Mohamed Mahgoub Azooz • Parvaiz Ahmad

Legumes under Environmental Stress
Yield, Improvement and Adaptations
9.1 Introduction

Various biotic and abiotic factors limit crop productivity, affecting nearly 1 billion people around the world (Munns & Tester, 2008; UNEP 2009). Malnutrition is recognized as the world’s most serious health problem, while agricultural development is considered as the most effective sector in reducing hunger and poverty, through improvements in crop productivity (Godfray et al., 2010). Crop losses due to salinity and drought are a major area of concern in coping with increasing food requirements (Egamberdiyeva et al., 2007; Shanker & Venkateswarlu, 2011; Davranova et al., 2013). Salinity alone affects 33% of the world’s potential arable land, whereas 950 million ha of salt-affected lands occur in arid and semi-arid regions (UNEP, 2008). Major factors increasing salinity include irrigation of cultivated lands with saline water, poor cultural practices and low precipitation. The ability of plants to take up water are inhibited by salinity stress, causing ion imbalance and, in turn, resulting in a reduction of root and shoot growth (Munns, 2002).

In such situations, the presence of salt-tolerant genetic variants in a particular crop is a prerequisite for its successful cultivation (Mahmood et al., 2000). Numerous studies have been reported on the management and identification of salt-tolerant crops such as cotton, wheat, maize and alfalfa (Chauhan & Singh, 2000; Soltani et al., 2012). In addition, organic farming practices, such as application of farm manure, compost, biofertilizer and recycling of crop residues and/or green manures, also improve degraded soils affected by salinity (Pathma & Sakthivel, 2012; Adesemoye & Egamberdieva, 2013).

Legumes are very important crop plants for human and animal consumption, and the use of legumes in crop rotations can be a useful management strategy to increase the supply of nitrogen to non-legume plants (Lüscher et al., 2011; Nyfeler et al., 2011). The legume-Rhizobium symbiosis is known to be the most efficient system for biological nitrogen fixation (BNF) through nodulation in legume roots (Molla et al., 2001). It has been estimated that some 44–66 million tons of N₂ are fixed annually by leguminous plants, providing nearly half of all N used in agriculture worldwide (Alberton et al., 2006).

The response of legumes to environmental stresses such as salinity and drought varies and depends on soil type, salt toxicity and climatic factors (Cordovilla et al., 1995; Serraj et al., 2001; Predeepa & Ravindran, 2010; Jabborova et al., 2013a). Numerous studies have shown that soil salinity inhibits legume growth and development and decreases nodulation and N₂ fixation (reviewed by Zahran, 1999; Mensah & Ihenyen, 2009; Egamberdieva et al., 2013a). Grain legumes are known to be salt-sensitive crops, but differences in salt tolerance exist among genotypes (Dua, 1992; Gandour, 2002). Genotypic variation in leguminous crops for traits affecting nodulation and N₂ fixation has been found (Montealegre et al., 1995). Bliss (1993) observed that the selection and breeding of common bean cultivars tolerant to salinity could improve nodulation and N₂ fixation. Thus, the selection of improved chickpea cultivars with salt-tolerant symbioses is an absolute necessity to enable its cultivation in salt-affected soils. Available reports indicate that legumes show improved
yield and nodulation when co-inoculated with plant-growth-promoting rhizobacteria (PGPR) under hostile environmental conditions compared to inoculation with rhizobia alone (Rokhzadi et al., 2008; Yang et al., 2009; Jabborova et al., 2013b).

This chapter examines recent studies on the impact of salt and drought stresses on legumes and the genotypic variation among legumes for germination, seedling growth and other plant traits under hostile conditions, and the microbial technologies that can improve growth, development and symbiotic performance of legumes. In addition, some possible mechanisms of plant resistance to stress, growth stimulation and improved symbiotic performance by rhizobacteria are described.

9.2 Abiotic stresses affecting legume crop productivity

9.2.1 Plant growth and stress

Previous studies have shown that soil salinity and drought decrease rhizobial colonization, inhibit infection processes and nodule development, and reduce N₂ fixation and nitrogenase activity in legumes (Zahran & Sprent, 1986; Zahran, 1999; Kulkarni et al., 2000; Serraj, 2002; Egamberdieva et al., 2013b). In earlier reports the inhibition by salinity of growth, nodulation and N fixation was observed in chickpea (Singh et al., 2001), common bean (Ferri et al., 2000) and lentil (Golezani & Yengab, 2012). In subsequent studies, saline soil conditions inhibited germination and seedling growth, nodulation and biomass accumulation in soybean (Essa, 2002; Li et al., 2006). Similar findings were observed for soybean by Hamayun et al. (2010), where the plant length, biomass, chlorophyll content, number of pods, 100-seed weight and yield were all significantly reduced by salinity stress. Leaf chlorosis, leaf bleaching and necrosis were also observed as effects of salt stress on soybean (Parker et al., 1987). In lentil, plant growth and nodulation were significantly reduced over the whole growing season under saline soil conditions (Van Hoorn et al., 2001). The decreased nodule formation resulted in reduction of leghaemoglobin content and N₂ fixation activity (Parida & Das, 2005). Limitation of oxygen diffusion in the nodules could be the reason for inhibition of nitrogenase activity and respiration of the nodules (Serraj et al., 1995). Further, salt stress affects protein synthesis, lipid metabolism and photosynthesis, and reduces the growth of roots and root hairs, thereby decreasing sites for potential rhizobial infection and further nodule development (Katerji et al., 2001; Bouhmouch et al., 2005). The decrease in root growth was related to endogenous levels of phytohormones such as gibberellins, abscisic acid, jasmonic acid and salicylic acid, which declined under NaCl-induced salt stress (Debez et al., 2001).

Several reports have indicated that germination and seedling growth of chickpea are reduced in saline soils, with responses varying according to cultivars (Gandour, 2002; Al-Mutawa, 2003). Krouma (2009) evaluated the growth, nodulation, nitrogen fixation and ionic repartition in two chickpea varieties, and found that the salt-tolerant cultivar was able to protect its photosynthetic and symbiotic apparatus against the toxic Na⁺and Cl⁻ions.

We have also observed a significant effect of salinity (salt concentration) on germination, and on shoot and root length of chickpea genotypes (Table 9.1). The 29 genotypes differed significantly for germination and shoot and root length. There was a significant genotype × salinity interaction on germination and shoot and root length. According to Almansouri et al. (2001), seed germination is usually the most critical stage in seedling establishment. According to Sadiki and Rabih (2001), chickpea is a salt-sensitive species, and conditions of 25 mM NaCl resulted in a 71% reduction in growth. We have also observed that most chickpea genotypes were salt sensitive, with germination capacity decreasing with increasing salinity. The present result agrees with the work of Gandour (2002) and Vadez et al. (2007), who observed decreases in percentage germination and seedling emergence of chickpea with increases in salinity. Atak et al. (2006) and Neamatomallahi et al. (2009) pointed out that higher salinity may reduce germination due to higher osmotic pressures. The seeds of six chickpea genotypes, namely Jahongir, Uzbekiston-32, Lazzat, Zimiston, Flip 1-22 and Flip 1-31, showed better germination (40–45%) than other chickpea genotypes. According to Tejovathi et al. (1988) the ability of a seed to germinate under salt stress indicates that it has genetic potential for salt tolerance. The 29 genotypes of chickpea differed in their response to different salinity levels (Table 9.2).

