Harnessing Soil Rhizobacteria for Improving Drought Resilience in Legumes

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Abstract

There are multiple challenges like population growth, food security imperatives, hunger and malnutrition, climate change, economic access to food, decreasing factor in productivity. Such challenges necessitate an appropriate research and policy framework. The aim of this chapter is to focus on the sustainability of the soil and crop and commodity production support systems. Sustainability in agriculture is more important for input delivering resources rather than the output. It is also more important than all biological attributes, including the beneficial microbes, which is the key to it. The nexus of soil microbes-legumes-is an inseparable entity. This is the recent focus on soil biological health and legumes in achieving sustainability. Soil rhizobacteria are important especially in legume-based farming systems. This is because the resource constraints such as water and nutrients often limit the productivity of such systems. There are substantial evidences based on research findings to build a valid premise. This premise should deal with legume-rhizobial associations which can be optimally harnessed. The objective behind this is to not only enhance productivity under favourable systems but also to improve resilience to stresses such as drought. Soil rhizobacteria colonise the endo-rhizosphere/rhizosphere to drought tolerance by producing phytohormones, 1-aminocyclopropane-1-carboxylate (ACC), deaminase, volatile compounds and antioxidants, inducing accumulation of osmolytes. They also decrease the regulation of stress-responsive genes and alteration in root morphology during the acquisition of drought tolerance. The ability of soil microbes to transfer their intrinsic resilience to legume hosts opens up an amazing world of opportunities. These opportunities can be harnessed by identifying optimal legume-microbe associations. On the research front, there is a need to identify resilience mechanisms. Besides this, the underlying genetic factors and the mechanisms in host plants that optimise associations have to be identified. On the management front, there is need to create enabling conditions in soil systems that enhance the population and functionality of native and introduced microbial systems. These systems can favourably enhance output especially under resource-constrained conditions.

Keywords

Legumes · Drought stress · Rhizobacteria · Sustainability

Abbreviations

ACC	1-aminocyclopropane-1-carboxylate
BNF	Biological nitrogen fixation
CGIAR	Consultative Group on International Agricultural Research
EPS	Exopolysaccharides
PGPR	Plant growth-promoting bacteria
PSB	Phosphate-solubilising bacteria

8.1 Introduction

Global population is poised to reach ~8 billion by 2020, an increase of about 35% over the 1995 population and is projected to exceed 9.8 billion by 2050 and 11.2 billion by 2100 (UN 2017). Therefore, the major challenge would be ensuring food security while lowering the risk of climate change (Stagnari et al. 2017). As such, the demand for plant products that satiate the human requirements especially the food will rise by an even higher proportion. This is in the light of the fact that the average income is also growing, diets have diversified and greater urbanisation has occurred. A major challenge is that majority of the population living in developing countries will be at a serious risk of food and nutritional security. This situation is further complicated by looming threats of climate change. The sections of populations have less adaptive capacities for the climate change. Governments ensure sustained investments in this regard. However, apart from outputs from national and international agricultural research systems and a matching technology support, the food grain and livestock production, during the period 1995–2020, is expected to increase by only 1.5% and 2.7% per year, respectively. Even though the poverty situations may have improved, the malnutrition would continue as the greatest ever challenge before scientists and policymakers across the globe. Climate change is another major challenge to agriculture as it will dent one's efforts to ensure sufficient and economically accessible food to increasing global population (Vadez et al. 2011; Yadav et al. 2017a). With regard to food legumes, climate change implications will be manifested as increased frequencies and intensities of water stress. The change is visible especially in the legumes that are sensitive to water stress (Liu et al. 2006).

The food crops across diverse classes and all production systems are vulnerable to projected changes in climate. However, owing to certain inherent bottlenecks of smallholder subsistence farmers, such systems are more likely to be hit hard. This is because they lack adaptive capacities (Menike et al. 2015). Food legumes are important components of such farming systems, which are invariably resource constrained (Odendo et al. 2011). The food and nutritional security imperatives, coupled with population pressures and ecological costs of agriculture, are compelling situations. These situations demand a paradigm shift in research approach towards managing natural resources for better agricultural output. Food legumes are important components of farming systems that can help in transforming agriculture into a sustainable intensification mode from chemical input-based intensification mode. This will not only improve productivity and sustainability but also optimise resource utilisation and improve the resilience of the system (Mungai et al. 2016).

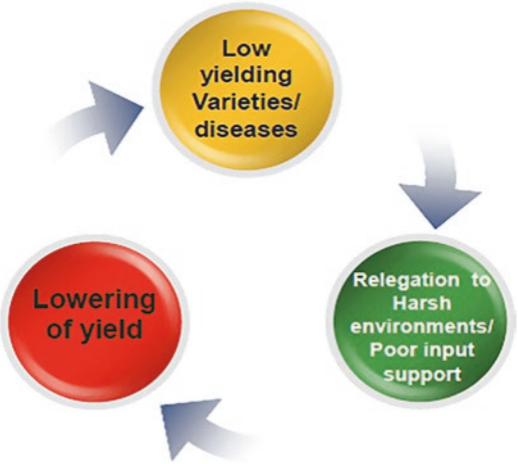
Chemical-based intensification of farming has, undeniably, transformed farming by contributing significantly to increases in food production worldwide. An appraisal of impacts reveals that there has been a disproportionate impact especially in marginal low-input systems (Bhattacharya and Majid 2013). Even in the high-input farming system, the productivity gains have come at the cost of deterioration of biophysical resource base of agriculture especially the soil. Chemical fertilisers may have favourably changed the physics and chemistry of the soil, but they have deteriorated the biology of the soil. The decline in soil health and microbial populations, as well as unfavourable changes in the structure of the soil, has been recognised as major offshoots of increased use of chemicals. This is in addition to the environmental as well as the energy cost of manufacturing chemical fertilisers (Gliessman 1998). Therefore, it is now increasingly being appreciated that the biology of the soil should be restored by harnessing the soil microbes and legume associations. The obvious benefits not only include a growth promotion but also an increase in the resilience of the systems (Prashar and Shah 2016; Meena et al. 2015a). This is all the more important, keeping in view that grain legumes are invariably grown in low-input marginal farming systems with minimal support and face resource constraints including water. It is imperative to improve the health to optimise the benefits of microorganisms because the grain legumes have evolutionary history of coexistence with microbes. This chapter will discuss the potential role of soil rhizobacteria in the context of improving sustainability and resilience of legume-based farming systems.

8.2 Agricultural Importance of Legumes

Food legume crops represent an indispensable component across all types of farming systems in both developing as well as developed countries. They are important determinants of food and nutritional and livelihood security. Nutritionally, food legumes are a cheap source of protein, especially in areas where animal protein is not affordable and more importantly in the light of increased carbon footprints of animal protein consumption and minerals, while agronomically they serve as important components of cereal-legume rotation. Besides this, they reduce soil-borne pests and supply nitrogen (N) to the companion crops through belowground complementation. Despite being valuable crops, the yields of legume crops have remained disappointingly low. This is due to interplay of various factors ranging from inherent physiological mechanisms, relegation to harsh environments and diseases and pests (Fig. 8.1). Even though food legumes are regarded as subsistence crops, they invariably fetch higher prices than most of cereals. Moreover, they supplement farmers' income for improving livelihood opportunities (Gowda et al. 2009). Currently around 78 million hectares are under various food legume crops globally with a production of about 85 million tonnes (FAO 2015). Consultative Group on International Agricultural Research (CGIAR) has identified food legumes as ideal target crops for achieving its developmental goals of tackling poverty and hunger and improving human health and nutrition. Above all, it is aimed at enhancing resilience of ecosystems. Under this umbrella programme, food legumes have found renewed research focus and policy support that has seen legume productivity increase in countries like India, where they are an indispensable component of farming and diets (CGIAR 2012).

The food legumes, soil and smallholder family farmers together form a favourable nexus in the developing countries. Food legumes or pulses are largely grown by smallholder family farmers accounting for a major proportion of food and nutritional

Fig. 8.1 Nexus of low yield in food legumes



and livelihood security. Soils are central to any agricultural development, and legumes now derive most of their nutrition from soil as they are grown under low-input farming systems. The United Nations (UN) General Assembly has in succession for 3 years highlighted the importance of these three components of the nexus by proclaiming 2014 as the International Year of Family Farmers, 2015 as International Year of Soils and 2016 as the International Year of Pulses (Belhassan 2017). The UN has during these 3 years made honest attempts to promote awareness about the importance of family farmers and also soils and pulses. This has been done through a series of programmes in collaboration with FAO, CGIAR, Crop Science Society of America, American Society of Agronomy and Soil Science Society of America as well as through National Agricultural Research systems (Anderson 2016). As part of this initiative, grain legumes were vigorously promoted for use as nearly perfect foods in terms of their nutritional benefits. This was for the protein source besides their environmental and economic benefits. Legumes form effective relationships with plant roots and in turn fix atmospheric N that not only increases the soil N supply to the legume crop (up to 70%) and in its companion crops in intercropping but also ensures an adequate N supply. This gives rise to better crop sequences when compared to sequences without legumes (Peoples et al. 2015; Verma et al. 2015a).

