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Actinobacterial Biofertilizers: An Alternative Strategy for Plant Growth Promotion

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A B S T R A C T

The problem of food security arises along with the increase in world population. To meet the enormous food demands of growing population, farmers use traditional agricultural practices which mainly rely on use of chemical fertilizers and pesticides which are extensively harmful to the humans as well as environment. Therefore, there is an immense demand for an alternate strategy to increase the food productivity and quality which does not rely on use of these harmful chemicals. This increasing demand of lesser use of these chemicals has led to the use of soil microorganisms which possess the ability of nutrient cycling, improve soil quality and plant health as well as crop productivity. Among soil microorganisms, actino-bacteria represent an important group of microorganisms which has been reported to produce some useful substances which help in increasing soil quality and improve plant growth promotion as well as crop productivity. Hence, actino-bacteria represent a key component of agricultural ecosystems. This is important to increase our knowledge about interaction of these microorganisms with the soil ecosystem. On the basis of several studies, the present article highlights the importance of actino-bacteria in plant growth promotion by various means

Introduction

Rhizosphere is an area where a strong microbiological bustle takes place due to the release of various kind of plant metabolites, known as root exudates. These root exudates consist of various amino acids, sugars, fatty acids, proteins, vitamins, *etc*. which play an important role to dwell microorganisms in the rhizosphere. A vast group of microorganisms inhabit the rhizosphere and show ecological activities by interacting with plants and other microorganisms. Actinobacteria comprise a major group of microorganisms which is found in rhizosphere as well as inside the plant roots as endophytes (Bhosale and Kadam, 2015). Although, the population of actinobacteria in the rhizosphere is different from the endophytic environment due to the presence of root exudates and other microorganisms in the rhizosphere, both kinds of communities use related mechanisms to promote the plant growth. Actinobacteria are well known for their productive activities in nutrient recycling by degradation of chitin, cellulose, starch, lipids and complex carbohydrates and flouting them into simple sugars by the secretion of various kinds of hydrolytic enzymes in the rhizosphere (Vurukonda *et al.,* 2018). These microorganisms, when, reside around the plant root surfaces, perform an important role in breakdown of organic matter and make it available for the plant uptake. These microorganisms also show their potential role in solubilization of rock phosphate, production of siderophores, indole-acetic-acid (IAA), hydrogen cyanide (HCN), ammonia and lytic enzymes (Jog *et al.*, 2012; Damam *et al.*, 2016). Actinobacteria may also suppress the venomous microorganisms which could be responsible for inhibition of plant growth. These abilities of actinobacteria have positive effects on the plant growth promotion and thereby, actinobacteria are also known as “plant growth promoting rhizobacteria”.

Sustainable agriculture is a fundamental need of today’s world because it is the only mean to ensure food security and food quality. It has the potential to meet our imminent requirements of agricultural products. Traditional agricultural practices, which include the use of harmful chemical fertilizers and pesticides, will not be able to meet these colossal agricultural needs. To retain sustainable agriculture, it is essential to limit the use of these harmful chemicals and replace them with ecofriendly agricultural practices. Plant growth promoting actinobacteria, also known as biofertilizers, being environment friendly and renewable, offer superior alternative to these hazardous and non-renewable fertilizers and pesticides. Actinobacteria promote the plant growth by two possible mechanisms *i.e.* direct and indirect mechanisms (Aditi and Anupama, 2015). These mechanisms involve nitrogen fixation, phosphate solubilization, production of phytohormone such as indole-acetic acid (IAA), utilization of 1- aminocyclopropane-1-carboxylate (ACC), production of siderophores, cyanide (HCN), lytic enzymes and antibiotics. These mechanisms are either engaged in plant growth promotion directly by supplying nutrients to the plants or suppress the deleterious microorganisms dwelling around the plant roots which could be harmful to the plant growth. Therefore, these direct and indirect plant growth promoting characteristics of actinobacteria make them superior alternative to the hazardous chemicals.