The reduction in seed germination rate (at 10 days after sowing), as compared to the respective controls, was less than 25% for Sino, Flip 1-01, Flip 1-04, Flip 1-05, Flip 1-19, Flip 03-27c and Flip 06-155c. Seeds of
Table 9.1  Germination* of various soybean genotypes 2, 6 and 10 days after sowing in Petri dishes at different concentrations of NaCl.

| Variety         | 2 days |       |       | 6 days |       |       | 10 days |       |
|-----------------|--------|-------|-------|--------|-------|-------|---------|-------|
|                 | 0 5.0  | 10.0  | 0 5.0  | 10.0  | 0 5.0  | 10.0  |
| Jahongir        | 5.3    | 4.8   | 2.5   | 12.0   | 11.5  | 4.0   | 14.5    | 12.5  | 8.5   |
| Uzbekistan-32   | 11.0   | 6.0   | 2.8   | 15.3   | 13.5  | 4.3   | 16.5    | 14.3  | 8.0   |
| Lazzat          | 5.8    | 5.0   | 4.5   | 10.3   | 6.0   | 6.3   | 15.3    | 10.0  | 8.3   |
| Zimistoni       | 10.3   | 9.0   | 3.8   | 12.8   | 13.3  | 4.0   | 18.3    | 15.0  | 9.0   |
| Xalima          | 4.3    | 6.0   | 0.1   | 9.5    | 9.3   | 2.5   | 16.8    | 15.0  | 6.5   |
| Miroz           | 4.0    | 2.3   | 0.5   | 7.5    | 4.8   | 2.3   | 17.3    | 11.3  | 6.3   |
| Muqtadir        | 4.5    | 5.5   | 3.3   | 7.0    | 7.3   | 4.5   | 9.0     | 8.3   | 5.3   |
| Xisor-32        | 8.8    | 8.0   | 3.8   | 9.0    | 8.0   | 5.8   | 9.3     | 8.8   | 6.5   |
| Sino            | 3.5    | 2.8   | 1.0   | 7.0    | 5.3   | 2.3   | 8.0     | 7.0   | 3.3   |
| Flip 1-01       | 7.5    | 2.8   | 1.3   | 10.0   | 4.8   | 3.0   | 13.8    | 10.5  | 4.0   |
| Flip 1-04       | 3.8    | 2.8   | 0.8   | 7.5    | 4.3   | 2.3   | 14.0    | 11.0  | 4.8   |
| Flip 1-05       | 3.0    | 0.8   | 0.3   | 5.5    | 4.3   | 1.0   | 12.3    | 9.5   | 2.8   |
| Flip 1-19       | 7.8    | 4.8   | 0.3   | 12.8   | 10.5  | 2.5   | 19.0    | 16.3  | 5.0   |
| Flip 1-21       | 7.5    | 5.0   | 3.8   | 11.0   | 8.3   | 5.5   | 19.3    | 15.8  | 7.5   |
| Flip 1-22       | 12.3   | 8.8   | 2.0   | 14.8   | 11.3  | 3.0   | 18.8    | 15.0  | 8.3   |
| Flip 1-29       | 9.0    | 7.8   | 1.5   | 12.0   | 9.0   | 2.3   | 17.5    | 15.3  | 5.3   |
| Flip 1-31       | 2.8    | 2.8   | 0.8   | 6.5    | 5.3   | 3.8   | 15.0    | 11.3  | 8.5   |
| Flip 1-33       | 13.8   | 4.5   | 1.8   | 17.0   | 12.3  | 4.3   | 19.3    | 17.0  | 6.3   |
| Flip 03-102c    | 6.5    | 6.0   | 3.5   | 8.3    | 7.8   | 4.3   | 10.3    | 9.3   | 5.5   |
| CIEW-45         | 6.0    | 7.0   | 6.0   | 9.0    | 8.8   | 8.8   | 10.3    | 9.3   | 8.8   |
| Flip 05-69c     | 5.3    | 3.5   | 5.0   | 7.5    | 7.0   | 5.0   | 9.3     | 8.8   | 6.3   |
| Flip 03-74c     | 5.0    | 5.0   | 4.5   | 7.5    | 6.5   | 6.3   | 9.0     | 8.0   | 6.8   |
| Flip 06-102c    | 4.8    | 4.5   | 4.0   | 6.5    | 7.5   | 6.3   | 9.5     | 9.0   | 7.0   |
| Flip 06-66      | 5.5    | 6.0   | 5.0   | 8.5    | 7.0   | 6.3   | 10.3    | 9.5   | 7.8   |
| Flip 05-65      | 5.0    | 6.5   | 5.8   | 7.0    | 8.3   | 6.5   | 9.8     | 10.0  | 7.3   |
| Flip 06-124c    | 6.3    | 7.0   | 6.0   | 8.8    | 7.8   | 6.0   | 9.8     | 9.0   | 7.0   |
| Flip 06-80c     | 8.0    | 7.8   | 6.5   | 9.0    | 8.5   | 7.3   | 9.5     | 9.3   | 8.8   |
| Flip 03-27c     | 7.5    | 6.5   | 1.3   | 8.0    | 7.5   | 2.8   | 9.8     | 8.8   | 3.0   |
| Flip 06-155c    | 1.5    | 5.5   | 1.8   | 2.8    | 7.3   | 4.3   | 3.0     | 7.5   | 2.0   |
| LSD (5%)        | 1.4    | 2.0   | 1.4   | 1.4    | 1.8   | 1.4   | 0.6     | 1.8   | 1.4   |
| Mean (%)        | 6.4    | 5.3   | 2.9   | 9.3    | 8.0   | 4.4   | 12.9    | 11.1  | 6.3   |
| CV (%)          | 14.0   | 23.2  | 29.1  | 12.1   | 14.0  | 19.1  | 7.7     | 10.1  | 13.23 |

*Number of germinated seeds.
CV, coefficient of variation; LSD, least significant difference.

Table 9.2  Mean squares from analysis of variance for various plant traits of 29 genotypes of chickpea at three concentrations of NaCl.

| Source                  | df  | Germination | Shoot length | Root length |
|-------------------------|-----|-------------|--------------|-------------|
| Replication             | 2   | 1.7         | 1.9          | 3.1         |
| Concentration           | 2   | 1018.4**    | 1219.3**     | 841.9**     |
| Genotype                | 28  | 66.3**      | 63.9**       | 15.4**      |
| Genotype × concentration| 56  | 16.6**      | 29.8**       | 19.3**      |
| Error                   | 181 | 1.0         | 1.3          | 1.0         |

**Significant at P=0.01.
Jahongir, Uzbekistan-32, Lazzat, Zimistoni, Flip 1-22, Flip 1-31, CIEW-45 and Flip 06-80c showed better germination (40−45%) at 10 dS/m salt concentration than other chickpea genotypes (Table 9.1). Seed germination was decreased slightly with increasing salinity levels for Xisor-32, CIEW-45, Flip 06-66, Flip 06-124c, Flip 06-80c and Flip 03-27c. In contrast, significant differences between NaCl treatments were observed for seed germination ($P<0.05$) at 5 and 10 dS/m.