Therefore, food legumes can play a major role in ensuring global food security as well as sustainability and resilience of legume-based farming systems. However, despite their desirable features and a large number of species, only a handful of them have been harnessed to a level. Consequently, they define the productive capacities of farming systems, and most of them continue to enjoy the “orphan” or “underutilised” status (ICRISAT 1998). On one hand, the ecological benefits of incorporating food legumes to farming systems are fairly well recognised. On the other hand, the lack of recognition and evidence of the social and economic benefits precluded development and the utilisation of genetic and genomic resources of food legumes. Apart from this, they are invariably relegated to harsh environments with low-input support. As a result, they have become increasingly less competitive and cannot favourably compete with cereals. Even during the green revolution era, grain legumes have not witnessed similar research investment and output as that of cereals, which was partly driven by food security imperatives (Pingali 2012; Meena et al. 2015b).

8.2.1 Global Context: Rationale for Sustainable Intensification of Legumes in Cropping Systems

Increasing population will mean additional requirements of food legumes. The need is felt more so in resource-constrained countries where a large proportion of world's resource poor people live. Therefore, food legumes account for large requirement of protein. By the year 2050, the farm producers will need to create a supply, adequate enough, to feed an additional three billion people, most of whom will be added in developing regions of the world. Therefore, significant efforts would be needed to ensure the availability of adequate quantity of food legumes in the era of climate change and in a deteriorated biophysical resource base for agriculture. Together food and forage legumes are grown on some 180 million hectares that accounts for about 15% of the earth's arable area and contribute to 27% of the world's total primary crop production, with grain legumes alone accounting for 33% of the human dietary protein requirements (Vance et al. 2000). In order of rank, the food legumes that contribute to the dietary protein intake (Akibode and Maredia 2011).

The global demand for food legumes is expected to grow in the future, given the fact that incomes have increased, food consumption patterns are diversifying and consciousness towards healthy dieting is rather increasing (Tables 8.1 and 8.2). There is an increasing recognition of legumes, as nutraceuticals and functional foods. There are also greater health risks of consuming animal proteins, and the demand for legume-based products is expected to increase further. Most of the food legumes are rich sources of proteins (i.e. >20%) and soluble fibre and have a low glycaemic index and reduce the risk of cardiovascular diseases as well as certain forms of cancer (Duranti 2006). The global legume production has doubled from 150 million tons in the 1980s to around 300 million tons in the 2000s. Most of the

Table 8.1 Area, production and yield of major legume crops

Crop	Scientific name	Area (Mha)	Production (Mt)	Yield (Mg/ha)
Common bean	*Phaseolus vulgaris*	30.61	26.53	0.86
Chickpea	*Cicer arietinum*	13.98	13.73	0.98
Cowpea	*Vigna unguiculata*	12.61	5.59	0.44
Lentils	*Lens culinaris*	4.52	4.82	1.07
Pea	*Pisum sativum*	6.93	11.18	1.61
Pigeon pea	*Cajanus cajan*	7.03	4.89	0.69
Soybean	*Glycine max*	117.54	306.51	2.60
Groundnut	*Arachis hypogea*	26.54	43.91	1.65
Faba bean	*Vicia faba*	1.05	1.59	1.67

Data source: FAOSTAT (2014)

Table 8.2 Countries where pulses are major sources of protein intake (%)

Country	Percentage	Country	Percentage	Country	Percentage
Burundi	55	Rwanda	38	Uganda	20
Uganda	20	Kenya	20	Comoros	18
Eriteria	18	Comoros	18	Haiti	18
Cuba	16	Nicaragua	16	Malawi	15
Angola	15	Tanzania	14	India	13
Brazil	13	Mozambique	12	Korea	11
Mexico	10	Belize	10	Botswana	10

Data source: Maredia (2012)

production entails a nonfood legume like soybean, and the food legumes account for nearly 20% of total production during the same period (Gowda et al. 2009). However, with the projected increase of 40% in the population by 2050, food production needs to be increased by 70–100% to meet the increasing demands due to population growth (Price and Howitt 2014; Ashoka et al. 2017). This challenge is further compounded by the fact that legume crops will face severe competition for resources such as land and water from cereals, cash crops and biofuels. This will happen apart from developmental imperatives such as industrialisation and urbanisation. Such competition will further relegate legumes to marginal areas, where a lack of irrigation is a major constraint, limiting crop productivity. Moreover, the constraints of water availability and the season to season fluctuations in climatic parameters in such marginal areas tend to be relatively larger. This would significantly affect food security in such rain-fed systems (Postel 2000). Table 8.3 lists some of the major food legume crops that are components of different farming systems.

Food legumes are increasingly emerging as potential future crops in the light of certain desirable features such as shorter duration, low water requirements, deeper roots, ability to fix N and cheap source of proteins that make inherently the climate smart. However, given the current state of biophysical resources for agriculture, all the policymakers are equivocal in promoting a sustainable intensification (SI) of farming systems to address the concerns of food and nutritional security. This is done by increasing the production output without having an adverse effect on ecosystem services (Mungai et al. 2016). It involves increasing output per unit area, natural resources as well as social and human capital, with a concomitant increase in the flow of ecosystem services (Pretty et al. 2011). Food legumes are central to any sustainable intensification approach that seeks to transform the farming systems to become more productive, more resilient and more eco-friendly. Considering the increasing public concerns about the deleterious effects of chemical-based agriculture, more focus is now laid on optimising the biological balance, the microbial diversity and microbial dynamics in soil. SI is being proposed as a strategy for improved natural resource management with focus on reducing trade-offs between productivity, profitability and resilience (Kaczan et al. 2013; Pretty and Bharucha 2014; Meena et al. 2014). There are compelling situations encompassing social, economic and ecological justifications for promoting food legumes in the farming

Table 8.3 Major food legume crops

Crop	Scientific name
Common bean	*Phaseolus vulgaris*
Lima bean	*Phaseolus lunatus*
Scarlet runner bean	*Phaseolus coccineus*
Tepary bean	*Phaseolus acutifolius*
Adzuki bean	*Vigna angularis*
Mung bean	*Vigna radiate*
Rice bean	*Vigna umbellate*
Moth bean	*Vigna aconitifolia*
Bambara bean	*Vigna subterranean*
Faba bean (broad bean)	*Vicia faba*
Common vetch	*Vicia sativa*
Pea	*Pisum sativum*
Chickpea	*Cicer arietinum*
Cowpea	*Vigna unguiculata*
Pigeon pea	*Cajanus cajan*
Lentil	*Lens culinaris*
Hyacinth bean	*Lablab purpureus*
Sweet Jack bean	*Canavalia ensiformis*
Winged bean	*Psophocarpus tetragonolobus*
Guar bean (cluster bean)	*Cyamopsis tetragonoloba*
Velvet bean	*Mucuna pruriens*
African yam bean	*Sphenostylis stenocarpa*
Groundnut	*Arachis hypogea*
Soybean	*Glycine max*
Jack bean	*Canavalia ensiformis*
Sword bean	*C. gladiate*
Yam bean	*Pachyrhizus tuberosus*
Lablab bean	*Lablab purpureus*
Moth bean	*Vigna angularis*

Akibode and Maredia (2011); USDA National Nutrient Database (http://www.nal.usda.gov/fnic/foodcomp/search/)

systems. These farming systems help fulfil the food and nutritional security imperatives besides enhancing the ecosystem services associated with the reduced use of chemicals and lower water footprints and also promoting biodiversity on farms.

8.2.1.1 Social

8.2.1.1.1 Food Security

Food legume crops (consumed as grain, green pods, shelled beans and leaves) contribute to food security and dietary diversity goal besides improving overall nutrition and also preventing diseases due to their nutraceutical properties. Among the strategies that could help decrease the risk of hunger under looming threats of climate change, N-efficient crops are of paramount importance. This is followed by reduced tillage practices and integrated soil fertility management. They can also reduce hunger by 12%, 9% and 4%, respectively (FAO 2016a). Food legumes fulfil all these criteria and as such need to be promoted for ensuring food security. Compared to cereals, the food legumes contain twice the amount of protein and in most developing countries constitute the major source of protein. The nutritional qualities of legumes also make them extremely helpful in the fight against some non-communicable as well as some chronic diseases. Pulses also provide important vitamins and minerals such as iron, potassium, magnesium, zinc and B vitamins including folic acid, thiamin and niacin (FAO 2016b).

8.2.1.1.2 Farming System Compatibility

Most of the food legumes play diverse roles in the farming systems in most of the developing countries, where farming systems are characterised by marginality of scale, lower input support, fragility, inaccessibility, diversity and lower productivity. In such a situation, any sustainable intensification approach that seeks to increase the productivity of the system should seek to harness the advantages of food legumes integrated into the system. This will contribute to an overall social development in terms of adequate food, better nutrition and better livelihood opportunities (Dar et al. 2012).

