere were tested for PGP in a field trial [58]. Both strains significantly reduced the infection rates of several fungal pathogens (*Dactylonectria* sp., *Ilyonectria* sp., *Phaeoacremonium chlamydospora*, and *Phaeoacremonium minimum*) that caused young grapevine. These isolates also significantly reduced the mortality level of grafted plants in the nursery [58]. The overall PGP properties of actinobacterial strains isolated from the rhizosphere are shown in **Figure 1**.

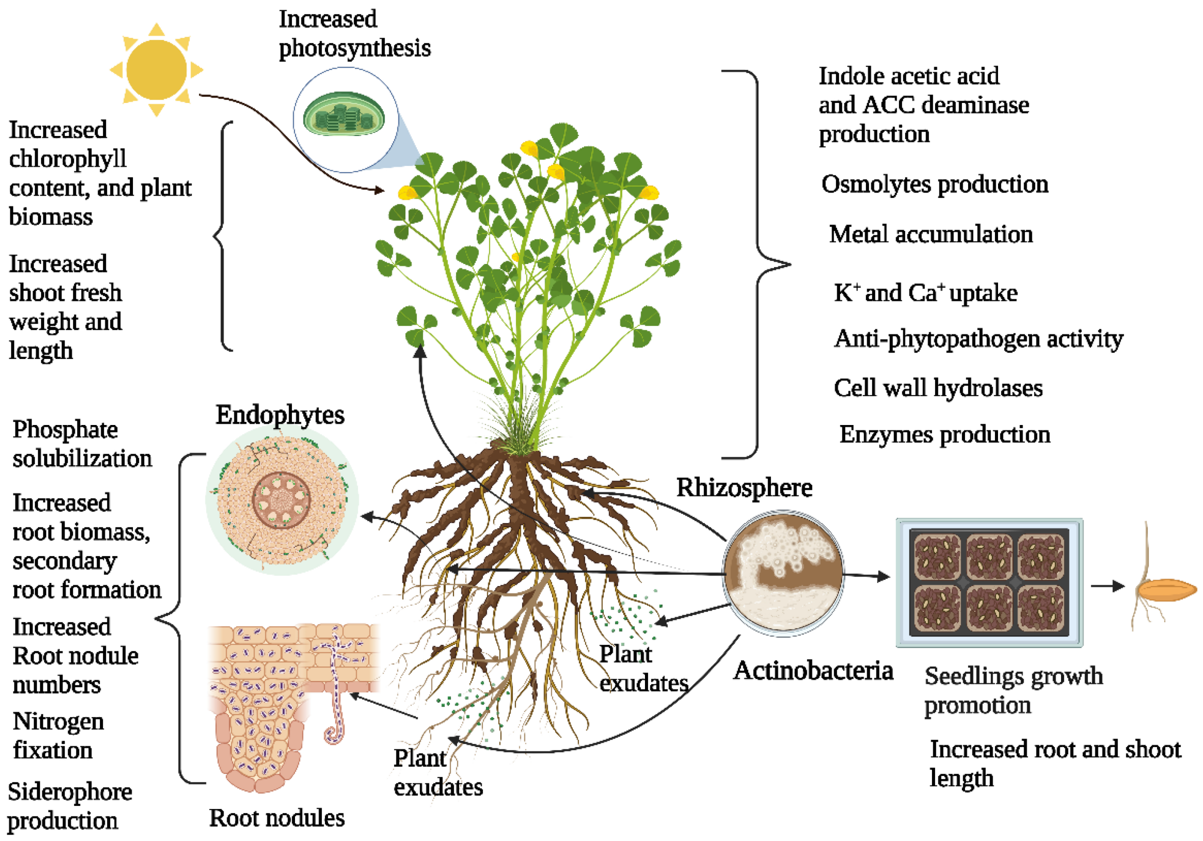

Figure 1. Role of Actinobacteria in various plant parts.

Microbial endophytes have co-evolved along with plants by colonizing apoplast and symplast regions of the host plant [59]. Among the endophytes, actinobacterial members are excellent dwellers in plant tissues, and their ecology in plants is exceptionally diverse [60]. It has been documented that actinobacterial members can colonize any tissue or organ of the host plant and they are prevalent in the roots, somewhat plentiful in the branches, and rare in the leaves [46][61][62]. The first actinobacterial endophyte to be isolated was *Frankia,* which is a nitrogen-fixing microorganism that induces nodulation on several angiosperm plant families and has received substantial attention due to its role in the nitrogen economy of its hosts [45][63]. *Frankia* sp. DDNSF-01 and *Frankia casuarinae* DDNSF-02 isolated from the root nodules of *Casuarina* sp. showed activity against phytopathogens including

Pseudomonas sp. and *Colletotrichum* sp. in addition to the production of IAA, siderophore, and ammonia, as well as phosphate solubilization [64].

In general, the endophytic actinobacterial members were the most commonly isolated from roots, followed by stems, and leaves [65]. *Streptomyces* spp. were the predominant species, followed by *Microbispora*, *Micromonospora*, *Nocardioides*, *Nocardia*, and *Streptosporangium* which were commonly found among the culturable endophytic actinobacteria [66][67]. In the past few years, various endophytic actinobacterial members were reported for PGP activity. For example, endophytic *Streptomyces* and *Amycolatopsis* isolated from *Camellia oleifera* increased the growth of *C. oleifera* seedlings [68]. Similarly, *Streptomyces* spp. and *Amycolatopsis* spp. were used in the hydroponic germination of wheat seeds, and promoted plant growth in terms of root and stem parts [68]. The genus *Streptomyces* was mostly dominant among the isolates recovered from leaf, stem, and root samples of tea, including *Actinomadura*, *Kribbella*, *Nocardia*, *Kytococcus*, *Leifsonia*, *Microbacterium*, *Micromonospora*, *Mobilicoccus*, *Mycobacterium*, *Nocardiopsis*, *Piscicoccus*, and *Pseudonocardia*, whereas *Mobilicoccus* and *Piscicoccus* were reported for the first time as plant endophytes [69]. These strains produced IAA and ACC deaminase, exhibited antimicrobial activity, and carried polyketide synthase (PKS-I and PKS-II) and non-ribosomal peptide synthetase genes [69].

Endophytic actinobacterial members also showed enhanced growth when co-inoculated with other microbial strains. Co-inoculation of endophytic *Microbispora* sp. CP56, *Actinomadura* sp. CP84B, *Streptomyces* spp. CP200B, and CP21A with *Mesorhizobium cicero* in chickpea seedlings showed growth promotion and enhancement of the rhizobia–chickpea symbiosis by increasing nodulation-related biological processes such as rhizobial chemotaxis, biofilm formation, and *nod* gene expression [70]. When PGP endophytic strains *Microbispora* sp. GKU 823 and *Streptomyces* sp. GKU 895 were co-inoculated with the PGP diazotrophs *Bacillus* sp. EN-24 and *Enterobacter* sp. EN-21, the growth of sugarcane was increased when compared with individual inoculation [71]. In addition, endophytic *Streptomyces* spp. isolated from plant roots grown in contaminated soil showed PGP features such as phosphate solubilization and production of ACC deaminase, IAA, biosurfactant, and siderophores with the ability of phytoremediation by degradation of petroleum increasing up to 98% after 7 days of incubation [72].

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