In our work the increase in salt concentration reduced shoot and root length in all genotypes, and it seemed to reduce the availability of the nutrients required for the growth and development of the plants. Growth response of chickpea to NaCl treatment (0, 5 and 10 dS/m) varied with the genotype, as shown by shoot and root lengths. The influence was more pronounced at 10 dS/m salinity level (Table 9.3). Genotypes Flip 1-04, Flip 1-05, Flip 1-22, Flip 06-66, Flip 03-27c, Flip 06-155c and Sino were

| Genotype               | Root length (cm) | Shoot length (cm) |
|------------------------|------------------|-------------------|
|                        | 0    | 5.0  | 10.0 | 0    | 5.0  | 10.0 |
| Jahongir               | 16.7 | 16.2 | 15.8 | 11.2 | 10.4 | 9.4  |
| Uzbekistan-32          | 14.3 | 13.2 | 13.9 | 10.5 | 14.0 | 9.9  |
| Lazzat                 | 15.1 | 15.2 | 12.1 | 15.8 | 11.9 | 10.5 |
| Zimistoni              | 18.4 | 14.9 | 9.3  | 22.6 | 13.3 | 7.6  |
| Xalima                 | 17.0 | 9.4  | 10.6 | 15.4 | 13.3 | 10.5 |
| Miroz                  | 18.6 | 18.5 | 13.6 | 14.3 | 12.5 | 8.8  |
| Muqtadir               | 15.6 | 14.3 | 11.6 | 10.4 | 9.6  | 7.7  |
| Xisor-32               | 16.2 | 13.4 | 10.5 | 17.6 | 12.8 | 7.8  |
| Sino                   | 19.0 | 14.9 | 0.0  | 19.1 | 13.3 | 0.0  |
| Flip 1-01              | 18.4 | 15.3 | 12.4 | 16.7 | 12.2 | 8.8  |
| Flip 1-04              | 16.4 | 14.0 | 11.7 | 11.7 | 11.8 | 10.5 |
| Flip 1-05              | 19.6 | 15.9 | 6.3  | 11.3 | 13.3 | 9.0  |
| Flip 1-19              | 16.2 | 16.7 | 11.6 | 12.9 | 13.0 | 10.0 |
| Flip 1-21              | 19.8 | 17.1 | 10.9 | 15.5 | 13.8 | 10.2 |
| Flip 1-22              | 7.7  | 6.1  | 5.7  | 12.4 | 10.6 | 8.3  |
| Flip 1-29              | 17.9 | 16.4 | 10.0 | 15.5 | 13.8 | 10.2 |
| Flip 1-31              | 21.2 | 19.7 | 14.4 | 13.9 | 12.1 | 10.0 |
| Flip 1-33              | 13.0 | 11.6 | 10.9 | 14.5 | 11.5 | 8.5  |
| Flip 03-102c           | 16.3 | 16.1 | 11.3 | 13.2 | 11.4 | 8.9  |
| CIEW-45                | 19.6 | 16.9 | 10.8 | 13.5 | 11.3 | 8.8  |
| Flip 05-69c            | 22.5 | 16.9 | 11.4 | 13.1 | 11.3 | 9.0  |
| Flip 03-74c            | 14.2 | 13.2 | 9.9  | 14.5 | 12.2 | 10.2 |
| Flip 06-102c           | 22.0 | 11.0 | 10.5 | 14.5 | 12.0 | 9.8  |
| Flip 06-66             | 12.6 | 11.5 | 6.8  | 14.1 | 11.8 | 8.6  |
| Flip 05-65             | 11.4 | 9.6  | 8.1  | 12.2 | 9.8  | 9.2  |
| Flip 06-124c           | 18.1 | 15.8 | 10.4 | 11.9 | 11.6 | 9.3  |
| Flip 06-80c            | 22.2 | 15.6 | 14.2 | 18.7 | 13.3 | 8.7  |
| Flip 03-27c            | 16.1 | 14.3 | 0.0  | 16.7 | 13.2 | 0.0  |
| Flip 06-155c           | 24.7 | 5.4  | 0.0  | 14.5 | 11.2 | 0.0  |
| LSD (5%)               | 2.4  | 1.6  | 1.5  | 1.6  | 1.8  | 1.1  |
| Mean                   | 17.7 | 14.2 | 10.0 | 14.4 | 12.2 | 8.0  |
| CV(%)                  | 8.4  | 6.9  | 9.3  | 0    | 9.0  | 1.8  |

CV, coefficient of variation; LSD, least significant difference.
found to be salt-sensitive whereas genotypes Jahongir, Uzbekistan-32, Xalima, Miroz, Xisor 32 and Flip 06-102 were found to be salt-tolerant at 10 dS/m salinity level. There was a significant interaction between salt and shoot and root growth \((P<0.05)\) (Table 9.2).

However, other genotypes remained intermediate in their salt tolerance with respect to seedling shoot and root length. This would suggest the possibility of exploiting genotypic variation in chickpea for tolerance to specific concentrations of salts. The present observations are in line with earlier reports in bean (Kaymakanova, 2009), ground nut (Mensah et al., 2006) and chickpea (Al-Mutawa, 2003), where increased salinity also led to decreased radicle lengths.

Salinity also affects uptake by plants of nutrients such as phosphorus, nitrogen and potassium (Egamberdiyeva & Hoflich 2004). According to Van Hoorn et al. (2001) salinity strongly reduced soil nitrogen content, probably through inhibiting nitrogen fixation and soil biological activity responsible for transformation of organic nitrogen. Salehi et al. (2008) reported that salt stress reduced plant dry weight, nitrogen content and the number of active nodules in alfalfa cultivars.

9.2.2 Rhizobia-legume symbiosis and stress

It has been reported that the colonization and infection of root hairs by rhizobial cells is sensitive to environmental stresses (Zahran, 1999; Räsänen et al., 2003). Several environmental stresses, including salinity, drought, extreme temperature and nutrient deficiency, are known to decrease survival and proliferation of rhizobia in the rhizosphere, and inhibit the infection process leading to symbiotic association with their plant host (Biswas et al., 2008; Ali et al., 2009). Salt inhibits the absorption of Ca, which reduces the growth of roots, root tips and root hairs, thereby decreasing sites for potential rhizobial infection and further nodule development (Bouhmouch et al., 2005). The number of rhizobial cells was found to be reduced in the root of soybean, common bean and chickpea grown under salt stress conditions (Zahran & Sprent, 1986; Bouhmouch et al., 2005).

We have also observed that increased salt content decreased the ability of Rhizobium galegae sv. officinalis cells to colonize goat's rue roots (Egamberdieva et al., 2013b). Similar observations were made about the decrease of root colonization of liquorice (Glycyrrhiza uralensis) by Mesorhizobium sp. under salt stress, where a salt concentration of 100 mM NaCl totally inhibited bacterial survival (Figure 9.1).

