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Field Application of Rhizobial Inoculants in Enhancing Faba Bean Production in Acidic Soils: An Innovative Strategy to Improve Crop Productivity

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Abstract

Faba bean is the most vital legume crop in Ethiopia, but abiotic stresses primarily soil acidity are an obstacle for its production. Soil acidity disturbs and potentially limits nitrogen-fixing symbiosis. The interruption of nitrogen fixation and faba bean rhizobia interaction as a result of soil acidity leads to decreasing crop production. Sole dependence on chemical fertilizers for agricultural growth would mean further loss in soil quality and increased environmental damage. Rhizobial species show off sizable metabolic abilities to mitigate abiotic and biotic stresses, and mechanisms in stress tolerance are advancing fast, offering a strong foundation for the choice and engineering of rhizobia and legume hosts with better tolerance to soil acidity accordingly. The vast efforts to pick bioinoculants that can restore nitrogen under acid-affected soils are producing competitive crop yields. The main challenge of using single-type bioinoculant in field application can lead to variable and inconsistent outcomes. Co-inoculation of compatible microbes with organic farming which does not involve use of synthetic pesticides and chemical fertilizers is an imperative element in sustainable agriculture. Therefore, the present chapter focuses on the field application of faba bean rhizobial inoculants in acidic soils as a promising potential input in organic farming system. Moreover, the mechanism of N_2 fixation and plant growth promotion systems under severe salt, drought, acidity, temperature, and heavy metal stresses is also highlighted.

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7.1 Introduction

Legumes play a predominant role in lowering poverty and improving human health and nutrition while restoring ecosystem services (Jaiswal et al. 2018). Among legume crops, faba bean (*Vicia faba* L.) is one of the important food legumes to satisfy human protein needs in the era of escalating price of animals' meat. Strong demand for food requires unique efforts for ample production. Today's agriculture is characterized by soil fertility loss, local weather alternates, and multiplied pest attacks (Mabrouk et al. 2018). Population growth and reduction in land on hand for cultivation with endless environmental constraints (extremely low/high temperature, soil acidity, salinity, drought, flooding, and heavy metals) are principal threats for agricultural sustainability (Shahbaz and Ashraf 2013). Agriculture is the predominant monetary endeavor in the growing countries including Ethiopia appealing over 50% of the population with low crop productivity owing to environmental stresses which include soil acidity (Alori et al. 2017). Moreover, increasing demand for food production with shrinking land resources is a principal venture to agricultural sustainability (Owen et al. 2015). Currently, the use of rhizobacteria and rhizobia has been of great help in combating the aforementioned stressful factors that limit the overall performance of faba bean crop (Kabata et al. 2017). The need of more sustainable agriculture practices, specifically the reduction of chemical fertilizers, highlights the significance of biological nitrogen fixation by symbiotic legume-rhizobia associations (Adesemoye and Kloepper 2009).

Faba bean is one of the earliest domesticated food legumes and occupies nearly 3.2 million hectares worldwide and is a major component of a daily diet in Ethiopia (Abebe et al. 2014). Due to its high dietary value and capability to grow over a wide range of climatic and soil conditions, cultivation of faba bean is appropriate for sustainable agriculture in many marginal areas (Youseif et al. 2017). Faba beans are fast growing and high-yielding crop with remarkably significant economic and ecological roles (Sahile et al. 2008). It has been considered as a meat extender or substitute due to its high protein content material (20–41%) (Crépon et al. 2010). In Ethiopia faba bean is grown mainly by using subsistence farming, during the cool season (June–September) (Weldua et al. 2012). In 2017–2018 cropping season, faba bean occupies about 437,106 hectares of land with an annual countrywide production of 1,016,068.2 tons, with a productivity of 2.11 tons ha^{-1} (Damtie Mengistie 2018). However, the productivity of the crops under smallholder farmers is not greater than 1.89 t ha^{-1} (Demissie et al. 2016). The low yields per hectare have been related with susceptibility of the plants to biotic and abiotic stresses (Sahile et al. 2009). The main cereal crop production constraint in most sub-Saharan Africa nations is the loss of soil fertility (Nyoki and Ndakidemi 2016). Soil acidity is a primary issue to crop production in the world. Declining soil fertility due to soil acidity is the most determinant factor. Annual nutrient deficit is also estimated to be −41 kg N, −6kg P, and

−26 kg K ha^{-1} (Kebede and Yamoah 2009). In addition, the highland location is a place that receives excessive rainfall and characterized as acidic soil which causes high phosphorus fixation, leaching nitrogen and potassium.

Modern farming practices have an effect on our world, via land degradation, nutrient runoff, soil erosion, water pollution, and destruction of traditional knowledge systems (Patil et al. 2013). When the soil contains a significant proportion of non-nodulating or ineffective nitrogen-fixing rhizobia as a result of soil acidity, it leads to decreasing crop production. Sole dependence on chemical fertilizers for crop cultivation would mean further loss in soil quality and extremely increased environmental damage. The chemical provides an instantaneous impact on crop production and however creates long-term ill outcomes on environment (Das and Singh 2014).

As a result of un-affordability of the cost of chemical fertilizers and their long-term negative ecological impact, there is a great need to explore biological means to improve soil health and crop productivity. Organic farming has emerged as an important priority area to realize safe and healthy food and continuing agriculture protecting environmental damage (Mahdi et al. 2010). These can be achieved by reducing(avoiding) the use of synthetic fertilizers, pesticides, growth regulators, and livestock feed additives (Das and Singh 2014). Organic farming comprises biofertilizers and organic amendments which are ready to use phytobeneficial live microorganisms and biowastes. The use of microbial inoculants has a prominent role in enhancing productivity due to their ability to release the bound nutrients in most organic matter at required times for crop utilization (Parr et al. 1994). Recently studies have shown that several plant species require microbial associations for stress tolerance and survival (de Zelicourt et al. 2013). Plant growth-promoting rhizobacteria (PGPR) and rhizobia can improve the growth of crops under abiotic stresses for sustainable agriculture (Egamberdieva and Kucharova 2009). The beneficial roles of PGPR and rhizobia have been achieved via nutrient availability and uptake and support the health of soil and plants (Alori et al. 2017). Field experimental results from acidic soils of Western Kenya showed that rhizobial inoculation increased nodule number and weight per plant and inoculation accounted for 58.91% and 78.95% in increased fixed N levels (Ogega et al. 2018). Generally, agricultural practices in the past 60 years have been dependent on external inputs (pesticides and fertilizers). All these environmental- and health-related problems in the world inspired the use of eco-friendly bio-tools to maximize growth and productivity of legumes by alleviating different stresses. Therefore, the present chapter focuses on the field application of faba bean rhizobial inoculants in acidic soils as a promising potential input in organic farming system. Moreover, the mechanism of N_2 fixation and plant growth promotion systems under severe salt, drought, acidity, temperature, and heavy metal stresses is also highlighted.

7.2 Legume-*Rhizobium* Symbiosis Under Soil Acidity Constraints and Their Performance

Rhizobia-legume symbiosis is the most environment-friendly gadget that money owed for nearly 40% of all biologically fixed nitrogen estimated at 70 million lots per annum (Yadav and Verma 2014). Symbiotic nitrogen fixation is in need of host plant cultivar, *Rhizobium* strain and the interactions of these symbionts with the pedoclimatic elements and the environmental conditions. Extremes of soil acidity have an effect on nodulation by way of lowering the colonization of soil and the legume rhizosphere by means of rhizobia. Highly acidic soils ($pH < 4.0$) regularly have low ranges of phosphorus, calcium, and molybdenum and high concentrations of aluminum and manganese which are regularly poisonous for each partner. The terrible results of soil acidity on soil biodiversity and crop boom are associated to the deficiency of principal nutrients and toxicity of metals (Bordeleau and Prévost 1994; Chimdi 2015). Soil acidity influences soil productivity in the Ethiopian Highlands the place where faba bean cultivation is distinguished (Birhanu 2014). Most species of legume family can fix atmospheric nitrogen (N_2) by using symbiotic microorganism (rhizobia) in root nodules. Lateral gene transfer of particular symbiosis genes inside rhizobial genera is a vital mechanism permitting legumes to form symbiosis with rhizobia adapted to particular soils (Andrews and Andrews 2017). Symbiotic nitrogen fixation is an essential contributor to soil fertility. The nodulation process for almost all legumes studied is initiated by means of the legume production of a mix of compounds, mainly flavonoids, which persuade the synthesis of NodD protein in rhizobia leading to root nodule formation (Downie 2014).