8.2.1.1.3 Resilience to Harsh Environments

Most of food legumes can grow in harsh environments (drought prone) where the focus of production system is not on production per se but on the resilience of system as well. Intensive cereal-based farming cannot sustain profitably under such low-input farming systems. Simulation studies have suggested that such climate vulnerable sites may benefit from legume-based farming systems, although it still requires extensive on-farm validation (Smith et al. 2016).

8.2.1.1.4 Gender Specificities

Rural women are key agents for economic, environmental and social changes required for a sustainable development. On the other hand, limited access to education, resources and role in decision-making are among the many challenges they face (Sofi 2015). In fact, a recent FAO study indicates that, if women are equally empowered to make decisions in farming, the hunger will be reduced by about 15%. In smallholder situations and in low-income food-deficient nations, about 75% of women work in agriculture (Mungai et al. 2016). In developing countries, agriculture provides employment for about 38% of women with the proportion as high as 66% in Southeast Asia and 63% in Sub-Saharan Africa. In rural India, about 84% of women are dependent on agriculture for livelihood, about 33% formally participate in farming but only 10% own land and 9.7% are female-headed households (Kumar et al. 2016). In legume-based cropping systems, females are more involved and as such farming systems take care of gender specificities.

8.2.1.2 Economic

8.2.1.2.1 Livelihood

Food legumes are second to cereals in economic importance in agriculture with an annual production valued at around 31 billion US$. Legumes such as soybean, groundnut and common bean are an important cash crop, and they augment the income of smallholder farmers (ICRISAT 2013). Even crops like the common bean are an important cash crop especially in Central America where beans are among major income-generating field crops, while as in Myanmar, they contribute to about 10% of total export earnings. In fact, food legumes are only next to cereals in terms of contribution to food security (Akibode and Maredia 2011) and serve as a major source of subsistence and livelihood for more than 700 million smallholders in the developing countries valued at about US$ 31 billion annually. They mostly come from the soybean (83.8%), common bean (8.8%), groundnut (peanut) (4.9%) and chickpea (2.4%) (Abate et al. 2012).

8.2.1.2.2 N Economy

The major driving force for ensuring sustainability in agriculture is the efficient N management in the environment (Graham and Vance 2000). Since legume crops fix a sizeable proportion of N, they reduce the reliance on fossil fuels as nutrients such as N are produced by energy-intensive process of Haber-Bosch reaction. Nearly 40% of all population at present as well as in the future depend on the Haber-Bosch process for the synthesis of the key biomolecules (involving N) such as proteins, DNA and other N-containing molecules (Smil 1999). At present, more than 80 million tonnes of chemically fixed N are used in agriculture (Hawkesford 2014). The N fertiliser is extremely indispensable for the energy balance of the crop production. It is required in high quantities globally, for growing crops. The energy footprints of nitrogenous fertilisers are a little over 7.5 times larger than phosphatic and potash fertilisers. In countries like Canada, inorganic fertilisers (mostly N) account for nearly 70% of the total non-renewable energy used in crop production. Since energy is going to be a key limiting factor to determine the sustainability of fertiliser-intensive farming systems, the economic value attributable to food legumes is extremely enormous (Murrell 2016; Datta et al. 2017a).

8.2.1.2.3 Productivity of Farming Systems

Food legumes improve the productivity of rotations especially under marginal farming systems. There is substantial evidence that intercropping systems are better than sole crops in terms of productivity because they optimise the use of resources such as water and nutrients, both spatially and temporally. The observed yield advantages have been attributed to both above- and belowground complementation between component crops of intercropping sequences such as greater interception of sunlight, efficient conversion of the intercepted radiation, better root interactions as well as resource sharing (Rodrigo et al. 2001).

8.2.1.2.4 Lower Cost of Production

Most of the legumes are cultivated at a lower cost as they are grown under the conservation tillage system. In countries like Brazil, Australia and Turkey as well as in North America, agriculture is being implemented on a large scale using legume crops such as soybean, lentil, chickpea, pea and faba bean, involving reduced or no till (NT) systems that leads to a reduction in cost and makes significant positive impact on soil organic carbon (Alpmann et al. 2013; Christopher and Lal 2007).

8.2.1.3 Ecological

8.2.1.3.1 Biological Nitrogen Fixation

Sustaining optimum soil fertility is one of the major challenges in low-input marginal farming systems, and as such, the ability of grain legumes to fix N makes them important under such conditions. Food legume crops have a unique role in the global N cycle, as they fix atmospheric N in soils, thereby reducing chemical N requirements of the legume crop itself, as well as the succeeding crop. Yu et al. (2014) reported that the process of BNF favourably affects soil N availability and also furthers an enhancement of 9.7–20.5% in residual N content in the rice field; these were observed also in rice-bean and rice-vetch sequences. About 7–11% of total legume N is partitioned to roots and nodules with roughly around 11–14 kg N-fixed contributed towards per tonne of belowground dry matter, representing almost half of the total aboveground plant (Carranca et al. 2015). Annually, legume crops, put together, fix about 21.45 Tg of N, out of which a whopping 16.44 Tg is accounted for by soybean, whereas food legumes together account for 2.95 Tg of N-fixation mainly through chickpea followed by common bean, pea, faba bean, cowpea and lentil (Herridge et al. 2008).

An alarming situation has recently come up in a report by Fagodiya et al. (2016), wherein they have analysed the trends in sources of N use in agriculture from 1961 to 2010. As per the report, the N sourced from chemical fertilisers has increased from 15.47% to 51.38%, whereas the amount sourced from N-fixation has reduced from 29.33% to 12.31%. Similarly, N sourced from crop residues has reduced from 18.75% to 14.40% and that sourced from animal manure has reduced from 32.30% to 15.41%. The situation points to the decline in BNF possibly due to largely cereal-based farming systems under high-input agriculture and deterioration in soil health owing to less contribution of food legumes towards global agricultural productivity. The differential contribution of various legume crops in developing and developed world in terms of species diversity may also contribute to the drop in the share of N through BNF (Fig. 8.2). An appraisal of trends of changes in food legume area and production (Table 8.4) reveals that, during the period 1961–2012, the area under food legumes has increased by 27.86%, and the production has increased by 70.73%, much of which has possibly come from synthetic fertilisers. To add to the misery, it is estimated that, by 2015, more than half of the world population will rely on Haber-Bosch process increasing the N emissions. In countries like China and India, synthetic fertilisers account for about 60% of total N inputs (Ma et al. 2010).

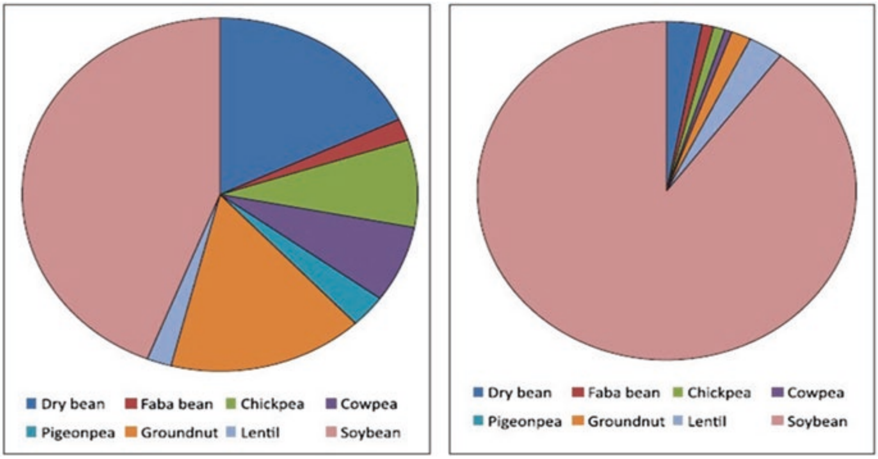


Fig. 8.2 Share of area under different legume crops in developing (left) and developed nations 2008–2010 (Nedumaran et al. 2015)

Table 8.4 World total pulse area, yield and production, 1961–2012

Area (m ha)			Production (M tones)			Yield (Kg/ha)		
1961	2012	Change (%)	1961	2012	Change (%)	1961	2012	Change (%)
61.0	78.0	+27.86	41.0	70.0	+70.73	637.0	908.0	+42.54

Data source: FAO STAT (2014)

8.2.1.3.2 Reduced Carbon Footprints

Legume crops are known as climate smart as they help in both adaptation and mitigation of climate change. In fact, an important climate change mitigation strategy would be the diversification of diets towards less animal-sourced foods especially for meeting protein requirements (FAO 2016a, b). The incorporation of food legumes into cropping system greatly reduces chemical fertiliser and energy footprints and consequently lowering the greenhouse gas emissions (Reckling et al. 2014; Yadav et al. 2017a). Food legumes offset the carbon footprints on account of reduced fertiliser use and consumption of fossil fuels on account of tillage and irrigation. Around one-fifth of all greenhouse gases are contributed by agriculture. This is a global responsibility and requires all economic sectors to shift to low emission intensity. The bulk of direct emissions of methane and nitrous oxide, two potent GHGs, is the result of fermentation in livestock, rice production, flooded fields and the application of N fertiliser and manure (FAO 2016a).