However, the species vary in tolerance to environmental stresses (Sridhar et al., 2005; Wei et al., 2008; Biswas et al., 2008). The rhizobial strains from various grain legumes may tolerate 100–300 mM concentrations of NaCl (Predeepa & Ravindran, 2010). Leguminous plants growing in saline environments require both the rhizobia and the host to be tolerant to salt. The salt tolerance of rhizobia is important for improved symbiotic performance of legumes under stress conditions, where they may enhance the nodulation and nitrogen fixation ability of plants (Shamseldin & Werner, 2005; Ali et al., 2009). Salt-tolerant strains of rhizobia improved the salt tolerance of host plants (Zou et al., 1995; Hashem et al., 1998; Shamseldin & Werner, 2005). Zahran (1999) reported that rhizobia use distinct mechanisms for osmotic adaptation to salt stress. Rüberg et al. (2003) reported the accumulation of low-molecular-weight organic solutes (osmolytes) by rhizobia to equilibrate internal and external osmotic concentrations under salt stress.

9.3 Improving legume yield by inoculation with rhizobacteria

The utilization of root-associated bacteria that interact with plants to mitigate the effects of various stresses opens a novel, inexpensive and advanced technology for

*Figure 9.1 The effect of NaCl concentration on the colonization of Mesorhizobium sp. in the rhizosphere of Glycyrrhiza uralensis.*
combating the problems of salinity (Egamberdieva & Hoflich, 2003; Berg et al., 2010; Pliego et al., 2011; Lugtenberg et al., 2013). In our previous work, we reported increased dry matter yield, nodulation, seed yield and protein content of soybean seeds grown under saline soil after inoculation with salt-tolerant strains of Bradyrhizobium spp. (Egamberdieva et al., 2004). Similar results were observed for chickpea, where shoot, root length and dry matter increased after inoculation of PGPR strain under stressful soil conditions (Mishra et al., 2010).

The tripartite bacterial-mycorrhizal-legume symbiosis also showed improvement in legume growth and development under stressful conditions. For example, Estévez et al. (2009) observed that co-inoculation of Rhizobium tropici CIAT899 with Chryseobacterium balusti-
nunum Aur9 improved growth and symbiotic performance of salt-stressed soybeans compared with the single inoculation (CIAT899). Molla et al. (2001) also showed that total root length, root number, dry matter, root hair development, number of nodules and shoot dry matter of soybean were significantly increased by Azospirillum lipoferum and Bradyrhizobium japonicum. Dardanelli et al. (2008) also observed improved rhizo-
bio-legume symbioses under saline conditions by co-inoculation of common bean with Rhizobium and Azospirillum strains.

Dual inoculation of Rhizobium with Azotobacter showed increased nodulation and plant growth of faba bean under drought conditions (Dashadi et al., 2011). Han and Lee (2005) also observed alleviation of induced stress in plants and improvement in root and shoot growth of soybean by dual inoculation with Bacillus sub-
tilis and Bradyrhizobium japonicum.

There are also several reports on the improvement of nodulation and plant growth of legumes by phosphate-solubilizing bacteria. For example, Rosas et al. (2006) reported on the positive effect of phosphate-solubilizing bacteria Bradyrhizobium japonicum and Pseudomonas putida on the root and shoot growth of soybean. Similar results were observed by Kumar and Chandra (2008), who showed that phosphate-solubilizing bacteria improved the symbiotic performance of introduced rhizobia in field-grown lentils. In another study, Pseudomonas spp. inoculated together with rhizobia significantly increased the number of pods per plant, number of seeds per pod per plant and seed yield per hectare of soybean (Argaw, 2012). Phosphate-solubilizing bacteria (PSB) are known to help plants to acquire more phosphorus from soil, thus stimulating P uptake by plants and also improving nodulation and nitrogen fixation (Elkoca et al., 2008). El-Azouni (2008) observed significant increases of dry matter, N and P uptake and yield of soybean grown in Egyptian soil inoculated with the phosphate-solubilizing fungi Aspergillus niger and Penicillium italicum. In another study, the sulphur-oxidizing bacteria Thiobacillus sp. stimulated nodule number, plant biomass and yield of groundnut, and increased soil available S (Anandham et al., 2007).

Rabie and Almadini (2005) observed that the dual inoculation of faba bean (Vicia faba) with nitrogen-fixing bacteria (NFB) Azospirillum brasilense and the arbuscular mycorrhizal (AM) fungus Glomus clarum increased salt tolerance of plants and improved growth and development under saline conditions. In their study significant effects of inoculation were reported in the plants for salinity tol-
erance, mycorrhizal dependency, phosphorus level, phosphatase enzymes, nodule number, nitrogen uptake, protein content and nitrogenase enzymes.

A greenhouse experiment demonstrated that the salt tolerance of goat’s rue was clearly improved when the plant was inoculated with its own specific symbiont Rhizobium galegae sv. officinalis and Pseudomonas extremor-ientalis TSAU20 (Egamberdieva et al., 2013). Dual inoculation with Rhizobium and plant growth-promoting rhizobacteria (PGPR) Pseudomonas could also enhance formation of nodules on soybean grown in salinized potting soil. In recent studies, Aamir et al. (2013) demo-
strated that combined inoculation of mung bean enhanced nodulation, grain yield (up to 30%) and protein content (up to 48%) compared to an individually inoculated control.

The survival of introduced PGPR strains in the roots of legumes is important, as bacteria may deliver biologically active compounds directly to the rhizosphere of plants. We have investigated the effect of salinity on the colonization of two selected plant-growth-promoting bacteria P. extremorientalis TSAU20 and P. chlororaphis TSAU13 in the rhizosphere of common bean, using a gnotobiotic sand system, and determined their survival on the plant roots in pot experiments under salinated soil conditions (Egamberdieva, 2011). Results showed that bacterial strains were able to colonize the rhizo-
sphere of bean at the highest salinity (12.5 dS/m) and were also able to survive in the root of bean grown in saline soil.
9.4 Biomechanisms regulating growth and development

Although the mechanisms playing in the PGPR stimulation of plant growth are not yet well understood, it is likely that PGPR can promote plant growth through several different mechanisms, which might function in tandem or separately, and depend on the species of plant and bacteria, the environment, and the nature and degree of stress (Ashraf et al., 2004; Adesemoye & Egamberdieva, 2013; Berg et al., 2013). Mechanisms by which bacteria are able to promote plant growth and prevent physiological plant disorders caused by salinity include production of phytohormones like indole acetic acid (IAA), gibberellic acid and cytokinins (Mishra et al., 2010), solubilization of phosphates and micronutrients (Medeot et al., 2010), production of 1-aminocyclopropane-1-carboxylate (ACC) deaminase to reduce the level of stress ethylene in the roots (Dey et al., 2004) and symbiotic nitrogen fixation (Ardakani et al., 2009). It has also been reported that PGPR strains can produce exopolysaccharides (EPSs), which may bind Na and decrease the content of Na available for plant uptake. Dardanelli et al. (2008) suggested that inoculation with Azospirillum spp. combined with rhizobia in common bean induced the synthesis of flavonoids by roots.