Field competition experiments carried out in Southern Spain and one of a kind inoculant strains of *Sinorhizobium fredii* have been selected that can nodulate soybean in alkaline or acidic soils (Albareda et al. 2009). Novel strains of the β-proteobacteria *Burkholderia* are successfully nodulating herbaceous legume *Rhynchosia ferulifolia* with attainable position in nitrogen fixation adapted to acid, infertile soils (Garau et al. 2009). Nodulation and quantities of nitrogen fixed via legumes in acidic soils are reduced both through direct effects on the survival and multiplication of rhizobia and on the boom of the host flora (Giller 2001). The establishment of an effective symbiosis requires (a) colonization and survival in soil by way of rhizobia as saprophytes in competition with other endogenous microbes; (b) a fast colonization of the rhizosphere prior to root infection and genetic compatibility between host and root nodule bacteria to establish an effective nodule; and (c) a favorable environment to permit maximum fixation (Bordeleau and Prévost 1994). Therefore, the production of legumes in agriculture often requires the introduction of symbiotically potent root nodule bacteria as inoculants.

7.3 Phytobeneficial Traits of Rhizobia

PGPR greatly and rhizobia singly perform necessary function in improving plant growth through numerous mechanisms. The mode of action of these microbes to promote plant growth embraces (1) abiotic stress tolerance in plants; (2) nutrient fixation for easy uptake by using plant; (3) plant growth regulators; (4) production of siderophores; (5) production of unstable (volatile) organic compounds; and (6) production of protection enzyme like chitinase and ACC deaminase for the prevention of plant diseases as displayed in Fig. 7.1 (Choudhary et al. 2011; García-Fraile

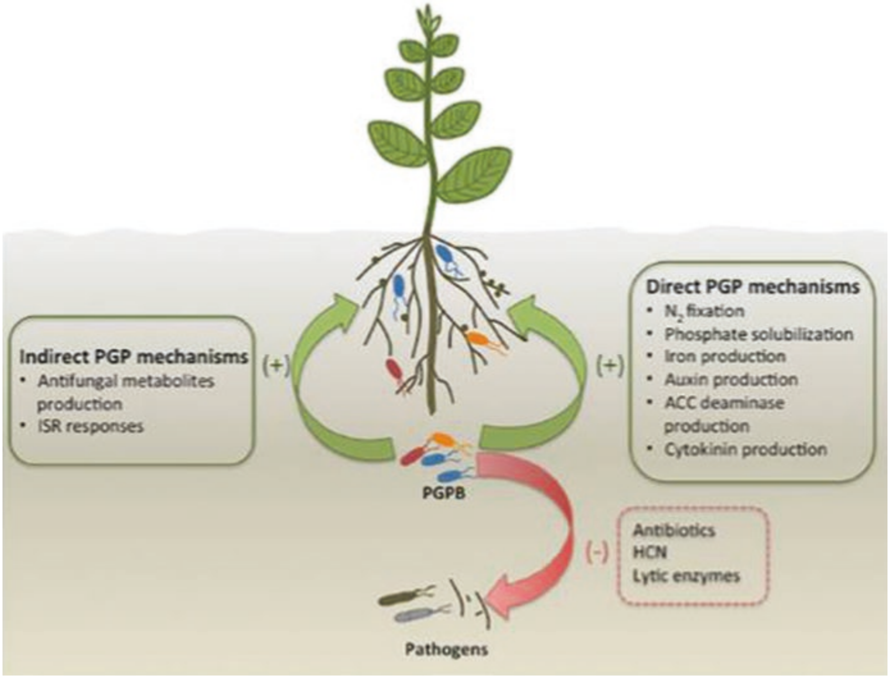

Fig. 7.1 The modes of action for PGPR are based on either direct and/or indirect mechanisms. (Adapted from Di Benedetto et al. 2017).

et al. 2015). However, the mode of action varies depending on the type of the host plants. Plant growth is influenced via a range of stresses due to the soil environment, which is a fundamental constraint for sustainable agricultural production. Beneficial interactions among plants and microbes are essential for stabilizing natural communities and restoring degraded lands for plant productivity (Premachandra et al. 2016). PGPR and rhizobia improve plant growth either directly, by facilitating resource use or modulating plant hormone levels, or indirectly by reducing the inhibitory outcomes of various pathogenic agents (Di Benedetto et al. 2017). The current knowledge of rhizosphere microorganisms in biotechnology and environment applications has been suggested by numerous scholars (Bakker et al. 2013; Glick 2012; Mendes et al. 2013). The main plant growth-promoting potentials (traits) of rhizobia are discussed below:

7.3.1 Siderophore Production

Iron is an integral nutrient for ideal plant development, and it is a cofactor in metabolic pathways. In contrary, its deficiency can also lead to disruption of respiration or photosynthesis (Rajkumar et al. 2010). Under stipulations of iron hindrance, various rhizosphere microbes produce siderophores, ferric iron-specific ligands, which may additionally beautify plant growth with the aid of increasing availability of iron close to the roots. Study done on chickpea (*Cicer arietinum* L.) with the application of *Rhizobium ciceri* has shown siderophore production for plant growth (Berraho et al. 1997). The utilization of rhizobia may also be one way to extend soil iron availability in the rhizosphere. Bacteria are capable to synthesize low molecular weight siderophores involved in the process of chelating ferric iron from the environment. As studies indicate, they have a strong ability to chelate ferric ions allowing their solubilization and extraction from most mineral or organic complexes (Sandy and Butler 2009). When iron is limited in the soil, iron-solubilizing microbes furnish vegetation with iron and better their growth. Experiment done on strawberries (Flores-Félix et al. 2015) confirmed siderophores producing *Phyllobacterium* strain resulted in its growth and quality. In the soil the quantity of bioavailable iron is very low due to its accumulation as iron oxides and hydroxides that cannot be simply utilized with the aid of residing organisms (Kraemer 2004). Thus, there is a competition for iron, wherein siderophore-producing PGPR facilitates plant iron acquisition from iron-limited environment, which helps to sequester iron from neighboring microorganisms outcompeting them (Yu et al. 2011; Ahmed and Holmström 2014). Likewise, plant pathogens send off low amounts of bioavailable iron behind (Fones and Preston 2013). Different strains of rhizobia have been suggested nowadays to produce siderophores. This ability also confers upon nodule bacteria a selective advantage and may additionally lead to both direct and indirect management of plant pathogens (Arora et al. 2001).

7.3.2 Plant Growth Regulators

Plant growth regulators (plant exogenous hormones) are artificial elements that are comparable to herbal plant hormones. They are used to adjust the growth of plant life and are necessary measures for boosting agricultural production. One of the terms for the prominent modes of action for growth promotion of rhizobial species is plant growth regulator. This is described as microorganisms that have the capability to produce or alter the concentration of growth regulators such as indole-3-acetic acid (IAA), gibberellic acid (GA), cytokinins (CK), and ethylene (Somers et al. 2004).