In Europe, the N economisation in legume-based rotations is around 277 kg ha^{-1} of CO_2 per year (1 kg $N = 3.15$ kg CO_2). Considering a baseline of 2.6–3.7 kg CO_2 generated per kg of N synthesised, approximately 300 Tg of CO_2 will be annually released into the atmosphere. All the CO_2 released during the process of N fertiliser synthesis is derived from fossil energy, thus indicating a net contribution of CO_2 to atmosphere (Jensen et al. 2012). On the contrary, the CO_2 released by root nodules wholly comes from the atmosphere through the photosynthetic activity. Legume-based cropping systems reduce nitrous oxide (N_2O) emissions by about 18–33%, compared to systems without legumes. N_2O accounts for about 5–6% of the total atmospheric greenhouse gases (GHGs), but are more damaging than CO_2 in terms of global warming potential (Crutzen et al. 2007). Agriculture contributes majority (60%) of total anthropogenic N_2O emissions (IPCC 2007). Most of GHG emissions result from the application of N fertilisers (Reay et al. 2012) evident from the fact about 1.0 kg of N_2O is released for every 100 kg of N fertiliser (Jensen et al. 2012) with denitrification as the major process of N_2O in most cropping systems (Soussana et al. 2010; Meena et al. 2017a). In the context of the quantum per unit area, legumes emit around five to seven times less GHGs compared to other crops (Jeuffroy et al. 2013)

8.2.1.3.3 Reduced Food Waste Footprints

Approximately, one-third of globally produced grains never reaches the plates as it is wasted along different stages of production value chain (amounting to a whopping US$ 750 billion), with most of the loss taking place during production and processing and lower during consumption (FAO 2011). Increasing primary food production is undoubtedly the major focus of farming research and policy. This is aimed at meeting the future increase in food demand. The economic accessibility of food to the poor is also important that can, to a large extent, be mitigated by reducing food losses. In view of a longer shelf life, the food waste footprints of legume crops are lower than cereals, vegetables and fruits. As per the FAO estimates, the oil crops and pulses together undergo a wastage of around 43.1 million tonnes as compared to 316.9 tonnes in cereals with around 70% occurring in low-income nations. These nations in turn have far greater food security concerns as compared to high-income nations (FAO 2011).

8.2.1.3.4 Sustainability

Legumes are an indispensable component of sustainable agriculture. The major advantages of legumes include the N-fixation to help both current and following crop as well as release of organic matter into the soil in terms of a balanced C/N ratio. Many of the legumes are characterised by deep root systems, which facilitate solubilisation of nutrients such as P, K and Zn by root exudates (Stagnari et al. 2017; Datta et al. 2017b). The food legumes used as rotation crop or intercrop in cereal-based farming systems reduce the soil pathogen inoculums and help achieve the N environmental sustainability goal. In case of the maize-legume system, the leguminous component contributes significantly to N requirement of the maize crop. As a result of such nutrient compensation, intercropped maize responds to a relatively lower fertiliser dosage as compared to sole maize. Similarly, in maize-cowpea intercropping system, it has also been observed that the N content of intercropped maize, especially under low N supply, is higher than that of sole maize (Francis 1986). This indicates some transfer of fixed N from cowpea to maize. In sorghum/black gram intercropping system, reduction of the N requirement of sorghum to the extent of 9 kg N/ha has been reported (Dusad and Morey 1979).

8.2.1.3.5 Increased Adaptive Capacities

There are ~475 million smallholder farmers worldwide (FAO 2016a, b) which are at a greater risk of climate change implications as they inherently lack adaptive capacities and resilience. The legume-based farming systems promote diversification and increased water use efficiency as compared to cereal crops, thereby increasing the adaptive capacity. The incorporation of legumes increases both structural diversity and genetic diversity that leads to pest suppression, nutrient recycling and land use optimisation and increases over all buffering capacity of farming systems (Hossain et al. 1984; Zhu et al. 2005).

8.2.1.3.6 Resource Recycling

Resource recycling is an important characteristic of multiple cropping systems that is accomplished through nutrient recycling and soil formation, especially in systems where legumes are component crops. Legumes have the ability to fix N and solubilise phosphorous and have the capacity to increase rhizosphere biodiversity that helps in such resource recycling. Additionally, the ability of legumes to promote higher rates of soil organic carbon accumulation compared to cereal-based systems can lead to enhanced sequestration of carbon (Bachinger et al. 2013).

8.2.1.3.7 Improving Soil Properties

Legume-based systems help improve soil fertility and soil organic carbon (SOC) as well as increase the availability of N and P. This is all the more important in the case of sandy soils where grain legumes can increase SOC content. The intercropping of soybean with maize has been reported to increase the SOC accumulation to up to 23.6 g C kg^{-1} as against 21.8 g C kg^{-1} under sole maize (Jensen et al. 2012). In fact, Bichel et al. (2016) reported that just by adding soybean residues to the soil increased the SOC by 38.5%. Hydrogen gas (H_2), which is as a by-product of BNF, favourably changes the composition microbial population of the soil, further enhancing the activities of rhizobacteria (Angus et al. 2015; Verma et al. 2015a).

8.2.1.3.8 Promoting Biodiversity

Modern agriculture is far more specialised and is mostly based on a monoculture involving very few crops that have reduced on-farm diversity. The dominance of cereals and other crops vis-à-vis legumes is largely due to the inherently low yielding ability of legume crops. However, with better input support and input-responsive varieties and better management, legumes could well become competitive and replace cereals. In fact, crop diversification is seen as a major driving force towards sustainable intensification. The intercropping systems are characterised by higher species diversity than monocropping. Greater species diversity increases the resource use efficiency that is invariably translated into higher yields and lowers the risk of crop failure due to increasing buffering of heterogeneous systems (FAO 2016a, b).

8.3 Implications of Drought Stress on Legumes

Abiotic stresses are major limiting factors that negatively affect crop growth. This consequently reduces crop productivity substantially, across all crops and farming systems, given that they are widespread. These factors often intensify in magnitude and occur almost every year (Wortmann et al. 1998; Mittler 2006). The crop growth rates are significantly influenced by the availability of water in the soil (Song et al. 2009). In fact, water availability is the most important abiotic factor that has shaped the plant evolution (Kijne 2006). The scenario of water availability is expected to deteriorate more owing to a decline in precipitation and unpredicted weather extremes that have created a proactive international policy and research interest in crop drought tolerance. In the United States alone, during the last 50 years, drought-related crop losses have been estimated at about 67% (Comas et al. 2013; Meena et al. 2015c). Drought stress is not a regional phenomenon, but a globally prevalent production constraint of all major crops including food legumes. The negative effects of prolonged water stress striking as early season, intermittent or terminal drought, are largely enhanced by high temperature (as drought and heat stress invariably come together) and low air relative moisture (vapour pressure deficit), and such situations are the most damaging for legume crops. Water stress especially during the flowering and grain filling periods causes precocity and greater reductions in the seed set, seed weight and seed yield in crops like dry bean (Singh 1995; Sofi et al. 2017).

Drought stress: Key concerns

- *Water is the most important resource for agriculture; any undesirable change in availability of water is going to severely dent our efforts to ensure food availability for the world population that is expected to cross 9 billion by 2050. In fact, agriculture accounts for the largest (70%) withdrawals of water (Siebert et al. 2010).*
- *The water utilisation between 1916 and 2016 has increased twofold in global population (UNO 2015).*
- *By 2025, there will be an upsurge in water withdrawals, and around 1.8 billion people will face acute shortage of water, and 66% people will be living under water-stressed conditions (UNO 2015).*
- *Alarmingly, 84% of economic impacts of drought will be on agriculture (www.fao.org).*
- *Under the predicted phenomenon of climate change, where temperatures are expected to increase by 1–2°, for each degree of increase in temperature will lead to 20% decrease in renewable water resources (www.fao.org).*
- *Increase in sea level will cause intrusion of saline water and cause salt stress.*

Legumes are considered as being inherently sensitive to water stress (Sprent 1972). For majority of grain legumes, the process of N_2 fixation seems especially more sensitive as it shows a decline early during the soil drying. Daryanto et al. (2015) has provided an excellent overview of the effect of drought stress on food legume production around the world. In dryland areas, legumes face up to 70% shortage of water, whereas under non-dryland systems, 60% reduction in water availability is reported causing a yield reduction of 30% and 40%, respectively. They reported that, across all food legume crops, early season water stress (at vegetative stage) reduces productivity by around 20%, water stress at either the early (flowering) or late (pod filling) reproductive stages caused yield reductions of up to 40%, whereas, water stress at both of these stages causes yield reduction in excess of 40%. Among crops, field pea, lentil, groundnut, soybean and pigeon pea suffer relatively lesser yield reduction under drought (20–30%); faba bean, chickpea, green gram and cowpea suffer mild reduction under drought (30–50%), whereas bambara bean, lablab bean, common bean and black gram suffer heavy reductions (60–80%) under drought (Verma et al. 2015b). The challenge of producing enough food for the increasing population is further complicated by the severe competition for already shrinking land and water from industry and urbanisation (Postel 2000) that further relegates legume-based farming to marginal areas, where water-limiting conditions often constrain crop productivity. The limitation posed by water availability in such areas is invariably persistent and season to season fluctuations tend to be large, significantly affecting food security in such rain-fed systems. Despite the fact that water stress adversely affects legume production, yet, about 70% of production occurs in regions such as sub-Saharan Africa, India and China that invariably experience water shortage (Gowda et al. 2009) resulting in lower yields. The variable rainfall patterns in these regions render legume cropping systems highly vulnerable to drought. Even in countries like Brazil where legumes like soybean are cultivated under sufficient precipitation, water deficiency may still surface resulting in significant yield reduction (Oya et al. 2004).