9.4.1 Phytohormone production

Phytohormones play an important role in plant physiology, and regulate many aspects of plant development, including the differentiation of vascular tissues, elongation growth, apical dominance, lateral root initiation, and stress responses and adaptation (Sharma et al., 2005; Egamberdieva, 2009; Javid et al., 2011). The exogenous application of auxins to alfalfa (Gruodien & Zvironaite, 1971), groundnut (Srinivasan & Gopal, 1977) and mung bean (Hayat et al., 2008) promoted plant growth and nodulation. Abiotic stresses inhibit phytohormone synthesis in plants, resulting in decreased plant growth and development. According to Figueiredo et al. (2008) drought stress causes a change in the balance of plant hormones, like cytokinin, zeatin, IAA and gibberellins in common bean. Phytohormones produced by root-associated bacteria will be taken up by plant cells, and can stimulate plant cell proliferation; this mechanism might be responsible for the enlarged root system and increased number of infection sites prior to nodulation, especially under stressed conditions (Tanimoto, 2005; TIlak et al., 2006; Jabborova et al., 2013a). Root-associated bacteria synthesize and release phytohormones such as auxins and gibberellins as secondary metabolites because of the rich supplies of substrates exuded from the roots (Egamberdieva & Hoflich, 2002; Tsavkelova et al., 2007; Shahab et al., 2009). Nutman (1977) reported that the IAA-producing abilities of Rhizobium strains have a positive influence on plant growth and also play an important role in the formation and development of root nodules. In another study Sridevi and Mallaiah (2007) reported IAA production by 26 Rhizobium strains isolated from the root nodules of the green manure crop, Sesbania sesban.

The comparative effects of auxin (IAA) and IAA-producing bacteria on the amelioration of salt stress on seedling growth of soybean under saline conditions were studied by Jabborova et al. (2013b). They observed that seedling growth of soybean was inhibited at 100 mM NaCl concentration and salt stress reduced the length of root by up to 56%. The plant growth regulator IAA did reverse the growth-inhibiting effect of salt stress to a certain extent in both shoot and root, whereas the IAA-producing bacterial strain Pseudomonas putida TSAU1 significantly increased seedling root growth by up to 29% in non-salinated conditions and by up to 86% at 100 mM NaCl compared to control plants. This study suggests that the application of low concentrations of auxin (IAA) or IAA-producing bacteria may improve the growth of soybean seedlings, which could enhance the tolerance of plants to soil salinity.

9.4.2 ACC (1-aminocyclopropane-1-carboxylate) deaminase

Ethylene is one of the endogenous hormones that play important roles in plant growth and development. Its production by plants is also considered as one of the stress responses, and is closely associated with various stress factors such as salinity, drought, metal toxicity and nutrient deficiency (Lynch & Brown, 1997; Schmidt, 2001; Li et al., 2009). It has been reported that in leguminous plants, extra ethylene production inhibits nodulation by rhizobia (Hirsch & Fang, 1994). The level of ethylene in stressed plants can be reduced by ACC deaminase enzyme, which can cleave the ethylene precursor ACC to α-ketobutyrate and ammonium (Hontzeas et al., 2005; Glick et al., 2007). It has been reported that many root-colonizing PGPR have the ability to produce ACC deaminase and may enhance the survival of
seedlings under stressed conditions (Glick et al., 1998). We have also observed in our previous work that *Pseudomonas trivialis* 3Re27 was able to utilize ACC as an N source, indicating the presence of ACC deaminase, and thereby increase the salt tolerance of goat’s rue under salinated soil conditions (Egamberdieva et al., 2013b). Similar results were observed by Shaharoona et al. (2006), who reported that co-inoculation of *Bradyrhizobium* with PGPR isolates possessing ACC deaminase activity enhanced nodulation in mung bean compared with inoculation with *Bradyrhizobium* alone. In another study Ma et al. (2003) reported that ACC deaminase-producing *R. leguminosarum* could lower ethylene production in pea roots and improve nodulation. Similar results were observed for lentil (Shahzad et al., 2010; Zahir et al., 2011) and chickpea (Aslam et al., 2010). Arshad et al. (2008) studied the effect of ACC deaminase-producing PGPR strains on plant growth of pea under water stress conditions, and found that plant inoculation with PGPR decreased the effects of water stress and improved plant growth and yield. PGPR strains that produce ACC deaminase showed positive effects on plant growth of chickpea (Roopa et al., 2012) and lentil (Zafar-ul-Hye et al., 2013), resulting in increased number of nodules, root and shoot growth, and yield of plant under stressful conditions.

### 9.4.3 Cell wall degrading enzymes

The complete erosion of the plant cell wall through which the bacterial symbiont penetrates to establish an intracellular endosymbiotic relationship with the host is a key event of the infection process (Robledo et al., 2008). Cellulase enzyme may help rhizobia penetrate more easily into intercellular spaces of root cells, which may result in development of more nodules. Sindhu and Dadarwal (2001) explained the improvement of nodulation and symbiotic performance of rhizobia in legumes through production of hydrolytic enzymes such as cellulases by root-colonizing *Pseudomonas* strains. In their study, co-inoculations of five cellulase-producing *Pseudomonas* strains with *Mesorhizobium* increased the number of nodules and especially nodule biomass in chickpea. Robledo et al. (2008) showed that both the cell-bound cellulase enzyme from *R. leguminosarum* bv. *trifolii* and the purified enzyme could erode cell walls at the tip of the root hair of the host, white clover, making a localized hole of sufficient size to allow rhizobial cell penetration. Co-inoculation of the cellulase-producing strain *P. trivialis* 3Re27 with *R. galegae* HAMBI 540 significantly increased nodulation and nitrogen content of fodder galega, whereas cellulase-negative *P. extremorientalis* TSAU20 showed no significant stimulation (Egamberdieva et al., 2010).

### 9.5 Conclusions and future prospects

The negative effect of abiotic factors such as salinity on plant growth, development and yield has been described by many studies. Agricultural biotechnology, particularly the use of rhizobia or consortia of plant-beneficial microbes, can be an effective approach for enhancing a plant’s tolerance to adverse environmental stresses, increasing legume productivity and the supply of biologically fixed N at low cost under stressed conditions. Several mechanisms of action are used by PGPR to alleviate salt stress, improve symbiotic performance of legumes and stimulate plant growth; however, more detailed studies are needed on the induction of salt stress tolerance at the plant tissue, cell and molecular levels. Recent studies have demonstrated that tripartite bacterial-legume symbioses represent the best microbial strategy for arid and saline regions, and are of great interest as the subject of future research. Revelations about the mechanisms of PGPR action on improving legume symbioses open new doors for improving the efficacy of microbial strategies under harsh environments.

### References

Aamir M, Aslam A, Khan MY, et al. (2013) Co-inoculation with *Rhizobium* and plant growth promoting rhizobacteria (PGPR) for inducing salinity tolerance in mung bean under field condition of semi-arid climate. *Asian J Agri Biol* 1: 17–22.

Adesemoye AO, Egamberdieva D (2013) Beneficial effects of plant growth promoting rhizobacteria on improved crop production: the prospects for developing economies. In: Maheshwari DK, Saraf M, Aeron A (eds), *Bacteria in Agrobiology: Crop Productivity*. Springer-Verlag, Berlin, Heidelberg, pp. 45–63.