Auxin is one of the indispensable molecules, regulating most plant processes at once or in a roundabout way (Tanimoto 2005).The result found that auxin-producing *Bacillus* spp. inflicts a tremendous effect on *Solanum tuberosum*'s growth (Ahmed and Hasnain 2008). The most active and famous auxins in vegetation are IAA (Hayat et al. 2010). IAA impacts plant nutrition and improvement via altering cell division, extension, and differentiation with the aid of increasing the rate of xylene and root development (Glick 2012). According to Vacheron et al. (2013), a wide range of processes in plant developmental growth are controlled by exogenous IAA via stimulate primary root elongation in lower dose and primary root length, root hair, and formation of lateral roots in higher dose. IAA promote root hair elongation significantly and this help the plant to more nutrient uptake and promote their growth. Species of *Bradyrhizobium*, *Rhizobium*, and *Mesorhizobium* have been found to produce a considerable quantity of IAA under in vitro conditions (Ahmad et al. 2008). Studies have proven that inoculation of CK- or GA-producing PGPR stimulated plant growth (Xie et al. 1996; Joo et al. 2009). IAA producing PGPR increased plant growth in mung beans (Xie et al. 1996), rice (Bal et al. 2013), and *Brassica juncea* L. (Indian mustard) (Shim et al. 2015).

Ethylene is a hormone that serves many physiological tactics in plants. It acts at trace levels during the life of the plant by stimulating or regulating the ripening of fruit, the opening of flowers, and the abscission of leaves and synthesis of volatile organic compounds responsible for aroma formation in fruits to mention a few (Frankenberger Jr 2002; Glick 2014). The rhizobial species increase growth and induce physiological changes in plants via synthesis of enzyme 1-aminocyclopropane-1-carboxylate (ACC) deaminase. Moreover, the higher dose of ethylene induces the defoliation and cellular processes that lead to the inhibition of root and stem growth and nitrogen fixation in legumes all of which in turn affect crop performance (Li et al. 2005; Ahmad et al. 2013). The plants synthesized ACC in response to exposure to more than a few types of environmental stress, such as cold, acidity, drought, pathogens, and heavy metals (Glick 2012). As a result rhizobia have the ability to degrade ACC in the rhizosphere and may want to shorten the deteriorating cycle and reconstruct a healthy root system that can withstand environmental stress. Ahmad et al. (2013) found that ACC deaminase-producing species of *Rhizobium* and *Pseudomonas* can improve the growth, physiology, and quality of mung beans under salt-affected environments. By lowering ACC levels in plants, rhizobia limit plant ethylene ranges which when exist in high concentrations can lead to a decreased plant growth and ultimately plant loss of life (Glick et al. 2007). The use of ACC deaminase-producing bacteria in association with different types of biotic and abiotic stresses results in enhanced plant tolerance to the stresses (Ma et al. 2003; Nascimento et al. 2012). ACC deaminase-producing rhizobial strains are 40% more environmentally friendly and effective at forming nitrogen-fixing nodules than non-producer (Ma et al. 2003). Generally, plants nodulated with the engineered strain of rhizobia resulted in a larger dry weight, a diminished ethylene level in roots, and a higher total copper uptake, in relation to indigenous strain.

7.3.3 Growth Modulation Enzyme

The synthesis of different antibiotics is often related with the potential of the bacteria to stop the proliferation of plant pathogens (generally fungi) (Mazurier et al. 2009). PGPR promote plant growth by producing different lytic enzymes together with chitinases, cellulases, glucanases, proteases, and lipases that can degrade part of the cell walls of many pathogenic fungi. Microorganisms that produce one or more of these lytic enzymes have been found to have biocontrol activity toward a range of pathogenic fungi inclusive of *Botrytis cinerea*, *Sclerotium rolfsii*, *Fusarium oxysporum*, *Phytophthora* spp., and *Rhizoctonia solani* (Kim et al. 2008; Glick 2012). The *Sinorhizobium fredii* KCC5 and *Pseudomonas fluorescens* LPK2 produce chitinase and beta-glucanases and dictate the fusarium wilt produced by *Fusarium udum* (Kumar et al. 2010). Apart from exhibiting the production of chitinase and beta-glucanases, *Pseudomonas* spp. inhibits *Rhizoctonia solani* and *Phytophthora capsici*, two of the most destructive crop pathogens in the world (Arora et al. 2008).

7.3.4 Nutrient Availability for Plant Uptake

Both free-living PGPR and symbiotic rhizobia have the potential to boost the availability of nutrient concentration in the rhizosphere by means of fixing nutrients, therefore stopping them from leaching (Choudhary et al. 2011). For instance, nitrogen is the most limiting nutrient for synthesis of amino acids and proteins in plants. It is a nitrogen present in the atmosphere (dinitrogen, N_2 or elemental nitrogen) and a relatively nonreactive molecules which is converted into ammonia through biological nitrogen fixation by most microorganisms (Lloret and Martínez-Romero 2005). The free-living PGPR *Azospirillum*, often related with cereals in temperate zones, is able to enhance rice crop yields (Tejera et al. 2005). Plants can't directly take up compounds like nitrogen, iron, and phosphate which are plentiful in the soil unless atmospheric nitrogen is converted via nitrogen fixation process (Chaparro et al. 2014; Richardson et al. 2009). Many researches have shown that *Rhizobium* spp. is the main nitrogen-fixing organism agriculturally known and regularly used to inoculate plants to increase nodules and plant biomass (Uribe et al. 2010). Some PGPR have phosphate solubilization capacity (Wani et al. 2007), insuring an increased phosphate ion availability and ease of uptake by plants. Agronomically vital rhizospheric actinobacteria *Kocuria turfanensis* strain 2M4 was discovered to be a phosphate solubilizer and IAA and siderophore producer (Goswami et al. 2014). Yadav et al. (2014) studied the positive effect of PGPR on nutrient uptake in rice via the inoculations of *Pseudomonas fluorescens* and *P. putida*. Phosphorus is also plant growth-limiting nutrient following nitrogen. Phosphorus is an essential nutrient required relatively in large amount and critical determinant of plant growth and productivity (Haileselassie et al. 2011). The requirement of phosphorus for faba bean is pretty high between 20 and 30 kg P ha^{-1} (Hungria et al. 2005). Moreover, it has precise roles in N_2 fixation, nodule initiation, nodule number, growth, and development (Schulze et al. 2006). It additionally performs an essential position in increasing legume yield through its impact on plant and fixation process by *Rhizobium* (Saraf and Dhandhukia 2005). On the other hand, phosphorus deficiency reduces N_2 fixation due to lowered nodule formation and decreased nodule sizes which ultimately affect the yield and grain quality and quantity (Sadeghipour and Abbasi 2012). Inoculation of high-quality *Rhizobium* had distinguished results on nodulation, growth, and yield parameters of faba bean (Desta et al. 2015).

7.4 Soil Acidity-Tolerant *Rhizobium* and the Symbionts for Sustainable Agriculture

Due to an extremely fast population growth and environmental pressure, it is mandatory to increase agricultural productivity with reduced environmental impacts. With the framework of sustainable agriculture, soil inoculation with PGPR and rhizobia is regarded as a promising bio-tool (Di Benedetto et al. 2017). The legume-*Rhizobium* symbiosis has tremendous ecological and agronomic importance with a full-size supply of nitrogen (Dita et al. 2006). Globally, N_2 fixed by using nodulated legumes makes contributions of 21.45 Tg nitrogen yearly in the world (Herridge et al. 2008). Among legumes, faba bean contributes to sustainable agriculture via fixing atmospheric nitrogen symbiotically with rhizobia. Effective symbiotic nitrogen fixation of faba bean with fast-growing species of *Rhizobium leguminosarum* bv. *viciae* is well known. Later, *R. fabae*, *R. laguerrereae*, *R. etli*, and *Agrobacterium tumefaciens* had been also recognized as faba bean-nodulating micro-symbionts (Tian et al. 2008; Youseif et al. 2014).