Nitrogen fixation

Nitrogen is a very critical element for limiting the growth of plants due to its unavailability to the plant uptake. It is a vital component of the most needed pigment for photosynthesis *i.e.* chlorophyll, in addition to amino-acids, proteins, ATP molecules and nucleic acids. Nitrogen is the most abundant element on earth’s atmosphere in its molecular form (N_2) (Vance, 2001). However, plants can use only reduced form of nitrogen as either ammonium (NH_4^+) or nitrate (NO_3^-). The molecular nitrogen is generally reduced via physical, chemical and biological means. Over physical and chemical means of nitrogen fixation, biological nitrogen fixation is an efficient method to fix the molecular nitrogen into its reduced forms which are more readily taken up by the plants. Nitrogen fixation via biological means entails the role of microorganisms. Among actinobacteria, *Frankia* is a resourceful microorganism which can fix the molecular nitrogen in non-leguminous actinorhizal plants under symbiotic as well as free living conditions (Sathya *et al.,* 2017). It infects the actinorhizal plant roots either by forming a thread like structure intracellularly or by intercellular cell incursion. *Frankia* form vesicles in the roots of the actinorhizal plants under N deficient and normal oxygen tension conditions where nitrogen fixing enzyme, nitrogenase, carry out the fixation of molecular nitrogen.

Beside *Frankia,* non-*Frankia* actinomycetes have also been found to fix the nitrogen under non-symbiotic conditions. An unusual group of actinomycetes showing positive acetylene-reduction activity has been illustrated in literature which was retrieved from surface-sterilized roots of *Casuarina equisetifolia* growing in Mexico and their distinction from *Frankia* was confirmed using 16S rRNA gene phylogenetic analysis and DNA-DNA homology which was found very low with *Frankia* (Valdes *et al.,* 2005). These non-*Frankia* actinomycetes, found to be closely related to Thermomonosporaceae and the Micromonosporaceae, were not only able to grow on N-free medium and found positive to acetylene-reduction activity but also found to possess *nifH* gene responsible for N-fixation. Therefore, the potential of some special actinobacteria to fix atmospheric nitrogen plays a significant role to supply nutrients for the growth of plants.

Phosphate solubilization

Like nitrogen, phosphorous is another essential element for all living life on the earth and in soil environment, it is an important limiting factor for plant growth. Soil phosphorous occurs in organic as well as in inorganic forms. The amount of organic and inorganic phosphorous in soil depends largely on soil properties, like pH and type of soil. Organic phosphorous accounts for 29-65% of total soil P content, but in some soil types, it contributes upto 90% total soil P (Ghorbani-Nasrabadi *et al.,* 2013). Usually, P content in the soil is present in excess for the use of plants. Nonetheless, a very little fraction of this huge amount of P in soil is readily available to the plants because P, being highly reactive, makes complexes with other elements which are not taken up by the plants. Plants can uptake only monobasic and dibasic form of P. To fulfill the requirements of P, traditional agricultural practices make use of rock phosphate fertilizers which result in depletion of phosphate reservoirs.

Actinobacteria are prime microorganisms in the soil representing crucial role in nutrient recycling. They have recently been reported to solubilize complexes of phosphate and making P available to the plants uptake. These microorganisms have the potential to carry out hydrolysis of phytate which is the most prevalent form of organic (inositol) phosphate in soil.

Actinomycetes *Streptomyces alboniger, S. venezuelae, S. ambofaciens* and *S. lienomycini* have been demonstrated to produce extracellular phytate-degrading enzymes *i.e.* phytases which correspond to a group of phosphomonoesterases that commence the stepwise breakdown of phytate (Ghorbani-Nasrabadi *et al.,* 2012). On the basis of pH, these phytases have been recorded as acid and alkaline phytases.

Another mean of solubilization of phosphate by soil microflora is the production of various acids *i.e.* gluconic acid, citric acid, malic acid, succinic acid and oxalic acid which depends on metabolic pathways to utilize different carbon sources. However, mechanism of acidification in phosphate solubilization by actinobacteria is rarely reported (Jog *et al.,* 2014). Therefore, enzymatic degradation of phosphate complexes plays a critical role in making P available to the plants. The ability of actinobacteria to solubilize P makes them a better candidate to use as natural fertilizers.