Anandham R, Sridar R, Nalayini P, Poonguzhali S, Madhaiyan M, Tongminsia (2007) Potential for plant growth promotion in groundnut (*Arachis hypogaea* L.) cv. ALR-2 by co-inoculation of sulfur-oxidizing bacteria and *Rhizobium*. *Microb Res* 162: 139–153.

Alberton O, Kaschuk G, Hungria M (2006) Sampling effects on the assessment of genetic diversity of rhizobia associated with soybean and common bean. *Soil Biol Bioch* 38: 1298–1307.
Ali B, Hayat S, Fariduddin Q, Ahmad A (2009) Nickel: essentiality, toxicity and tolerance in plants. In: Ali B, Hayat S, Ahmad A (eds), Nickel in Relation to Plants. Narosa Publishing House, India, pp. 69–88.

Almansouri M, Kinet JM, Lutts S (2001) Effect of salt and osmotic stresses on germination in durum wheat (Triticum durum Desf.). Plant Soil 231: 243–254.

Al-Mutawa MM (2003) Effect of salinity on germination and seedling growth of chickpea (Cicer arietinum L.) genotypes. Int J Agro Biol 5: 227–229.

Arshad M, Shaharoona B, Mahmood T (2008) Inoculation with plant growth promotion rhizobacteria containing ACC-deaminase partially eliminates the effects of water stress on growth, yield and ripening of Phaseolus sativum L. Pedosphere 18: 611–620.

Ashraf M, Berge SH, Mahmood OT (2004) Inoculating wheat seedlings with exopolysaccharide producing bacteria restricts growth, yield and nutrient composition in four grain legumes-Rhizobium symbiosis. J Plant Nutr 27: 1595–1609.

Chauhan MP, Singh IS (2000) Variability estimates and identifying chick pea genotypes for yield and yield attributes in salt affected soil. Legume Res 23: 199–200.

Cordovilla MP, Ocana A, Ligero F, Lluch C (1995) Salinity effects on growth analysis and nutrient composition in four grain legumes-Rhizobium symbiosis. J Plant Nutr 18: 1595–1609.

Dardanelli M, Fernández de Córdoba F, Espuny M, et al. (2008) Effect of Azospirillum brasilense co-inoculated with Rhizobium on Phaseolus vulgaris flavonoids and Nod factor production under salt stress. Soil Biol Bioch 40: 2713–2721.

Davranova N, Egamberdieva D, Ismatov Z, Wirth S (2013) Impact of crop management practice on soil microbial populations in a semi-arid soil of Uzbekistan. Soil Water J 2: 921–927.

Debez A, Chaibi W, Bouzid S (2001) Effect du NaCl et de régulateurs de croissance sur la germination d’Atriplex halimus L. Cahiers Agr 10: 135–138.

Dey R, Pal KK, Bhatt DM, Chauhan SM (2004) Growth promotion and yield enhancement of peanut (Arachis hypogaea L.) by application of plant growth-promoting rhizobacteria. Microbes Res 159: 371–394.

Dua RP (1992) Differential response of chickpea (Cicer arietinum L.) genotypes to salinity. J Agric Sci 119: 367–371.

Egamberdieva D (2009) Alleviation of salt stress by plant growth regulators and IAA producing bacteria in wheat. Acta Phys Plant 31: 861–864.

Egamberdieva D (2011) Survival of Pseudomonas extremorientalis TSU20 and P. chlororaphis TSU13 in the rhizosphere of common bean (Phaseolus vulgaris) under saline conditions. Plant Soil Env 57: 122–127.

Egamberdieva D, Hofflich G (2002) Root colonization and growth promotion of winter wheat and pea by Cellulosomonas spp. at different temperatures. J Plant Growth Reg 38: 219–224.

Egamberdieva D, Hofflich G (2003) Influence of growth promoting bacteria on the growth of wheat at different soils and temperatures. Soil Biol Bioch 35: 973–978.

Egamberdieva D, Hofflich G (2004) Importance of plant growth promoting bacteria on growth and nutrient uptake of cotton and pea in semi-arid region Uzbekistan. J Arid Env 56: 293–301.

Egamberdieva D, Qarshieva D., Davranov K (2004) The use of Bradyrhizobium japonicum to enhance growth and yield of soybean varieties in Uzbekistan conditions. Plant Growth Reg 23: 54–57.

Egamberdieva D, Gafurova L, Ismail KR (2007) Salinity effects on irrigated soil chemical and biological properties in the Syr Darya basin of Uzbekistan. In: Lal R, Sulaimanov M, Stewart B, Hansen D, Doraismwamy P (eds), Climate Change and Terrestrial C Sequestration in Central Asia. Taylor-Francis, New York, pp. 147–162.

Egamberdieva D, Berg G, Lindstrom K, Rasaran L (2010) Root colonizing Pseudomonas spp. improve growth and symbiosis...
performance of fodder galega (Galega orientalis LAM) grown in potting soil. *Eur J Soil Biol* 46: 269–272.

Egamberdieva D, Jabborova D, Wirth S (2013a) Alleviation of salt stress in legumes by co-inoculation with *Pseudomonas* and *Rhizobium*. In: Arora NK (ed.), *Plant Microbe Symbiosis – Fundamentals and Advances*. Springer India, pp. 292–299.

Egamberdieva D, Berg G, Lindström K, Räsaänen LA (2013b) Alleviation of salt stress of symbiotic Galega officinalis L. (goat’s rue) by co-inoculation of rhizobium with root colonizing *Pseudomonas*. *Plant Soil* 369: 453–465.

El-Azouni I (2008) Effect of phosphate solubilizing fungi on growth and nutrition uptake of soybean (Glycine max L.). *Plants J Appl Sci Res* 4: 592–598.

Elkoca E, Kantar F, Sahin F (2008) Influence of nitrogen fixing and phosphorus solubilizing bacteria on the nodulation, plant growth, and yield of chickpea. *J Plant Nutr* 31: 157–171.

Essa TA (2002) Effect of salinity stress on growth and nutrient composition of three soybean (Glycine max (L.) Merrill) cultivars. *J Agron Crop Sci* 188: 86–93.

Estévez J, DardANELLI MS, Megías M, Rodriguez-Navarro DN (2009) Symbiotic performance of common bean and soybean co-inoculated with rhizobia and *Chryseobacterium balustinum* Aur9 under moderate saline conditions. *Symbiosis* 49: 29–36.

Ferri A, Lluch C, Ocana A (2000) Effect of salt stress on carbon metabolism and bacteroid respiration in root nodules of common bean (*Phaseolus vulgaris* L.). *Plant Biol* 2: 396–402.

Figueiredo MVB, Martinez CR, Burity HA, Chanway CP (2008) Plant growth promoting rhizobacteria for improving nodulation and nitrogen fixation in the common bean (*Phaseolus vulgaris* L.). *World J Micr Biotech* 24: 1187–1193.

Gandour G (2002) Effect of salinity on development and production of chickpea genotypes. PhD thesis, Aleppo University, Syria.

Glick BR, Penrose DM, Li JA (1998) Model for the lowering of plant ethylene concentrations by plant growth promoting bacteria. *J Theor Biol* 190: 63–68.