The application of *Rhizobium* in faba bean performs major functions in soil acidity enhancement. These bacteria can facilitate the overall growth of legumes and related nonlegumes directly by means of transferring symbiotically formed N to crops like cereals, growing in intercrops (Hayat et al. 2008). Besides N_2 fixation, rhizobia promote the growth of plant life via means of different mechanisms together with production of plant growth-promoting substances like phytohormones; auxins, cytokinins, and abscisic acids; and vitamins (Ahmad et al. 2008; Wani et al. 2007). Declining in soil fertility, acidity, decreased N_2 fixation, over cultivation, and poor soil management resulted in lower yields in leguminous crops (Abubakari et al. 2016). The different stages of plant host and rhizobial interaction in the interaction have been affected by acidity via limiting production of nodulation factors, attachment of rhizobia to roots, number of root nodules, and the nitrogenase activity (Graham 1992; Morón et al. 2005). To keep away from acidic soil losses in leguminous crop productivity, the improvement and viable strategies in legume-rhizobia associations or the selection of rhizobia capable to tolerate acidity has been designed (Ruiz-Díez et al. 2009). The key in acidity tolerance is the improvement of acid-tolerant and effective rhizobia inoculants (Tittabutr et al. 2006). Many experimental results have shown that it is feasible to enhance the growth of leguminous trees with superb rhizobia inoculation (Bogino et al. 2006; Maia and Scotti 2010).

Soil pH is one of the most limiting factors in legume and *Rhizobium* symbiosis as it renders rhizobial survival, nodulation, and N_2 fixation. McDonald (2014) noted that rhizobia are extremely sensitive to acidic pH and soluble aluminum ions between soil pH 4.8 and 5.0 as pH much less than 4.6 inhibits their activity. Legumes and *Rhizobium* form efficient symbiosis and fix high quantity of nitrogen when soil pH is no less than 5.6–6.1. On contrary, nitrogen fixation can be decreased up to 30% below $pH<4$. Findings of Ambrazaitienė (2003) and Hartwig and Soussana (2001) have been showed that soil acidity inhibited the root hair infection and nodulation; this disrupts the communication process. Furthermore, experimental outcomes have been revealed that soil acidity hinders the distribution and symbiotic efficiency of *R. leguminosarum* bv. *trifolii*, *R. leguminosarum* bv. *viciae*, *Sinorhizobium meliloti*, and *R. galegae*. In a slightly acidic soil, the average number of rhizobia has been 540.0×10^3cfu $g^{-1}$of soil, whereas, in high and medium acidic soil (pH KCl 4.1–5.0), *R.galegae* and *Synorhizobium meliloti* are no longer available. The symbiotic effectiveness is strain-specific where some that are outcompeted under normal pH conditions ($pH > 5.5$) might become dominant under low pH ($pH < 5.5$) conditions (Ferguson et al. 2013). *Bradyrhizobium* sp. are generally more acid-tolerant than most *Rhizobium* sp. (Brockwell et al. 1991). Although few rhizobia thrive at $pH < 5$, certain strains of *R. tropici* and *R. loti* are highly acid-tolerant (Appunu and Dhar 2006).

7.5 Role of *Rhizobium* Inoculation in Organic Farming Systems

Soil is a crucial and biologically active resource in agricultural ecosystem. It is to mean industrial agriculture that involves the application of agrochemicals (synthetic fertilizer, pecticides, herbicides and other fabricated inputs) (Pelletier et al. 2008). The experimental outcomes of Muleta (2007) have validated that the rational exploitation of microbial inputs in Ethiopian *Coffea arabica* production systems deserves inoculum development while retaining environmental quality. Due to these advantages, organic agriculture reached 43.1 million hectares by the end of 2013, with a yearly escalation of 14% (Syswerda et al. 2012; Cavigelli et al. 2013). Biological nitrogen fixation (BNF) is becoming economically feasible and eco-friendly eye-catching agricultural input (Bekere et al. 2012). As a result, legume plants symbiotically fix about 33 to 46 teragram (Tg) of nitrogen per year in the world (Herridge et al. 2008). Faba bean alone can fix nearly 150–300 kg N ha^{-1} in a growing season (Singh et al. 2012). BNF can be more desirable by means of effective and persistent *Rhizobium* seed inoculation. In this regard, pulse crop *Rhizobium* inoculation can fix better nitrogen to eliminate the need for nitrogen fertilizer inputs (Walley et al. 2007). Numerous studies proved that in improved yields with inoculation, Haile et al. (2008) reported a yield gain of 61–68% and 52% in *R. leguminosarum* var. *viciae*-inoculated faba bean in Bulie and Chencha districts of Southern Ethiopia, respectively. In Iran similar result has been mentioned that inoculation of faba bean seed with an appropriate strain increased faba bean grain yield by 35–69% (Khosravi et al. 2001). Abdel-Aziz and El-Din (2015) of Egypt described yield increments between 5.6–20% in Kantara and 6.5–15.4% in Gelbana at North Sinai via *Rhizobium* inoculation as compared to uninoculated treatment (control). The bacterial genera of *Pseudomonas*, *Klebsiella*, *Enterobacter*, *Azospirillum*, *Bacillus*, *Rhizobium*, *Alcaligenes*, and *Arthrobacter* have been said to enhance plant growth directly or indirectly (Saharan and Nehra 2011). In Australia competent and reliably faba bean rhizobial inoculant strains have been observed that can form nodules in soils above pH 5.0; however they are restricted below this level. The performance of strains of rhizobia with improved acidity tolerance to improve pulse nodulation and N_2 fixation on acidic soils has been also suggested (Denton et al. 2018).

7.6 Molecular Basis of *Rhizobium*-Mediated Mitigation of Soil Acidity Stresses

Environmental stress such as soil acidity, salinity, drought, and temperature imposes a foremost threat to each symbiotic nitrogen fixation and agriculture. For this reason, the *Rhizobium*'s tolerance to one of a kind environmental stresses is a preferred property for use in nitrogen-depleted soils (Lebrazi and Benbrahim 2014). Many research outcomes have mentioned unfavorable consequences of the aforementioned constraints on the survival and proliferation of rhizobia (Elboutahiri et al. 2010). Of these, soil acidity adversely impacts the survival, multiplication, and development of symbiosis of rhizobia and can affect each symbiosis partners. Nearly neutral or slightly acidic soil has been preferred for the growth of nitrogen-dependent leguminous plants (Zahran 1999). The most appropriate pH for rhizobial growth is considered to be 6.0 and 7.0. Acidic soil can have an effect on the production and excretion of nodulation factors of *R. leguminosarum* bv. *trifolii* (Kantar et al. 2010). The rhizobial strains vary extensively in their acidity tolerance. Although some previously proven acid-tolerant rhizobia strains have been chosen (Laranjo and Oliveira 2011), the mechanisms that appoint life on and growth in acidic soils have not been fully explained; consequently the molecular basis for variations in pH tolerance among strains of rhizobia is still no longer clear. In the last decades, the most important strategies employed to reduce the negative results of unfavorable environment on legume production have been centered on the selection of host genotypes adapted to drastic conditions (Bargaz et al. 2013; Farissi et al. 2011). Nevertheless, the exploration on rhizobial strains may represent any other approach to enhance plant productiveness via symbiosis or adaptation to a number of environmental hindrance (Keneni et al. 2010).

7.6.1 Molecular Basis of Soil Acidity Tolerance

The find out the molecular basis of stress response in rhizobia is fascinating considering that they are exposed to the soil conditions (da-Silva et al. 2017). The physiological and biochemical mechanisms of rhizobial adaptation to acidity conditions includes (1) exclusion and expulsion or extrusion of protons H^+ (Lebrazi and Benbrahim 2014); (2) increasing potassium and glutamate contents in the cytoplasm of stressed cells (Aarons and Graham 1991); (3) the change in the lipopolysaccharides composition (Vriezen et al. 2007); (4) the accumulation of polyamines (Fujihara and Yoneyama 1993); (5) the production of acid shock proteins (ASPs) (Foster 1993); and (6) the involvement of myriad genes such as *actA*, *act P*, *actR*, *actS*, *exoR*, *lpiA*, and *phrR* (Abd-Alla et al. 2014). All these mechanisms are valuable in rhizobial growth in acidic soil. These genes are proven to be crucial for rhizobia survival at lower pH soils (de Lucena et al. 2010). The work done by Kurchak et al. (2001) has identified 20 genes in *R. leguminosarum* that are responsible for acid stress, namely, *act* genes (acid tolerance).