8.3.1 Implication of Water Stress on N-Fixation

The legume-*Rhizobium* symbiotic N-fixation is a biological phenomenon of paramount importance and also a major contributor towards improving soil fertility in legume-based farming systems. There is sufficient evidence to state that water and salt stress cause a substantial reduction in plant biomass accumulation (root and shoot), nodule development, and N activity as well as these strongly declined the yield (Egamberdieva et al. 2014). As a biological process, symbiotic N-fixation is highly sensitive to water stress, which results in decreased N accumulation and also in the yield of companion legume crops. With this premise, one can safely conclude that crops dependent on N-fixation in nodules, under drought stress, will experience N deficiency on account of reduced N_2 fixation. In fact, the increased sensitivity of N-fixation to water stress relative to leaf gas exchange is a major constraint on N_2

accumulation and yield of legumes grown under moisture stress (Serraj et al. 1999). The legume-rhizobacterial symbiotic system efficiency under stress is based on individual and interactive ability of various components such as plants, the N-fixing microbes and certain helper microbes to function optimally. Of the two component partners in the legume-rhizobium association, the *rhizobium* is more sensitive than the plant. This is evident from the observation that symbiotic association is more sensitive to environmental stress (especially drought) than the uninfected legume (Swaine et al. 2007; Meena et al. 2017b).

8.4 Association of Legumes with Soil Rhizobacteria

The interface of root and soil systems constitutes a dynamic associative as well as interactive system known as the *rhizosphere* where the roots, soil and microorganisms interact (Lynch 1990; Kennedy 1998). Hiltner (1904) was the first to describe the term "rhizosphere" as a zone of maximum microbial activity. Rhizosphere is a unique zone of soil near plant roots and formed under the influence of a plant root system (Berendsen et al. 2012). All the three components of soil environment, viz. physical, chemical and biological, of the rhizosphere are clearly different from the rest of the soil (outside the rhizosphere), where entirely different microbial diversity and activity have been reported (Kennedy and Smith 1995). Especially the biological component (microbes) of rhizosphere is clearly distinct from that of the bulk soil, both in abundance and in diversity, primarily due to the root exudates that create an enabling habitat by providing nutrition for microbial growth (German et al. 2000). The microorganisms may be present in the rhizosphere, root tissue and/or in a specialised root structure called a nodule. Very important and significant interactions have been reported among plant, soil and microorganisms present in the soil environment (Antoun and Prevost 2005). The rhizosphere comprises not only the wide array of microbial diversity (ranging from beneficial to harmful to neural microbes) but also a complex set of interactions (beneficial, harmful and/or neutral) between the roots and microbes (Ahmad et al. 2011; Bakker et al. 2013). The increased population of bacteria in the rhizosphere may be due to the root exudates that not only attract but also promote bacterial growth (Bais et al. 2006). The microorganisms colonising plant roots generally include bacteria, algae, fungi, protozoa and actinomycetes. Enhancement of plant growth and development by application of these microbial populations is well evident (Bhattacharyya and Jha 2012; Hayat et al. 2010; Meena et al. 2013). Of the different microbial populations present in the rhizosphere, bacteria are the most abundant of microorganisms (Kaymak 2010). Various genera of bacteria, *Pseudomonas*, *Enterobacter*, *Bacillus*, *Variovorax*, *Klebsiella*, *Burkholderia*, *Azospirillum*, *Serratia and Azotobacter*, cause a significant effect on overall plant growth and are referred to as plant growth-promoting rhizobacteria (PGPR). The PGPRs are reported to increase plant growth both under favourable and stressful conditions through various direct and indirect mechanisms (Nadeem et al. 2010) including biological N-fixation,

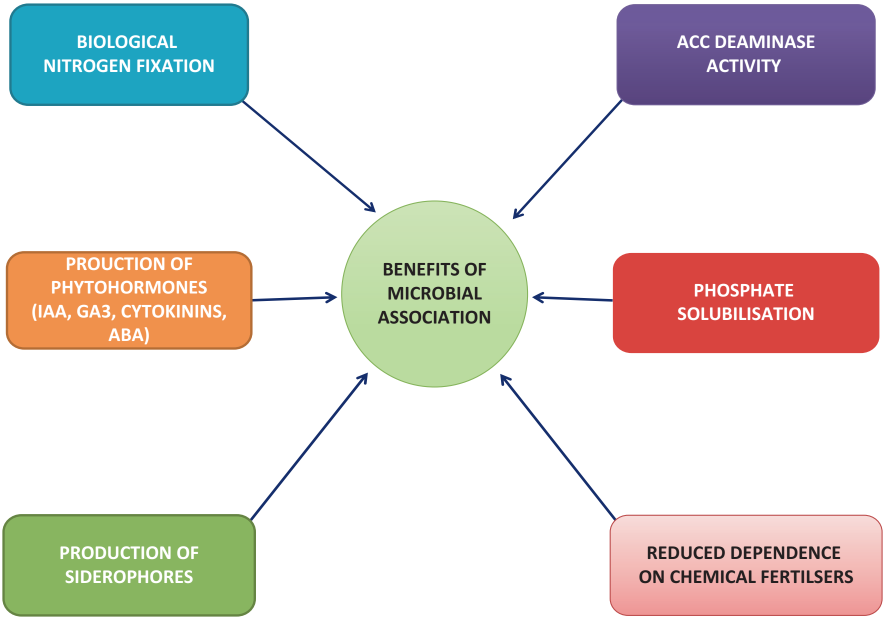


Fig. 8.3 Mechanisms of plant growth promotion by rhizobacterial association

phosphorus solubilisation, siderophore production, phytohormones and organic acids as well as enzymes such as ACC deaminase, chitinase and glucanase (Fig. 8.3) that have all protective roles under stress (Berg 2009; Glick et al. 2007).

The beneficial bacteria may either form a symbiotic relationship, involving the formation of nodules as in *rhizobia*, or may be free-living in the soil (Valdenegro et al. 2000). The beneficial free-living bacteria, commonly referred to as plant growth-promoting rhizosphere bacteria (PGPR), have been found in association with many different plant species (Majeed et al. 2015). The beneficial plant growth-promoting bacteria belong to a heterogeneous group of microorganisms inhabiting the rhizosphere, in diverse forms of associations, and thus enhancing the growth of plants as well as protecting them from various biotic and abiotic stresses (Dimkpa et al. 2009; Grover et al. 2011; Glick et al. 2007). In addition to the growth-promoting characteristics, some of these PGPRs have also been implicated in restricted pathogen proliferation through production of various biostatic compounds that stimulate the immune system (Berendsen et al. 2012).

Various types of plant-microbe (Fig. 8.4) interactions such as symbiotic, endophytic or associative are operative in the rhizosphere with distinct degrees of proximity with the roots and the rhizosphere. Endophytic rhizobacteria are invariably good candidates for use as inoculants on account of their ability to efficiently colonise roots. Therefore, they create a favourable environment for proliferation and effective function, while the non-symbiotic endophytes colonise the intercellular spaces of plant tissues, containing high levels of carbohydrates, amino acids and

Fig. 8.4 Various types of rhizobacterial cultures and products for legume crops. (Source: Z A Baba)

inorganic nutrients (Bacon and Hinton 2006). The success and efficiency of the different types of PGPRs for agricultural crops is determined by factors such as:

- *Root-colonising ability of bacteria*: This is invariably influenced by the nature and extent of competition and survivability of the different microbes, as well as with the changes in gene expression (quorum sensing) in response to the population dynamics (Meneses et al. 2011).
- *Composition of root exudates*: Plant roots secrete a wide range of root exudates in response to the variations in the immediate environment. These root exudates influence the plant-microbe interaction that is an important consideration in the efficiency of the PGPR's use as inoculants (Carvalhais et al. 2013).
- *Soil health:* Soil health is collectively determined by physical, chemical and biological parameters of soil such as soil structure and texture caused, nutrient pool

and toxic metal concentrations, soil moisture, microbial diversity as well as management practices and affects the inoculation efficiency due to several characteristics.

Rhizosphere functionality significantly influences the overall fitness of plants and the soil health, especially under stress conditions as they can help the host plant to adapt to stress conditions, as well as ward of certain soil-borne pathogens (Bowen and Rovira 1991). Nearly all plants have a well-established association with a wide variety of soil microbes in the rhizosphere (Brundrett 2009). Such a system not only provides an enabling habitat for proliferation of microorganisms but also improves plant growth as well as soil health. A large number of such microorganisms establish an endophytic relationship with the root system of host plants (Stone et al. 2015). Climate change mainly increased CO_2 and is expected to change the plant physiology and consequently the root exudation, mainly by changes in carbon allocation to the roots. Such alterations may also include changes in the availability of attractants and/or signal molecules as well as changes in C/N ratio or the availability of certain nutrient (Haase et al. 2007; Meena et al. 2016).