Production of phytohormone

Root exudates secreted by the plants in rhizosphere help to modulate the microflora around the roots of plants and construct potential environment for the synthesis of IAA by the microorganisms dwelling in the rhizosphere. Actinobacteria have been studied to produce phytohormone belonging to class of auxins *i.e.* IAA which is a common plant hormone (Kamal *et al.*, 2014). Indole-acetic acid production helps in growth and development of plants by promoting cell division and elongation. Among actinobacteria, the production of IAA (71 g/mL and 197 g/mL) by two different *Streptomyces* sp. have been revealed to enhance seed germination and seedling growth of a folk ethno-medicinal plant of Meghalaya, *Centella asiatica* (Dochhil *et al.*, 2013). The production of IAA has also been mentioned in other *Streptomyces* sp. also, including *Streptomyces violaceus, Streptomyces griseus, Streptomyces exfoliates, Streptomyces coelicolor, Streptomyces lividans etc.* (Vurukonda *et al.*, 2018). Their ability to produce IAA makes them a potential candidate for use in agricultural practices as natural fertilizers to maintain sustainability of agricultural products.

Utilization of 1- aminocyclopropane-1-carboxylate (ACC)

Some actinobacteria have the ability to use ACC which acts as a precursor molecule for the biosynthesis of ethylene in the plants. Ethylene is often called as ‘aging hormone’ because of its role in enhancing plant developmental processes which include ripening, senescence and abscission (Schaller, 2012). An enzyme, ACC-deaminase catalyzes the hydrolysis of ACC into ammonia and alpha-ketoglutarate. Among actinobacteria, streptomycetes have been evaluated to produce ACC-deaminase (El-Tarabily, 2008). Their study revealed increased plant growth promotion of tomato (*Lycopersicon esculentum* Mill.) by *Streptomyces filipinensis* and *S. atrovirens* due to the production of ACC-deaminase. Furthermore, *S. filipinensis* has been reported to promote plant growth more as compared to *S. atrovirens* due to the production of IAA and ACC-deaminase both by *S. filipinensis* while *S. atrovirens* has been reported to produce ACC-deaminase only. Therefore, it is deemed that actinobacteria showing more plant growth promoting properties are more prominent to use as bio-fertilizers.

Production of siderophores

Iron is a very essential element in all the living organisms as it plays an important role in catalysis of numerous enzymatic reactions where it acts as a co-factor. Earlier, iron was usually present in ferrous form (Fe^{2+}) in soil during oxygen deficient atmosphere, which was easily utilized by the microorganisms. However, with the passage of time, as the oxygen deficient atmosphere replaced by oxygen rich environment, iron get oxidized to ferric form (Fe^{3+}) which is not readily utilized by microorganisms. To overcome this challenge, microorganisms evolved to produce small, low molecular weight, iron chelating molecules *i.e.* siderophores which form complexes with iron (Wilson *et al.*, 2016). The competition for iron acquisition occurs between plants and phytopathogens as microbial siderophores have higher affinity towards iron chelation making it unavailable to the plants.

Streptomyces sp. have been reported to produce siderophores *i.e.* ‘coelichelin’, a peptide siderophores by *Streptomyces* *coelicolor* (Challis and Ravel, 2000), 'enterobactin' by *S. tendae* and *Streptomycin* sp. Tu 6125 (Fiedler *et al.,* 2001). Siderophore producing actinobacteria create iron deficient conditions for phytopathogens by chelating the iron present in the rhizosphere and help to protect plants from disease which leads to the better growth of plants.

Production of cyanide

Actinobacteria have the ability to produce hydrogen cyanide (HCN). The mechanism of action of HCN is considered to inhibit terminal 'cytochrome c oxidase' in the respiratory chain and binds to metalloenzymes which confers it the property of suppressing phytophathogens (Ramette *et al.,* 2003; Olanrewaju *et al.,* 2017). Different species of *Streptomyces* have been reported to produce HCN conferring important role in disease suppression (Passari *et al.,* 2015; Anwar *et al.,* 2016). Hydrogen cyanide has also been reported to contribute in mineral mobilization and phosphate release which results in indirect increase of nutrient availability to both actinobacteria and their host plants (Rijavec and Lapanje, 2016). Based on the ability of HCN to prevent plant pathogen and to enhance nutrient availability, HCN producing actinobacteria can be used as biocontrol as well as plant growth promoting agents.