The contribution of passive cytoplasmic buffering in maintaining active pH homeostasis has been mentioned. The main classes of active pH homeostasis mechanisms comprise coupling transmembrane proton movements to an energetically favorable exchange with cations (K^+, Na^+) or anions (Cl^-), a strategy that is the central active component of alkaline pH homeostasis (Padan et al. 2005; Krulwich et al. 2007), and metabolic switching to generate acidic or neutral end products (Stancik et al. 2002; Wei et al. 2006). Moreover, myriad outcomes has been recommended to retain optimal pH like acid-induced amino acid decarboxylases and base-induced amino acid deaminases (Foster 2004; Richard and Foster 2004); use of urease activity, sometimes working together with carbonic anhydrase activity, to regulate cytoplasmic and periplasmic pH (Stingl et al. 2002; Sachs et al. 2006; Sachs et al. 2005); and synthesis of acid-resistant membrane structures such as cyclopropane fatty acids (CFAs) (Cronan 2002) and tetra ether lipids (Baker-Austin and Dopson 2007) or increased synthesis of anionic phospholipids or specific neutral lipids at high pH and chaperone protection from temporary damage due to pH shift (Stancik et al. 2002). There is scant information on the physiological and genetic bases of acid tolerance in rhizobia. It has been shown that acid-tolerant strains of *R. meliloti* can more readily generate a pH gradient when grown in acidic soils to maintain a more conveniently internal pH as compared to acid-sensitive strains that failed to maintain it (O'Hara and Glenn 1994).

One approach microorganisms might also counteract changes in internal pH is via the buffering ability of cytoplasm with molecules including proteins, polyamines, polyphosphates, and inorganic phosphate. This buffering has been gained by protein amino acid side chains that can work over a wide range of pH. Both polyphosphates and inorganic phosphate have pKa values around 7.2 and thus may want to offer appropriate buffering ability near the most beneficial internal pH of neutrophils. As many studies suggested, polyphosphates have been involved in many extreme stress adaptations along with acid exposure of *Burkholderia* (Moriarty et al. 2006; Seufferheld et al. 2008). Polyamines are additionally related with acid resistance in bacteria (Wortham et al. 2007). Both polyphosphates and polyamines make a contribution to biofilm formation in which passive buffering would possibly furnish specific protection from pH shift.

Polyamines are low molecular weight natural compounds that exist in bacteria, animals, and plants consisting of putrescine (Put), spermidine (Spd), and spermine (Spm) (Hussain et al. 2011). These molecules are widely implicated in cell division and differentiation, root elongation, fruit ripening, leaf senescence, DNA synthesis, gene transcription, protein translation, and chromatin organization (Alcázar et al. 2011; Zhang et al. 2011; Alet et al. 2012; Tavladoraki et al. 2012). Polyamines additionally play vital roles in salt-, acid-, drought-, temperature-, ozone-, flood-, heavy metal-, and oxidative stressed environments (Cheng et al. 2009; Tavladoraki et al. 2012). Multiple abiotic stresses can modulate polyamine biosynthetic, metabolic pathway and its levels. Polyamines share common substrates with nitric oxide (NO), ethylene, and proline as well as N metabolism, so finding the link between polyamines and abiotic stress is complicated (Shi et al. 2013).

Root nodule microorganisms have employed a crucial mechanism of retaining intracellular pH. They exhibit acidity tolerance (adaptation) response by protecting against an extreme acid shock. Variations in acid tolerance within species of root nodule bacteria suggest a genetic basis to low pH tolerance, and studies of acid-sensitive mutants suggest that as many as 20 genes could be involved (Glenn and Dilworth 1994). Experimental results have found that there are a sensor and a regulator (actR and actS) genes in *S. meliloti* that encode for acid shock response (Tiwari et al. 1996a). The membrane-bound product of actA is basic and responsible for maintaining internal pH at around 7, when the external pH drops below 6.5 (Tiwari et al. 1996b). They demonstrated that mutants defective in this gene are unable to maintain intracellular pH and cannot grow at a pH lower than 6. Tiwari et al. (1996b) indicated that calcium is involved in acid tolerance mechanism of *S. meliloti*. Riccillo et al. (2000) reported that glutathione plays a key role in acid tolerance of *Rhizobium tropici.* Glutathione also provides protection against chlorine compounds in *Rhizobium leguminosarum* bv. *phaseoli* (Crockford et al. 1995). The activation of glutathione synthesis might be essential for tolerance to acid stress (Muglia et al. 2007). TypA acts as a regulator by controlling the phosphorylation of proteins and is required for growth at acidic condition (Kiss et al. 2004). Reeve et al. (1998) show that, in addition to the genes like actA, actS, and actR that are absolutely essential for growth of *S. meliloti* at low pH, there is phrR gene which, while not essential for growth, appears to be induced by exposure to low pH. Munns (2005) found that *Rhizobium* which produces greater amounts of exopolysaccharides is able to survive in acidic conditions more successfully than *Rhizobium* that can only produce smaller amounts.

Adaptation of microorganisms to stress is a complex multilevel regulatory process in which many genes may be involved (Srivastava et al. 2008). Microbial intrinsic metabolic and genetic capabilities make them suitable organisms to combat extreme conditions of the environment (Singh 2014). Their interactions with the plants evoke various kinds of local and systemic responses that improve metabolic capability of the plants to fight against abiotic stresses (Nguyen et al. 2016). A testament to the important attributes of the microbial interactions with plants is significant number of accumulating pieces of evidence that suggest in-depth mechanisms based on plant-microbe interactions that offer modulation of cellular, biochemical, and molecular mechanisms connected with stress tolerance (Bakker et al. 2012). Microbial interactions with crop plants are key to the adaptation and survival of both the partners in any abiotic environment. Induced systemic tolerance (IST) is the term being used for microbe-mediated induction of abiotic stress responses. The role of microorganisms to alleviate abiotic stresses in plants has been the area of great concern in the past few decades (Nadeem et al. 2014; Souza et al. 2015). The role of several rhizospheric occupants belonging to the genera *Pseudomonas* (Ali et al. 2009; Sorty et al. 2016), *Azotobacter* (Sahoo et al. 2014), *Azospirillum* (Omar et al. 2009), *Rhizobium* (Remans et al. 2008; Sorty et al. 2016), *Bacillus* (Vardharajula et al. 2011), and *Bradyrhizobium* (Tittabutr et al. 2006) in plant growth promotion and mitigation of multiple kinds of abiotic stresses has been documented. The selection, screening, and application of stress (acid)-tolerant microorganisms particularly rhizobia, therefore, could be viable options to help overcome productivity limitations of crop plants in stress-prone areas.

Nitrogen-fixing symbiotic bacteria known as rhizobia can exist in different soils and adapt to different environmental conditions (Janczarek et al. 2010). Rhizobia infect the roots of legumes and induce the formation of nodules where the rhizobia fix nitrogen. Some typical environmental stresses faced by both partners of symbiosis include salinity, drought, temperature, soil pH, heavy metals, and so on (Küçük and Kivanc 2008). Therefore, limiting factors impose restriction and may affect symbiosis and productivity (Keneni et al. 2010). *Rhizobium* species appear to be varying in their symbiotic efficiency under acidic or alkaline conditions (Ali et al. 2009). Extreme pH affects nodulation by reducing infection by rhizobia. Highly acidic soils and highly alkaline soils (pH 8.0) affect survival, the growth of both partners, and reduce nitrogen fixation (Bordeleau and Prévost 1994). The capacity of *Rhizobium* spp. to adapt to adverse soil acidic condition is fundamental for the establishment of an efficient symbiosis. More than one-quarter of the world's cultivable soils are acidic, which makes the study of the mechanisms implied in the survival to acid stress of great agricultural relevance (Tiwari et al. 1996a).