Glick BR, Cheng Z, Czarny J, Duan J (2007) Promotion of plant growth by ACC deaminase producing soil bacteria. *Eur J Plant Pathol* 119: 329–339.

Godfray HCJ, Beddington JR, Crute IR, et al. (2010) Food security: the challenge of feeding 9 billion people. *Science* 327: 812–818.

Golezani KG, Yengabad FM (2012) Physiological responses of soybean – inoculation of Bradyrhizobium japonicum with PGPR in saline soil conditions. *Res J Agr Biol Sci* 1: 216–221.

Hashem FM, Swelim DM, Kuykendall LD, Mohamed AI, Abdel-Wahab SM, Hegazi NI (1998) Identification and characterization of salt- and thermo-tolerant *Leucaena*-nodulating *Rhizobium* strains. *Biol Fert Soils* 27: 335–341.

Hayat R, Ali S, Ijaz SS, Chatha TH, Siddique MT (2008) Estimation of N₂-fixation of mung bean and mash bean through xylem ureide technique under rainfed conditions. *Pak J Bot* 40: 723–734.

Hirsch AM, Fang Y (1994) Plant hormones and nodulation: what’s the connection? *Plant Mol Biol* 26: 5–9.

Hontzeas N, Richardson AO, Belimov A, Safronova V, Abu-Omar MM, Glick BR (2005) Evidence for horizontal transfer of 1-aminoacyclopropane-1-carboxylate deaminase genes. *Appl Env Microb* 71: 7556–7558.

Jabborova D, Qodirova D, Egamberdieva D (2013a) Improvement of seedling establishment of soybean using IAA and IAA producing bacteria under saline conditions. *Soil Water J* 2: 531–539.

Jabborova D, Egamberdieva D, Räsaänen L, Liao H (2013b) Salt tolerant *Pseudomonas* strain improved growth, nodulation and nutrient uptake of soybean under hydroponic salt stress condition. In: *XVII International Plant Nutrition Colloquium and Boron Satellite Meeting Proceedings Book*. Sabanci University, Istanbul, pp. 260–261.

Javid MG, Sorooshzadeh A, Moradi F, Modares Sanavy AM, Allahdadi I (2011) The role of phytohormones in alleviating salt stress in crop plants. *Aust J Crop Sci* 5: 726–734.

Katerji N, Van Hoorn JW, Hamdy A, Mastrorelli M (2001) Salt tolerance of crops according to three classification methods and examination of some hypotheses about salt tolerance. *Agr Water Man* 47: 1–8.

Kaymakanova M (2009) Effect of salinity on germination and seed physiology in bean (*Phaseolus vulgaris L.*). *Biotech Equip* 23: 326–329.

Krouma A (2009) Physiological and nutritional responses of chickpea (*Cicer arietinum L.*) to salinity. *J Agric For* 33: 503–512.

Kulkarni S, Sarangnath PA, Salaliknop SP, Goddi AV (2000) Response of chickpea to rock phosphate and phosphate solubilizers in typic chromustert. *Legume Res* 23: 21–24.

Kumar R, Chandra R (2008) Influence of PGPR and PSB on *Rhizobium leguminosarum* bv. *viciae* strain competition and symbiotic performance in lentil. *World J Agr Sci* 4 (Suppl 3): 297–301.

Li H, Wong WS, Zhu L, Guo HW, Ecker J, Li N (2009) Phosphoproteomic analysis of ethylene-regulated protein phosphorylation in etiolated seedlings of Arabidopsis mutant ein2 using two-dimensional separations coupled with a hybrid quadrupole time-of-flight mass spectrometer. *Proteomics* 9: 1646–1661.

Li X, An P, Inanaga S, Enejci AE, Tanabe K (2006) Salinity and defoliation effects on soybean growth. *J Plant Nutr* 29: 1499–1508.

Lugtenberg B, Mallanova N, Kamilova F, Berg G (2013) Plant growth promotion by microbes. In: de Bruijn FJ (ed.), *Molecular Microbial Ecology of the Rhizosphere*. Wiley-Blackwell, Hoboken, pp. 561–573.

Lüscher A, Soussana JF, Huguenin-Elie O (2011) Role and function of *Pseudomonas* and *Bacillus* in plant growth promotion by microbes. In: de Bruijn FJ (ed.), *Molecular Microbial Ecology of the Rhizosphere*. Springer India, pp. 292–299.

Lugtenberg B, Malfanova N, Kamilova F, Berg G (2013) Plant growth promoting rhizobacteria for improving nodulation and nitrogen fixation in *Phaseolus vulgaris* L. (*Phaseolus vulgaris* L. genotypes). *Deserti Biotech* 2: 396–402.

Lugtenberg B, Malfanova N, Kamilova F, Berg G (2013) Plant growth promoting rhizobacteria for improving nodulation and nitrogen fixation in *Phaseolus vulgaris* L. (*Phaseolus vulgaris* L. genotypes). *Deserti Biotech* 2: 396–402.
gain from symbiotic N2 fixation. In: Lemaire G, Hodgson J, Chabbi A (eds), Grassland Productivity and Ecosystem Services. CAB International, Wallingford, UK, pp. 101–107.

Lynch JP, Brown KM (1997) Ethylene and plant responses to nutritional stress. Physiol Plant 100: 613–619.

Ma JH, Yao JL, Cohen D, Morris B (1998) Ethylene inhibitors enhance in vitro root formation from apple shoot cultures. Plant Cell Rep 17: 211–214.

Mahmood IA, Nawaz S, Aslam M (2000) Screening of rice (Oryza sativa L.) genotypes against salinity. Int J Agric Biol 2: 147–150.

Medoet DB, Paulucci NS, Albornoz Al, et al. (2010) Plant growth promoting rhizobacteria improving the legume-rhizobia symbiosis. In: Khan MS, Zaidi A, Musarrat J (eds), Microbes for Legume Improvement. Springer-Verlag, New York, pp. 473–494.

Mensah JK, Ihenyen J (2009) Effects of salinity on germination, seedling establishment and yield of three genotypes of mung bean (Vigna mungo L. Hepper) in Edo State, Nigeria. Nigerian Ann Nat Sci 8: 17–24.

Mensah JK, Akomeah PA, Ikhaijagbe B, Ekepekurede EO (2006) Effects of salinity on germination, growth and yield of five groundnut genotypes. Afr J Biotech 5: 1973–1979.

Mishra M, Kumar U, Mishra PK, Prakash V (2010) Efficiency of plant growth promoting rhizobacteria for the enhancement of Cicer arietinum L. growth and germination under salinity. Adv Biol Res 4: 92–96.

Molla AH, Shamsuddin ZH, Halimi MS, Morziah M, Puteh AB et al. (2010) Plant growth promoting bacteria that exhibit useful agricultural traits and waste post bacteria that exhibit useful agricultural traits and waste uptake from symbiotic and nonsymbiotic sources. Notulae Botanicae Horti Agrobotanici Cluj-Napoca 37: 190–194.

Nutman PS (1977) Study frameworks for symbiotic nitrogen fixation. In: Newton WE, Postgate JR, Rodriguez-Barrueco C (eds), Recent Developments in Nitrogen Fixation. Academic Press, London, pp. 443–448.