8.5 Soil Rhizobacteria in Relation to Drought Stress Amelioration

There are ample evidences to show that the crop-microbial interactions in legumes enhance productivity, quality as well as resilience to various abiotic stresses through mechanisms outlined above (Fig. 8.3). Several limiting factors such as water, salt and high-temperature stress cause cell and tissue dehydration and irreversibly damage plant tissues. Symbiotic N-fixing bacteria such as *Rhizobium* can synthesise trehalose (Suárez et al. 2008), a sugar that accumulates in bacteroids as well as in nodules and helps retain water in cells. Water stress changes the phytohormonal balance in the plants resulting in higher abscisic acid (ABA) content in leaves, small decrease in indole acetic acid (IAA) and gibberellic acid (GA3) and a large decline in zeatin content in leaves (Figueiredo et al. 2008). For legume crops that depend on N-fixation, water stress causes a corresponding negative effect on nodulation, nodule functioning as well as N-fixation, biosynthesis of protein, malate and leghaemoglobin and changes in enzymatic activities, plant growth and metabolism (Aydi et al. 2004; Mhadhbi et al. 2004). Water stress may decrease persistence and the survival of *rhizobia* in the soil and root hair colonisation as well as in the colonisation and infection process (Gray and Smith 2005). Legume crops are colonised both by endocellular and intracellular microorganisms including bacteria and fungi that can enhance plant growth especially under stress conditions and improve yields (Dimkpa et al. 2009). PGPRs directly stimulate plant growth and development by providing fixed N, phytohormones, iron as well as phosphate (Hayat et al. 2010; Yadav et al. 2017b), plant physiology and growth under various abiotic stress conditions, and some examples are summarised in Table 8.5.

Table 8.5 Rhizobacterial species reported to alleviate various stresses in legume crops

Rhizobacterial species	Crop	Stress	References
Aeromonas hydrophila	Soybean	Heat stress	Zhang et al. (1997)
Azospirillum brasilense	Common bean	Water stress	German et al. (2000)
Azospirillum brasilense	Faba bean	Salt stress	Hamaoui et al. (2001)
Sinorhizobium meliloti	Medicago	Water stress	Vazquez et al. (2001)
Glomus intraradices	Soybean	Water stress	Porcel and Ruiz-Lozano (2004)
Bradyrhizobium	Soybean	Lead toxicity	Andrade et al. (2004)
Pseudomonas marginalis	Pea	Heavy metals	Safronova et al. (2006)
Pseudomonas brasiliense	Soybean	Mercury toxicity	Gupta et al. (2005)
Mesorhizobium	Common bean	Heat stress	Rodriguez et al. (2006)
Ochrobactrum	Mung bean	Chromium toxicity	Faisal and Hasnain (2006)
Mesorhizobium ciceri	Chickpea	Salt stress	Tejera et al. (2006)
Brevibacillus	Clover	Zinc toxicity	Vivas et al. (2006)
Mesorhizobium	Chickpea	Acidity	Rodriguez et al. (2006)
Rhizobium leguminosarum	Trifolium	Nickel toxicity	Vivas et al. (2006)
Glomus etunicatum	Soybean	Salt stress	Sharifi et al. (2007)
Ensifer meliloti	Common bean	Water stress	Mnasri et al. (2007)
Pseudomonas fluorescens	Groundnut	Salt stress	Saravanakumar and Samiyappan (2007)
Rhizobium tropici	Common bean	Water stress	Figueiredo et al. (2008)
Azospirillum brasilense	Pea	Salt stress	Dardanelli et al. (2008)
Rhizobium etli	Common bean	Water stress	Suárez et al. (2008)
Mesorhizobium mediterraneum	Chickpea	Water stress	Romdhane et al. (2009)
Variovorax paradoxus	Pea	Water stress	Belimov et al. (2009)
Rhizobium and Azotobacter	Faba bean	Water stress	Dashadi et al. (2011)
Glomus mosseae	Trifolium	Salt stress	Zou and Wu (2011)
Pseudomonas pseudoalcaligenes	Chickpea	Salt stress	Patel and Jain (2012)
Pseudomonas extremorientalis	Common bean	Salt stress	Egemberdieva (2011)
Glomus mosseae	Mung bean	Water stress	Habibzadeh et al. (2012)
Rhizophagus irregularis	Trigonella	Salt stress	Basrnawal et al. (2013)
Bradyrhizobium spp.	Common bean	Water stress	Uma et al. (2013)
Bradyrhizobium spp.	Mung bean	Water stress	Tittabutr et al. (2013)

(continued)

Table 8.5 (continued)

Rhizobacterial species	Crop	Stress	References
Glomus mosseae	Faba bean	Chromium toxicity	Ismail (2014)
Pseudomonas aeruginosa	Mung bean	Water stress	Sharma and Saikia (2014)
Bradyrhizobium japonicum	Soybean	Water stress	Prudent et al. (2015)
Pseudomonas putida	Faba bean	Salt stress	Metwali et al. (2015)
Bacillus thuringiensis	Soybean	Water stress	Prudent et al. (2015)
Rhizobium phaseoli	Common bean	Water stress	Sofi et al. (2017)
Rhizobium spp.	Chickpea	Water stress	Khadraji and Cherki (2007)
Mesorhizobium	Chickpea	Salt stress	Chaudhary and Sindhu (2017)

Table 8.6 Shifts in biomass partitioning under drought in common bean without rhizobial inoculation (Sofi et al. 2017)

Treatment	Root to total biomass ratio	Shoot to total biomass ratio	Root shoot ratio
Drought	0.465	0.535	0.930
Irrigated	0.263	0.737	0.381
% Increase/ decrease	+76.80	−27.40	+144.09

There are various strategies and mechanisms implicated in enhancement of plant drought stress tolerance mediated by rhizobacteria. However, the exact mechanisms of enhancement by rhizosphere bacteria have remained mostly speculative. In terms of gross morphology and biomass partitioning, rhizobium is reported to cause changes in allocation to help plant adapt to resource. This resource deficiency entail rooting depth, root biomass and root volume (Table 8.6). Rhizobium has been reported to increase height, leaf area, photosynthetic rate and dry matter production in plants under irrigated conditions (Thakur and Panwar 1995). Sofi et al. (2017) reported that among plant growth parameters, rhizobial inoculation caused the largest increase in shoot biomass (184.44%) followed by a root volume of (91.81%) and root biomass of (74.64%), whereas the smallest increase was recorded for rooting depth was (10.87%). Interestingly, the rhizobia caused a decrease in root/shoot ratio by −38.60%. This is interesting in view of the fact that drought stress, without any rhizobial treatment, invariably causes a shift in allocation towards roots to enhance resource acquisition. However, such shift always has penalties on the overall biomass production as well as the subsequent remobilisation of resources (Table 8.7).

The rhizobacteria-mediated alleviation of stressful conditions may be accomplished through either of the following possible mechanisms:

- Hormones like ABA, GA, cytokinins and auxin that promote growth and development and modulate plant response to stress by improving its soil resource acquisition. Phytohormones such as IAA produced by bacteria also stimulate the

Table 8.7 Effects of rhizobium on various root and shoot traits in common bean (*Phaseolus vulgaris* L.) (Sofi et al. 2017)

Treatment	Rooting depth (cm)	Root biomass (g)	Root volume (cm^3)	Plant height (cm)	Shoot biomass (g)	Root/shoot ratio
Without rhizobium	74.222	6.0037	6.527	46.527	10.283	0.583
With rhizobium	82.291	10.485	12.520	45.500	29.250	0.358
% increase or decrease	+10.87	+74.64	+91.81	−2.01	+184.45	−38.60

activity of the ACC deaminase (Glick 2005). Enhanced production of abscisic acid (ABA) plays a key role in closing stomata and regulating aquaporins either via their gene expression or via post-translational regulations. This helps plants to regulate water fluxes within as well as absorption of nutrients (Acharya and Assmann (2009).