7.6.2 Survival and Persistence of Rhizobia in Acidic Soils

Soil acidity impacts on the number of population and survival of rhizobia in the soil. As a result, the number of rhizobia is generally less than 100 per g of soil below 5.5 pH ($CaCl_2$), the threshold below which there is a proper possibility of the response to inoculation (Drew et al. 2012). Similarly, Drew et al. (Drew et al. 2012) has indicated that rhizobia population are much less than 10 per g of soil below pH 4.5 in the fields of field pea. The growth, survival, abundance, and competitiveness in nodulation ability of rhizobia are incredibly influenced by soil pH (Brockwell et al. 1991). However, bacteria and archaea have the potential to maintain pH homeostasis usually closer to neutrality via cytoplasmic buffering (Slonczewski et al. 2009). Experimental finding stated that nearly 10^{-3} decreased the number of *S. meliloti* in soils with pH< 6 as compared to pH >7.0 (Brockwell et al. 1991). Although few rhizobia thrive at pH < 5, certain strains of *R. tropici* and *R. loti* are highly acid-tolerant (Graham et al. 1994). Some species of rhizobia are pretty tolerant to acidity. *B. japonicum* can continue to exist in acidic soils down to a pH of 4.0, whereas *R. leguminosarum* bv. *trifolii* and bv. *viciae* can't grow under pH 4.7; the lower limit for most *S. meliloti* strains is pH 5.0 (Hirsch 1996). The following different intracellular pH maintenance techniques have been appointed by rhizobia: (1) decreased membrane permeability; (2) internal buffering; (3) amelioration of external pH; (4) proton extrusion/uptake; and (5) prevention of metal ion toxicity. Changes in soil pH are regarded to be related with shifts in the dominant rhizobial groups within soil populations (Fig. 7.2). The result finds that, below a pH of 4.2, *Rhizobium* spp. of *R. etli*, *R. giardinii*, and *R. gallicum* groups has dominated the populations, while the

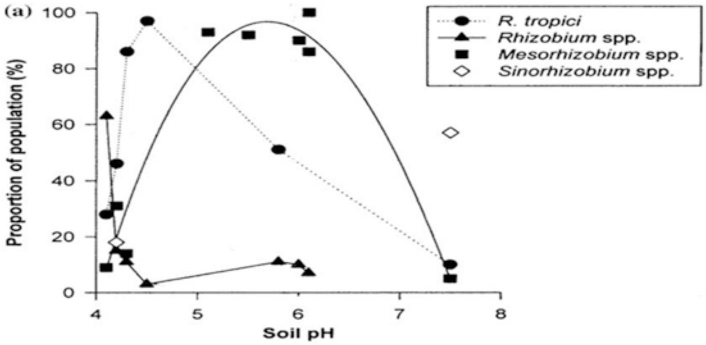

Fig. 7.2 Relationships between the relative dominance of rhizobial types and soil pH. (Adapted from Bala and Giller 2006)

R. tropici groups have been dominant between pH of 4.2 and 5.0. The *Mesorhizobium* spp. had been the most dominant between pH 5.0 and 6.5, whereas the *Sinorhizobium* spp. conquered above a pH of 6.5 (Bala and Giller 2006). Similar outcome has been forwarded in low pH (acidity) adaptation and dominancy of *R. tropici* (Graham et al. 1994). The rhizobial population in general has proved to greater survival capacity in acidic soils than in YEM broth at same low pH level. The reasons of tolerance and higher survival in rhizobia may be due to the attachment of rhizobia with cations/anions or organic molecules in the soil than in YEM broth (Appunu and Dhar 2006). Therefore, the establishment of a relationship between rhizobial types and soil conditions, mainly soil acidity, may want to have an extensive effect on the survival and persistence as well as to predict the adaptability of inoculant strains to specific soil types and conditions.

7.6.3 Rhizobium-Legume Molecular Signaling Exchange

The interaction of legume-*Rhizobium* symbiosis is initiated via a complex signaling dialogue between each partner to permit the entry of rhizobia into the root and the development of nodules for atmospheric nitrogen fixation to be available to and assimilated by plants. There has been a mutual symbiosis between rhizobia and legumes for the exchange of signal molecules among them (Downie 2014; Nelson and Sadowsky 2015). The signal molecules produced by each partner have been involved in early steps of symbiosis and have been identified through the evaluation of molecular mechanisms of plant-rhizobia communication primarily based on signal exchange (Tseng et al. 2009). Nodulation and symbiotic N_2 fixation contain many rhizobial genes commonly designated as symbiosis genes, such as *nod* and *nif* genes (Cooper 2007). As analyzed by the same author, the genes nod ABC (transcriptionally regulated by using NodD) encode enzymes that synthesize Nod elements (lipo-chito oligosaccharides). This gene has been perceived by using the plant, activating the root hair curling, and forming a hook for subsequent improvement of an infection thread (Cooper 2007). Nevertheless, preceding research has proven that chaperone proteins, such as GroEL and ClpB, typically involved in stress response, may also play essential roles in the symbiotic legume-rhizobia relationships (Brígido et al. 2012).

7.7 The Position of *Rhizobium* in Other Plant Stress Tolerance

Abiotic stresses are considered to be the most important sources that can be restricted in agricultural yield reduction. However, the depth of these stresses varies depending on the type of soils and plant factors (Nadeem et al. 2010). Due to their sessile nature, plants have continuously been confronted with myriad number of abiotic and biotic stresses in their immediate environment. All plants have been perceived and respond to one of the following stress signals of drought, soil acidity, heat, salinity, herbivory, and pathogens (Hirt 2009). PGPR can enhance plant growth under abiotic stresses and may consequently open new applications for sustainable agriculture (Egamberdieva and Kucharova 2009). A research suggests that the following bacterial genera *Rhizobium*, *Bacillus*, *Pseudomonas*, *Paenibacillus*, *Burkholderia*, *Achromobacter*, *Azospirillum*, and many others have been stated to provide tolerance to host plants under different abiotic stress environments (Grover et al. 2011).

7.7.1 Temperature

Temperature is one of the principal elements affecting rhizobial growth and survival and the symbiotic process (Niste et al. 2013). When soil temperature is either too high or too low, it can limit legume BNF, nodulation, and nodule establishment and nitrogenase activity although it varies among species. The optimal soil temperature for fixation has to vary between 25 and 30 °C. However, a consistently cool-temperature region around the root can significantly prolong the onset of nitrogen fixation in contrast to optimal temperature (Abendroth et al. 2006). Resistance/tolerance to excessive temperature is thus an acceptable property for rhizobial inoculants to be used. Various researches have been carried out to examine the growth responses of different *Rhizobium* strains to increasing temperatures.

7.7.2 Drought Stress

Drought stress is an increasing hassle that can limit crop production in the world under current climate change scenarios. As a result a great and renewed attention is paid for rhizosphere microorganisms that have been ameliorating plant stress with the aid of various mechanisms that span plant hormone level modification and bacterial exopolysaccharide production (Kaushal and Wani 2016; Naveed et al. 2014).