Production of lytic enzymes

Cell wall of any organism is accountable to maintain the integrity of cells under all kinds of environment *i.e.* isotonic, hypotonic and hypertonic. Cell wall of different organisms is composed of various kinds of complex polymeric substances, for instance, fungal cell wall is composed of chitin and β-1, 3-glucan while cell wall of oomycetes is mainly composed of cellulose and β-1, 3-glucan. Furthermore, bacterial cell wall is composed of peptidoglycan *i.e.* polysaccharide chain cross linked with unusual peptides. Actinobacteria have been observed to produce various lytic enzymes which hydrolyze the cell wall component of other bacteria, fungi and protozoa and thus, prevent harmful microorganisms to cause disease. *Streptomyces albovinaceus, S. caviscabies, S. griseus, S. setonii* and *S. virginiae* have been reported to produce chitinases (Macagnan *et al.,* 2008). *Streptomyces* RC1071 retrieved from cerrado soil was tested against phytopathogenic fungus which was observed having antifungal activity (Gomes *et al.,* 2001). Actinomycetes have also been illustrated to produce proteases, lipases and cellulases (Aditi and Anupma, 2015). The production of lytic enzymes by actinobacteria grants them biocontrol potential and aids the plant growth promoting characteristics.

Production of antibiotics

Actinobacteria have been extensively studied to produce a vast variety of secondary metabolites *i.e.* by-products of metabolism which are not generally essential for their own growth (Waksman *et al.,* 2010; Nanjwade *et al.,* 2010; Omran and Kadhem, 2016). These secondary metabolites are termed as 'antibiotics'. Antibiotics exhibit antitumoral (doxorubicin and bleomycin), antifungal (amphotericin B and nystatin), immunosuppressive (FK-506 and rapamycin), insecticidal (spinosyn A and avermectin B), herbicidal (phosphinotricin) and many clinically and commercially important activities (Grasso *et al.,* 2016). Most of the antibiotics with diverse biological activities are produced by actinomycetes. Among actinomycetes, *Streptomyces* sp. have been reported to produce a wide variety of antibiotics belonging to class β-lactam (Ram, 2014). Antibiotics differ in their chemical structure, mode of action and effects on different organisms. In rhizosphere, antibiotics produced by soil dwelling actinomycetes play a very significant role in inhibiting the growth of plant pathogens by targeting either essential molecules or biosynthetic pathways. Production of antibiotics depends upon several environmental factors, such as temperature, pH, aeration, presence of competitor microorganisms *etc*. (Omran and Kadhem, 2016). Therefore, actinobacteria present in soil produce a variety of antibiotics depending upon environmental conditions and these antibiotics inhibit a wide range of pathogenic microorganisms to cause disease in the plants. As a result, actinobacteria aid to the better plant health and development leading to the sustainability of agricultural products.

Conclusion and future prospectives

Actinobacteria possess a great potential to enhance plant growth and development by producing various substances which increase nutrient supply to the plants, provide essential phytohormones, inhibit the growth of harmful microorganisms in rhizosphere and suppress disease to occur. These abilities of actinobacteria make them a competent candidate to use as biofertilizers and biocontrol agents to attain sustainability in agriculture. Use of these plant growth promoting actinobacteria helps to limit the use of chemical fertilizers and pesticides which could either harm the environment and devastate agricultural sustainability to a very large extent.

Some actinobacteria are having a few while the other possesses several plant growth promoting characteristics. This can limit their use to attain sustainability in agriculture because a microorganism with maximum number of plant growth promoting characteristics is considered as an ideal candidate for use. Therefore, genetic manipulations of an optimal actinobacterial candidate to the better one are needed to be accepted upto safe and sound levels by the scientists, breeders and regulatory agencies to achieve a very giant goal of increased crop productivity without environmental hazards. Therefore, a lot of work is to be done genetically to improve the efficacy of actinobacteria in plant growth promotion and suppression of diseases by bioactive compounds.

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