- Enzymes such as ACC deaminase reduce ethylene level in the root of growing plants. Under stress conditions ACC deaminase reduces stress-induced ethylene production. The rhizosphere bacteria with ACC deaminase activity are reported to modify the sensitivity of the root and leaf growth to water stress through ethylene signalling. The reduced ethylene production upon inoculation improved recovery from water deficiency, although there was no effect on leaf relative water content (Mayak et al. 2004).
- Osmoprotective amino acids such as proline are enhanced under water stress. The *Medicago* plants infected by PGPR strains that produce higher quantity of phytohormones such as IAA were more tolerant to stress environmental conditions through accumulation of higher levels of proline (Verbruggen and Hermans 2008).
- Release of plant growth-promoting compounds in active form through hydrolysis of conjugated phytohormones and flavonoids in the root tissue as reported in case of *Azospirillum* inoculation (Dardanelli et al. 2008).
- Increased root growth, root biomass, enhanced lateral root formation as well as greater root hair proliferation that can result in higher tolerance to abiotic stress such as water stress as reported in case of *Rhizobia* (Sofi et al. 2017).
- PGPRs can also induce a reproductive delay leading to a better tolerance to water stress as in case of Arabidopsis (Bresson et al. 2013).
- Bacterially derived biofilms, i.e. extracellular matrix, trigger induced systemic resistance (Kim et al. 2013). Such extracellular matrix contains a wide variety of macromolecules, which are beneficial for plant growth and development. Biofilms also contain a number of sugars and polysaccharides that can play very essential roles in bacteria-plant interactions and in the improvement of their water retention capacity, thereby improving water availability in the root medium. Some of the polysaccharides have the capacity to retain water by severalfold of their mass (Timmusk and Nevo 2011). Even small polysaccharide such as

alginate in the biofilms can facilitate maintenance of hydrated microenvironment, by increasing the water retention capacity (Chang et al. 2007).

- Changes in the composition of cell envelope that may result in changes in proteins, periplasmic glucans and exo- and lipopolysaccharides. PGPRs such as *Pseudomonas* are known to survive under stress conditions due to the exopolysaccharide production that confers protection from water stress by increasing retention of water and regulating the diffusion of C sources in environment (Sandhya et al. 2009; Meena and Yadav 2015). Similarly, Klein et al. (1999) reported that, under osmotic stress, the composition of bacterial membrane is changed by changes in the length and branching of acyl chains as well as number of double bonds. Francius et al. (2011) reported the presence of loose, flexible surface appendage around the bacteria under low electrolyte concentration condition that acts as a protective barrier. Changes in phospholipid content in the cell membranes of cowpea have been observed upon inoculation with *Azospirillum* (Bashan et al. 1992).
- Certain osmolytes that increase the osmotic potential within cells are released into rhizosphere by root zone bacteria such as trehalose and glycine betaine (Farooq et al. 2009). Production of sugars like trehalose as reported in *R. elti* that help plants retain more water under stress conditions (Suárez et al. 2008).

The use of PGP microbes for stress alleviation can be used as a viable option for improving stress tolerance that is economically as well as ecologically sustainable. In this case, the native microbes could be more useful as they are relatively well adapted to the local environments on account of their competitive abilities (Mrabet et al. 2005). Rhizobacteria used as microbial inoculants have many direct and indirect growth-promoting properties including some tolerance mechanism against water stress, heavy metals and pesticides. Even though the response in legumes to various stresses is host plant centric reaction, this response can be favourably modulated by the rhizobia (Yang et al. 2009). Various accounts of role of *Rhizobium* and *Bradyrhizobium* in tolerance and nodulating capacity for alleviating problem soils, temperature and water stress conditions have been provided by Graham (1992) and Grover et al. (2010). The rhizobacteria have a remarkable ability to protect not only their own systems from stresses but also impart a fair amount of resilience to host plants, against abiotic stresses. Interaction of rhizobacteria with several crops in stress conditions is reported to reduce growth reduction and improve plant survival and performance in adverse conditions (Dimkpa et al. 2009).

8.6 Breeding Perspectives of Harnessing Soil Rhizobacteria

The crop-microbial interaction is a multi-partner association comprising plant roots, the rhizobacteria as well as certain helper microbes. These microbes facilitate recognition, colonisation as well as the functionality of the system. There are obvious genetic differences in both the partners of this association that determine the levels of interaction and effectiveness especially under stress conditions (Fig. 8.5). The

Fig. 8.5 Response of common bean under drought stress with and without rhizobium (top) irrigated (middle) drought with rhizobium (bottom) drought without rhizobium

different partners of the system are differentially susceptible to water stress, so they have to be considered as separate systems as well as on a whole system basis. This is done to find the combinations that effectively harness the potential of such combinations to alleviate water stress in food legume crops (Rengel 2002).

8.6.1 Selection for Differential Genotypic Response to Rhizobacterial Inoculation

The first step towards building effective crop microbial associations would be to understand natural variation in food legume crops, varieties, breeding lines and germplasm resources for their association capacities with different soil rhizobacteria. This would require extensive genotypic screening to identify the genotypes that have the ability to harbour effective microbial populations that can help improve overall growth and stress tolerance (Fig. 8.6). There are already ample evidences that indicate genotypic differences in legumes for rhizobacterial associations such as white clover (Ledgard 1989), faba bean (Caba et al. 2000), soybean (De Chueire and Hungria 1997), mung bean (Espiritu et al. 1993), common bean (Suárez et al. 2008), pea (Evans et al. 1995), groundnut (Ibrahim et al. 1995), lucerne (Hernandez

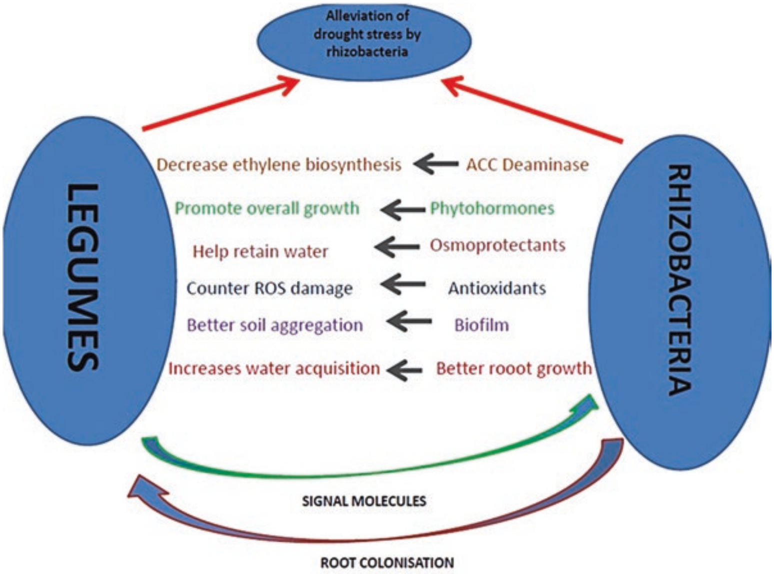


Fig. 8.6 Mechanistic representation of legume-rhizobacteria association for drought alleviation

et al. 1995) and chickpea (Sattar et al. 1995). The genotypic differences for glutamine synthetase and glutamate synthase activities in nodules have also been reported to be correlated to stress tolerance in faba bean (Caba et al. 2000). Therefore, increased activities of such enzymes can be used as selection criteria in the breeding programmes to increase stress tolerance of genotypes. Similarly, in chickpea, genotypic differences in the nodule number and weight have been reported (Dangaria et al. 1994). Genotypic differences for traits related to the nodule functionality such as N accumulation in shoots have also been reported in pea (Fesenko et al. 1995). The legume genotypes that are able to maintain a higher N-fixation under suboptimal levels of nitrate should also be selected (Blumenthal and Russelle 1996). This is especially relevant in the case of modern crop varieties that contain high N concentrations in the harvestable product by removing greater amounts of N on account of higher fertiliser use even in legume-based farming systems. Genotypic differences have also been reported in legumes in the level of tolerance of the N-fixation to nitrate. Such natural variation can be potentially harnessed for increasing the efficacy of symbiotic N-fixation by selecting the best combination of nitrate-tolerant plant genotype and rhizobia (Raffin and Roumet 1994).

Any breeding programme aimed at harnessing crop-microbial associations should tap this variation to identify the genotypes as well as elucidate the physiological and genetic factors underlying such a variation. However, a major problem in screening genotypes for differences in nodulation and N-fixing ability is the diversity of conditions that may occur in soils. This is especially the case of drought stress, where, in the screening process, different factors may confound the final results (Fig. 8.7). Under field conditions, a multitude of favourable and

Fig. 8.7 Genotypic differences in nodulation in common bean. (Source: P. A. Sofi)

unfavourable effects may come into play, and delineation of actual genotypic differences becomes practically impossible. Therefore, the experiments should be, as far as possible, conducted in controlled conditions such as hydroponics and green houses. However, a major issue with such a setup is failure to replicate actual soil-like conditions, which represent the real farmer conditions. This problem may be further complicated by differences in functionality of rhizobacterial strains at different locations. Another major focus in identifying desirable genotypic variation for effective rhizobacterial associations is that the wild relatives of legume crops may provide valuable sources of variation/genes, since the wild relatives might have retained all the regulatory and structural components of effective associations as they have not really suffered changes under domestication such as fertilisers and chemical pesticides. Similarly, mutagenesis can also be used as an approach to generate desirable variation for this trait (Andriolo et al. 1994).