From experimental findings, drought predominantly decreased world food production by 9–10% (Lesk et al. 2016). As studies suggest, plants can adapt (cope) to this devastating impact via morphological adaptations, osmotic adjustment, optimization of water resources, antioxidant systems of reactive oxygen species (ROS) linked to drought, and induction of a variety of stress-responsive genes and proteins (Farooq et al. 2009). To date, introduction of drought-tolerant cultivars has been the strategy used to mitigate the negative effects of this stress on crops and their yields (Eisenstein 2013). The aforementioned techniques overlook the ecological context of the soil environment in which the crops are grown. Therefore, there is a necessity for microbial-based tactics to mitigate drought stress. This is why rhizosphere microbial communities have received firsthand attention for enhancing crop productivity and stress resistance (Glick et al. 2007; Yang et al. 2009). Numerous studies forwarded the best studied plant-associated microbes comprising mycorrhizal fungi (Azcón et al. 2013), nitrogen-fixing bacteria (Lugtenberg et al. 2013), and plant growth-promoting rhizobacteria (Glick 2012). The beneficial roles of these microbes have been observed in nodulation, growth promotion, and biocontrol enhancement in plant growth under drought stress conditions. The capability of microorganisms such as rhizobia to live on drought stress environments depends on their competency to cope with radiation stresses, reactive oxygen species (ROS), solutes, and temperature extremes (Deaker et al. 2004). The progressive result of PGPR and rhizobia on plants under abiotic stresses is the improvement of leaf water status, especially under salinity and drought stress (Ahmad et al. 2013).The finding of Sarma and Saikia (2014) stated that *Pseudomonas aeruginosa* strain inoculation has improved the growth of *Vigna radiata* (mung beans) plants under drought conditions. Similarly, Ahmad et al. (2013) and Naveed et al. (2014) found that the stomatal conductance (water vapor exiting through the stomata leaf) of plant leaf has been greater in PGPR-inoculated plants than the noninoculated in drought situations. The discovering result from each research proves that PGPR-inoculated plants have a tendency to enhance the water-use efficiency of plants. This finding ought to be beneficial in terms of decreasing immoderate utilization of water (Mnasri et al. 2007). Similar result conducted in vitro by Swaine et al. (2007) reported that strain of *Bradyrhizobium elkanii* isolated from a drought environment has been more tolerant to osmotic stress than strains isolated from wet environments. *Achromobacter piechaudii* ARV8 which produced ACC deaminase conferred IST against drought and salt in pepper and tomato (Mayak et al. 2004). Moreover, Grover et al. (2014) has mentioned that sorghum plants treated with *Bacillus* spp. strain KB 129 under drought stress showed 24% increase in RWC over plants that have been no longer treated with PGPR. Similar consequences have been validated in maize crop (Naveed et al. 2014).

7.7.3 Salt Tolerance

Soils affected via salt harasses are known to destroy the growth of plants (Paul 2013). The true indications of the problem have been stated as nearly 40% of the world's land surface is affected by means of salinity-related issues (Zahran 1999). Enhanced salt tolerance in maize upon co-inoculation with *Rhizobium* and *Pseudomonas* is correlated with reduced electrolyte leakage and retention of leaf water contents (Bano and Fatima 2009). Similarly results from Marulanda et al. (2010) suggested that *Bacillus megaterium* strain inoculated into maize roots elevated the potential of the root to take in water under the salinity conditions. Gond et al. (2015) also found comparable behavior when *Pantoea agglomerans* is used to be inoculated into the maize roots. All these results forwarded that the capacity of the maize root to absorb water in saline conditions has improved. Here, microorganisms that can grow under hypersaline environments have better capability to colonize rhizospheres and external spaces of roots that are themselves exposed to high salinity conditions. Thus, the strategy was to first screen the bacterial isolates for their ability to grow under hypersaline conditions. More likely, Gonzalez et al. (2015) used *Azospirillum brasilense* in in vitro studies to enhance salt tolerance in jojoba plant. This finding forwards that *A. brasilense* can limit the undesirable effects of salinity on the jojoba rooting. This suggests that *A. brasilense* has greater plant tolerance to salt stress. Generally, the potential roles of co-inoculated *Rhizobium* and *Pseudomonas* in salt tolerance of *Zea mays* have been due to increased production of proline along with diminished electrolyte leakage, maintenance of relative water content of leaves, and selective uptake of K ions (Bano and Fatima 2009). Other experimental investigation found that inoculation of lettuce with *Azospirillum* sp. under salt-affected soil improves lettuce quality, extends the storage life, and increases yield (Fasciglione et al. 2015). Moreover, Yao et al. (2010) reported that inoculation of *P. putida* Rs198 promoted cotton growth and germination under conditions of salt stress.

7.7.4 Heavy Metals (HMs) Stress

In the era of civilization, HMs pollution has numerous environmental, human health, and agricultural problems. As different results indicated, the uptake of HMs from soil has both direct and indirect effect on microbial composition (Rathnayake et al. 2013), metabolism (Dostal et al. 2012), and differentiation (Harrison et al. 2007). The metal species, habitat of interacting organisms, structure and compositions, and microbial functions have been disturbing the interaction of metals with soil microbes. Heavy metals at minimal dose are required for more than a few metabolic activities of microbes along with rhizobia and legume crops. To the contrary, the elevated doses of HMs cause undeniable damage to rhizobia, legumes, and their symbiosis (Ahmad et al. 2012). Different findings presented the toxic effect of greater quantities of metals on physiological processes like synthesis of chlorophyll pigments of plants (Feng et al. 2010) and (Ahmad et al. 2008) inactivated protein synthesis. Similar result suggests that the destructive impact of sludge application on N_2 fixation in faba bean is pronounced as this amendment comprises toxic HMs (Chaudri et al. 2000). Certain metals like Cu, Zn, Co, and Fe are essential for survival and growth of microbes. However, these metals can have toxicity impact at greater concentrations and may inactivate protein molecules (Samanovic et al. 2012). Thus, microorganisms have advanced some mechanisms to overcome the inhibitory results of toxic HMs. Some of the HM cleaning techniques adopted via microbial communities are (i) metal exclusion using permeable barriers; (ii) active transport of HMs far from the cell; (iii) intracellular sequestration through protein binding; (iv) extracellular sequestration; (v) enzymatic cleansing of HMs to a less toxic form; and (vi) decreasing the sensitivity of cellular targets to metal ions. As results indicated, both single and multiple detoxification mechanisms have been affected by microbial types involved (Shoeb et al. 2012).

Rhizosphere microbes perform an extensive function in phytoremediation of HM-contaminated soil and have the mobility and availability to the plant by means of chelating agents, acidification, phosphate solubilization, and redox changes (He and Yang 2007). In order to live on HM-contaminated soils, tolerance has to be present in microbes and the host plants. Experimental results supported that application of nitrogen fixing rhizobia and PGPR in heavy metal contaminated soil resulted in significant reduction in the level of HMs in the soil. These soundful outcomes have been observed in the overall improvement in the growth and yield of chickpea and pea (Gupta et al. 2004; Wani et al. 2007). A similar finding recently suggested that *Methylobacterium oryzae* CMBM20 and *Burkholderia* sp. CMBM40 strain inoculation in nickel- and cadmium-treated soil appreciably decreased their toxicity effect in tomato via promoting growth in greenhouse test (Madhaiyan et al. 2007). Additionally, application of *Pseudomonas maltophilia* strain transformed the mobile and toxic form of chromium (Cr VI) to nontoxic and immobile form (Cr III) and also minimized the mobility of other toxic ions, such as Hg^{2+}, Pb^{2+}, and Cd^{2+} (Khan et al. 2009).

7.7.5 Induction of Plant Resistance

In the last few decades, the world has seen an increased application of un-ecofriendly synthetic fertilizers in agriculture. This situation shifts in the use of PGPR strains that can trigger the resistance in plants against pathogens. This phenomenon is referred as induced systemic resistance (ISR). Plants have the capacity to acquire a state of ISR to pathogens after inoculation with PGPRs (Pieterse et al. 2003). In plant roots, PGPRs can lead the plant innate immune system and confer resistance to a broad spectrum of pathogens with a minimal impact on yield and growth (van Hulten et al. 2006). Phytopathogenic microbes have massive effect in agriculture and considerably decreasing crop yields and causing total crop loss (Antoun and Prévost 2005). As different studies forwarded, root-colonizing species of *P. fluorescens*, *P. putida*, *B. pumilus*, *Serratia marcescens*, *Paenibacillus alvei*, *Acinetobacter lwoffii*, *Chryseobacterium balustinum*, and *Azospirillum brasilense* protect large variety of plant species against foliar diseases in greenhouse and field trials (Pieterse et al. 2003; van Loon 2007). In the same fashion, various rhizobial species of *R. etli*, *R. leguminosarum* bv. *phaseoli*, and *R. leguminosarum* bv. *trifolii* have been pronounced to induce systemic resistance in plants with the aid of producing bio-stimulatory agents (Gohel et al. 2006; Mishra et al. 2006). A number of phytobeneficial microbes of *P. fluorescens* (Peighami-Ashnaei et al. 2009) and *B. subtilis* (Dawar et al. 2010) have proven antagonism effect against *Fusarium* sp., *Pythium* sp., *Rhizoctonia* sp., *Sclerotium* sp., and diseases leading to enhancement in plant growth or yield. Moreover, application of *B. subtilis*, *Pochonia chlamydosporia*, and *P. fluorescens* can successfully manage the diseases brought on through nematode infection (Trabelsi and Mhamdi 2013). The excessive cost of pesticides, the emergence of fungicide-resistant pathogens, and different health-related influences of modern agriculture on the environment have increased interest in agricultural sustainability and biodiversity conservation by using phytobeneficial soil microorganisms (Van der Vossen 2005).

7.8 Co-inoculation of Rhizobia and Other Rhizobacteria

The inconsistency of results in single microbial inoculation under field application has brought an emphasis on co-inoculation (Bashan and De-Bashan 2005). Co-inoculation of rhizobia with PGPR plays an important role in promotion of nodulation and plant growth of leguminous plants. The statement is supported via co-inoculation of soybean with *Azospirillum* spp., and *Bacillus* sp. significantly increased 23.65 and 34.92% seed yield over single inoculation (Aung et al. 2013).

These outstanding findings push researchers focusing on co-inoculation of rhizobacteria and R*hizobium* to enhance the growth of legumes. PGPR provides a supportive role for *Rhizobium* inoculation in legumes by means of antibiotic, siderophore, and enzyme production to facilitate the infection sites for *Rhizobium* by colonizing the root surface (Contesto et al. 2008). The increase in the number of pods per plant of faba bean with co-inoculated *Rhizobium* strains and *P. fluorescens* is compared to the uninoculated (Radwan et al. 2005). Other finding also forwarded that co-inoculation of common bean with *Rhizobium* and PGPR sustainably increased shoot and root dry weights in respect to *Rhizobium* inoculation alone and the uninoculated control. Similarly, Figueiredo et al. (2008) reported a greater increase in shoot and root dry weight when CIAT 899 rhizobia strains and *Paenibacillus polymyxa* strain DSM 36 were inoculated together in common bean than single inoculation. Additionally, Elkoca et al. (2010) informed an elevated shoot dry weight as a result of co-inoculation of common bean with *Bacillus megaterium* (M-3) and *Rhizobium* strain. Once more, co-inoculation of P-solubilizing bacteria and *Rhizobium* stimulated plant growth over single inoculations (Charana Walpola and Yoon 2013). Experimental results of Tariq et al. (2012) indicated that non-rhizobial PGPR improved nodulation and grain yield of the legumes upon co-inoculation with crop-specific rhizobia. These improvement in growth and yield has been upon *Rhizobium* and *Pseudomonas* co-inoculation is related proline production, decreased electrolyte leakage, maintenance of relative water content and selective uptake of potassium ions in salt affected *Zea mays* (Bano and Fatima 2009). Furthermore, co-inoculation of PGPR and rhizobia has a synergistic effect on bean growth as PGPR allows *Rhizobium* with biofertilizers for common bean production

(Korir et al. 2017). Bai et al. (2003) also stated that co-inoculation of *Bacillus* strains in soybean plants with *Bradyrhizobium japonicum* provided the largest increases in nodule number, nodule weight, shoot weight, root weight, total biomass, total nitrogen, and grain yield.

Field study conducted in salt-affected soils has shown that single and combined inoculation of *Rhizobium* and PGPR enhanced growth, nodulation, and yield of mung bean in 1000 grain weight and grain yield up to 14 and 30%, respectively (Aamir et al. 2013). A comparable result has stated that dual inoculation of *P. pseudoalcaligenes* and *B. pumilus* protects paddy plant from abiotic stresses via induction of osmo-protectant and antioxidant proteins (Jha et al. 2011). Co-inoculation of *Bradyrhizobium* sp., *Paenibacillus polymyxa*, and *Bacillus* sp. brings increased nodulation and root dry matter in *Vigna unguiculata* (da Silva et al. 2007). Similarly, endophytic PGPR and nitrogen-fixing *Rhizobium* species have been found a synergism in N-fixation efficiency of lentils (Saini and Khanna 2012). Also, Wang et al. (2012) described that application of cucumber plants with a mixture of *Bacillus cereus* AR156, *Bacillus subtilis* SM21, and *Serratia* sp. XY21 increased leaf proline contents three- to fourfold relative to untreated controls. This finding suggested that the increased leaf proline contributed to drought tolerance from over-dehydration. A complementary field and greenhouse experiments in chick pea showed extensive outcomes as compared to control with a combined application of *Mesorhizobium* sp. BHURC02 and *B. megaterium* (Verma et al. 2012). Generally, all findings suggested an improved growth and yield of plants upon microbial inoculation; more importantly co-inoculation is the prominent solution.

7.9 Challenges and Opportunities in Using Rhizobial Inoculants

Inoculation of legumes with rhizobia inoculants has been more often used than BNF technology in agriculture, but in most African countries which include Ethiopia, this technology is not well established (Deshwal and Chaubey 2014). The commercial production of inoculant in Africa faces various challenges. Production and marketability of bioinoculants are highly small, due to the fact that legume production is an emerging industry. Since the product consists of bio-tools with exceedingly short shelf life, the production process and technologies and environment need to satisfy strict criteria to produce a quality product. Moreover, transport and storage facilities are required to maintain the quality of the product. The expense for the components has been limited which helps keeping the price for inoculants low. However, considerable investments either from the government or NGO are required for the production facility and equipment. Distribution is a challenge, particularly if the smallholder farmer community has to be served, taking small trading volumes required storage facilities into account. The economics values of rhizobium biofertilizer utilization in small-scale farming systems in Zimbabwe and the role for policy have indicated that a break-even point (where total revenue equals total cost) is reached at the production of around 40,000–50,000 units (100 g). The inconsistency laboratory and field outcomes are more compounded due to more than a few abiotic stresses that succeed under field conditions for a microbial inoculant to show the desired effect. Such problems can be overcome by the aid of sound screening program for efficient stress-tolerant and phytobeneficial PGPRs (Gupta et al. 2015). One of the principal limiting factors in widespread use of PGPRs is their selectivity. The available technologies for inoculant production and application have been abundantly reviewed in the past. An important point to underline is the relatively small quantities of inoculation technologies emerging from basic research on the genetics of rhizobia and the mechanisms of the legume-*Rhizobium* symbiosis. There is the possibility to get more productive, efficient, and competitive N_2-fixing bacteria.

7.10 Conclusion and Future Prospects

The world's ecosystems are affected with various processes carried out in/on the soil. Climate change and associated environmental stresses with soil acidity have been taking the prior position. The negative effect of synthetic agrochemicals on environment and human health shifts an urgent interest in improving and utilization of rhizospheric microbial populations. These lead bioinoculants the first choice in the current scenarios of chemical fertilizer and pesticide effects. Legumes and other plant inoculation with improved phytobeneficial microbes have been helpful for farmers specifically in stressed environments. Rhizobia and PGPR are reported to influence crop growth, yield, and nutrient uptake by different mechanisms. They fix nitrogen; help in promoting free-living nitrogen-fixing bacteria; increase supply of other nutrients, such as phosphorus and iron; produce plant hormones; enhance other beneficial bacteria; control bacterial and fungal diseases; and help in stress tolerance in plants. Since most single inoculant might in part account for the recorded inconsistencies in field application, the possible means to overcome this problem has been via co-inoculation. Hence, the better understanding of rhizobial physiological and molecular responses to different intrinsic and extrinsic stresses factors is very important to improve crop production by harnessing biological nitrogen fixation process.

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