8.6.2 Selection for Competitive Rhizobacterial Strains

Corresponding to the natural variation in the legume crop species, the rhizobacterial strains that have come under evolutionary forces also developed a variation in cross compatibility relationships for colonising, nodulating, and effective functioning. This process was in association with the appropriate legume species and consequently the rate of change of such traits that define the ability of the rhizobacteria to enter into symbiotic relationship with legume crops might be higher than host plants. This is due to their small size, greater generation turnover and ability to generate enormous variability. From a functionality point of view, the potential of association and colonisation is important, apart from the efficiency of N-fixation and the ability to transfer some degree of tolerance to stresses to plant partner. Since rhizobacteria have been reported to differ in their N-fixation capacity, it is possible to select the efficient strains that fix a higher quantity of N even under stress (Hungria et al. 2013). Since substantial natural variation for nodulation and the N_2-fixation is widely reported in different rhizobia-host combinations, it should be possible to identify the most efficient rhizobial strains as well as the underlying genetic factors that regulate the efficiency of the symbiosis. Once the genes are characterised, it would be possible to transfer them into commercial strains of rhizobia to improve the efficiency of their N-fixation. Even within the nodulating bacteria, substantial variability has been found in tolerance of the N-fixation process to nitrate (Nour et al. 1994; Varma and Meena 2016), an issue of paramount significance, while breeding for better symbiosis (Rengel 2002).

Superior rhizobia have better N-fixation. However, an increased N-fixing ability should not be the only index of selection. More than that, one should also consider differential competitive abilities vis-à-vis the native rhizobia which are invariably ineffective in N-fixation, yet competitive due to the adaptive advantage. Superior N-fixing strains invariably have the ability to outcompete the native rhizobial strains and occupy a greater proportion of the nodules. In order to increase the selection efficiency, the selection for competitive ability and functional efficiency should be done under natural conditions to identify superior ones. The effective rhizobia are characterized by better establishment in the soil and the rhizosphere (saprophytic competence), causing better nodulation, occupying larger proportion of nodules, and having better nitrogenase activity. Even though functionally efficient rhizobial strains can be selected from native populations (Howieson et al. 1995), achieving a larger nodule occupancy by rhizobia is also an important practical constraint as mass inoculation does not always ensure improved nodule occupancy (Kuykendall 1989). In fact, the quantum of required inoculum to outcompete the native rhizobia is invariably uneconomical (Vlassak and Vanderleyden 1997). Moreover, the inoculums load as well as number of bacteria is not the single deciding parameter for competitiveness. Other factors such as mobility of rhizobial may also equally be important in determining the capacity of rhizobial strains to effectively nodulate the crown and lateral roots. However, the competitive ability of introduced rhizobia strains can be increased through genetic engineering to produce compounds that inhibit the nod gene expression in native rhizobia. In fact, the nod gene repressor (NolA) in strain USDA110 upon transfer to *B. japonicum* caused a decline in Nod factor production. The native rhizobacterial strains of a particular geographical area hold greater promise on account of their adaptability to environmental conditions and long evolutionary history of coexistence with the local legume crops. The rhizobacterial cultures brought into the system by way of ruthless import of microbial formulations which may have more negative implications rather than potential benefits. This is because they may lack adaptability to the agroecological conditions, may not colonise the host plant optimally, may be invasive and may erode local microbial biodiversity. Besides, they may sometimes negatively influence plant growth parameters (Vlassak and Vanderleyden 1997).

8.6.3 Identification of Adaptive Crop-Microbial Associations

In order to identify stress adaptive crop-microbe associations, one needs to test one's functionality under appropriate stress environments. The host legume crop grown under stressful conditions have exhibited substantial natural variation in nod gene inducers found in their root exudates (Raghuwanshi et al. 1994) such as under low P (Mullen et al. 1988), low Ca (Munns 1970) and the soil acidity. Rhizobial strains with relatively higher nodulation capacity under low P or in acidic soils have been isolated (Howieson et al. 1995) and found to possess better symbiotic abilities under such stress conditions especially in acidic soils in tropical areas where subsistence farmers do not have sustainable options to alleviate soil acidity. In terms of the root phenes, the phenomic level potential root traits to be considered are length, angle, biomass and branching, while as at the level of transcriptome, proteome and metabolome, one needs to consider osmoprotectants, auxin-responsive factors, transcription factors, methionine and coumestrol. Similarly, in nodule partner, the traits at the phenomic level include number, density and biomass, while as traits at the level of transcriptome, proteome and metabolome include C/N/S metabolism, protein turnover and lipoxygenase Kunert et al. 2016; Dhakal et al. 2016).

8.6.4 Genetic Modification of Rhizobacteria

Use of genetically engineered microbes that can suitably alter plant response to stresses by overexpression of certain osmolytes is a viable option. There are already reports about the use of engineered *R. elti* over expressing trehalose conferring drought stress tolerance in common bean (Suárez et al. 2008). The strategy of using genetic transformation in rhizobacteria as against developing transgenic plants for improved plant performance under stresses has many practical advantages (Carman and Defez 2011; Hays et al. 2015):

- They are more robust in that they possess diverse mechanisms to environmental disturbances and in association can transfer a fair amount of tolerance to the host plant.
- It is comparatively much easier to perform genetic modification in bacteria as compared to complex higher plants.
- Many traits that promote plant growth can be simultaneously combined in a single organism thereby overcoming the need to engineering diverse crops, especially in the case of *Azospirillum* which is nonspecific.

8.7 Conclusion

Ensuring food and nutritional securities will be central to all research efforts and policy support systems and will assume much greater significance in the years to come due to predicted projections of climate change implications. Legumes will for sure be a key to any such endeavour owing to their unique features that in addition to increasing farm productivity also lend sustainability to the system at different levels. The sustainability would encompass the food system level where they ensure food and nutritional security to both human and animals; production system level where they ensure reduced dependence on chemical fertilisers especially for low-input farming systems, as well as their role in reducing carbon foot prints, improving soil health and mitigating greenhouse gases emissions; and cropping system levels where their role in diversification of agroecosystems helps enhance farm biodiversity, in reducing pest and disease vulnerability.

8.8 Future Prospective

Plant breeding has undeniably contributed heavily to enhancing productivity across a broad range of growing environments. New crop varieties, with better yields as well as inbuilt resilience to various stresses such as drought, have been continuously developed and released using both the conventional plant breeding and molecular breeding using MAS and genetic engineering through transgenic varieties (Atkinson and Urwin 2012). Depending upon the trait complexity, conventional plant breeding does suffer from being time consuming, as well as laborious and cost intensive (Ashraf 2011). The techniques of molecular biology and biotechnology have largely helped to reduce the time and labour costs of conventional breeding, as well as increase precision. Transgenics have been developed in crops like cotton, maize and soybean carrying genes for economically important traits, more often imparting resilience to biotic and abiotic stresses. Recently the focus has also shifted to traits such as growth regulators, antioxidants, osmolytes and other factors that have been implicated in improved tolerance to stresses (Eisenstein 2013).

Both, the conventional and molecular breeding, work on the premise that the plants function as autonomous organisms and are regulated solely by their gene composition (Barrow et al. 2008). However, there is substantial evidence to safely assume that plant-microbe interactions cannot be ruled out as significant modulators of crop response to abiotic stresses. Despite that, the field trials of newly released stress-tolerant cultivars barely address microbial influence on improved performance (Cooper et al. 2014). Even the greenhouse trials are invariably conducted with sterilised soil and soil amendments (Witt et al. 2012) to create a microbe-free growth environment, a situation hardly found in actual field conditions (Friesen et al. 2011). In doing so, the important determinants of phenotypic output are neglected, which often lead to overestimation of the effect of host genotype on plant phenotype and make the basis for our hypothesised view of plants as individual autonomous systems (Barrow et al. 2008).

Coleman-Derr and Tringe (2014) outlined the comparative advantages of using rhizobacteria approaches to improving stress tolerance as compared to seeking plant improvement per se for stress tolerance. They pointed out the following advantages of harnessing crop-rhizobacterial associations and for improving drought tolerance:

- Microbial systems are capable of conferring stress tolerance to a wide variety of diverse plants, across different genera and species (Zhang et al. 2008). One's ability to harness the stress-resistant substances across crop species through microbial inoculation can potentially save one several years of plant breeding effort. It has been experimentally shown that microbes isolated from the rhizosphere of a desert crop can equally improve the growth of a different host species when grown under water-limited conditions (Marasco et al. 2013).
- Rhizobacteria invariably confer tolerance through a diversity of tolerance mechanisms (Rodriguez et al. 2008). This is all the more important in view of the fact that crops grown in areas where water stress and high temperatures are more prevalent (arid and semiarid) typically suffer from multiple stress. Rhizobacteria, possibly modulate plant response to stress through manipulation of plant hormone pathways that involve substantial crosstalk (Glick et al. 2007; Atkinson and Urwin 2012).
- The plant-microbe system represents a highly flexible co-evolved system that can favourably add genetic flexibility to the stress adaptation of plants (Barrow et al. 2008). In fact, the concept of "habitat specific symbiosis" is one of the most intriguing scientific discoveries that defines the contribution of soil microbes to stress tolerance (Rodriguez et al. 2008).
- It is now fairly easy to characterise vast diversity of rhizobacterial species than ever before. A substantial proportion of microbes isolated from crops have exhibited significant effects on overall fitness of hosts (Friesen et al. 2011). Even for the strains that are otherwise difficult to culture, metagenomics has evolved as a powerful approach to asses such vast diversity spectrum of microbes in rhizosphere (Berg et al. 2016).

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