Nyleler D, Huguenin-Elie O, Suter M, Frossard E, Lüscher A (2011) Grass-legume mixtures can yield more nitrogen than legume pure stands due to mutual stimulation of nitrogen uptake from symbiotic and nonsymbiotic sources. Agric Ecos Environ 140: 155–163.

Parida SK, Das AB (2005) Salt tolerance and salinity effects on plants. Ecotox Environ Safe 60: 324–349.

Pathma J, Sakthivel N (2012) Microbial diversity of vermicompost bacteria that exhibit useful agricultural traits and waste management potential. SpringerPlus 1: 26.

Parker MB, Gaines TP, Hook JE, Gascho GJ, Maw BW (1987) Chloride and water stress effects on soybean in pot culture. J Plant Nutr 10: 517–538.

Pliego C, Kamilova F, Lugtenberg B (2011) Plant growth-promoting bacteria: fundamentals and exploitation. In: Maheshwari DK (ed.), Bacteria in Agrobiology: Crop Ecosystems. Springer, pp. 295–343.

Predeepa RJ, Ravindran DA (2010) Nodule formation, distribution and symbiotic efficacy of Vigna unguiculata L. under different soil salinity regimes. Emir J Food Agr 22: 275–284.

Rabie GH, Almadini AM (2005) Role of bioinoculants in development of salt-tolerance of Vicia faba plants under salinity stress. Afr J Biotech 4: 210–222.

Räsänen LA, Sajjets S, Jokinen L, Lindström K (2003) Evaluation of the roles of two compatible solutes, glycine betaine and trehalose for the Acacia senegal-Sinorhizobium symbiosis exposed to drought stress. Plant Soil 260: 237–251.

Robledo M, Jiménez-Zurdo JJ, Velázquez E, et al. (2008) Rhizobium cellulase CelC2 is essential for primary symbiotic infection of legume host roots. Proc Natl Acad Sci USA 105: 7064–7069.

Rokhzadi A, Asgharzadeh A, Darvish F, Nour-Mohammadi G, Majidi E (2008) Influence of plant growth promoting rhizobacteria on dry matter accumulation of chickpea (Cicer arietinum L.) under field conditions. J Agr Env Sci 3 (Suppl. 2): 253–257.

Roopa B, Maya C, Makari HK (2012) Effect of different PGPR strain along with rhizobium on nodulation and chick pea productivity. Asian J Exp Biol Sci 3: 424–426.

Rosas BS, Javier AA, Marisa R, Correa NS (2006) Phosphate solubilizing Pseudomonas putida can influence the rhizobia legume symbiosis. Soil Biol Biochem 38: 3502–3505.

Rüberg S, Tian ZX, Krol E, et al. (2003) Construction and validation of a Sinorhizobium meliloti whole genome DNA microarray: genome wide profiling of osmostatadapative gene expression. J Biotech 106: 255–268.

Sadiki M, Rabih K (2001) Selection of chickpea (Cicer arietinum) for yield and symbiotic nitrogen fixation ability under salt stress. Agronomie 21: 659–666.

Salehi M, Salehi F, Poustini K, Heidari-Sharifiabad H (2008) The effect of salinity on the nitrogen fixation in four cultivars of Medicago sativa L. in the seedling emergence stage. Res J Agr Biol Sci 4: 413–415.

Schmidt W (2001) From faith to fate: ethylene signaling in morphogenic responses to P and Fe deficiency. J Plant Nutr Soil Sci 164: 147–154.

Shahab S, Nuzhat A, Nasreen SK (2009) Indole acetic acid production and enhanced plant growth promotion by indigenous PSBs. Afr J Agr Res 4: 1312–1316.

Shahzad SM, Khalid A, Arshad M, Tahir J, Mahmood T (2010) Improvement nodulation, growth and yield of Cicer arietinum L. through bacterial ACC-deaminase induced changes in root architecture. Eur J Soil Biol 46: 342–347.

Shanker AK, Venkateswarlu B (2011) Abiotic Stress in Plants – Mechanisms and Adaptations. In Tech Publisher, Janeza Trdine Rijeka, Croatia. 428pp.
Sharma N, Abrams SR, Waterer DR (2005) Uptake, movement, activity, and persistence of an abscisic acid analog (80 acetylene ABA methyl ester) in marigold and tomato. J Plant Growth Regul 24: 28–35.

Serraj R (2002) Response of symbiotic nitrogen fixation to drought and salinity stresses. Phys Mol Biol 8: 77–86.

Serraj R, Fleurat-Lessard P, Benoit J, Drevon JJ (1995) Structural changes in the inner-cortex cells of soybean root-nodules are induced by short-term exposure to high salt or oxygen concentrations. Plant Cell Environ 18: 455–462.

Serraj RH, Vasquez-Diaz G, Hernandez, Drevon JJ (2001) Genotypic difference in response of nitrogenase activity (C\textsubscript{2}H\textsubscript{2} reduction) to salinity and oxygen in common bean. Agronomie 21: 645–650.

Shahroorna B, Arshad M, Zahir ZA (2006) Effect of plant growth promoting rhizobacteria containing ACC-deaminase on maize (Zea mays L.) growth under axenic conditions and on nodulation in mung bean (Vigna radiata L.). Lett Appl Microbiol 42: 155–159.

Shamseldin A, Werner D (2005) High salt and high pH tolerance of new isolated Rhizobium etli strains from Egyptian soils. Curr Microbiol 50: 11–16.

Singh AK, Singh RA, Sharma SG (2001) Salt stress induced changes in certain organic metabolites during seedling growth of chickpea. Legume Res 24: 11–15.

Sindhu SS, Dadarwal KR (2001) Chitinolytic and cellulolytic Pseudomonas sp. antagonistic to fungal pathogens enhances nodulation by Mesorhizobium sp. cicer in chickpea. Microb Res 156: 353–358.

Soltani A, Khodarahmpour Z, Jafari AA, Nakhjavan S (2012) Selection of alfalfa (Medicago sativa L.) cultivars for salt stress tolerance using germination indices. Afr J Biotech 11: 7899–7905.

Sridhar KR, Arun AB, Narula N, Deubel A, Merbeck W (2005) Patterns of soil-carbon- utilization by fast growing coastal and dune rhizobia of the Southwest coast of India. Eng Life Sci 5: 425–430.

Son TTN, Diep CN, Giang TTM (2006) Effect of Bradyrhizobium and phosphate solubilizing bacteria application on soybean in rotational system in the Mekong delta. Omorene 14: 48–57.

Srínivasan PS, Gopal KS (1977) Effect of plantfioxin and NAA formulation on groundnut var TMU-7. Curr Sci 46: 119–120.

Tanimoto E (2005) Regulation of root growth by plant hormones: Roles for auxin and gibberellin. Crit Rev Plant Sci 24: 249–265.

Tejovathi G, Khadeer MA, Anwer SY (1988) Studies on certain enzymes in salt tolerant and sensitive genotypes of sunflower. Indian J Bot 11: 113–117.

Tilak KVB, Ranganayaki N, Manoharachari C (2006) Synergistic effects of plant-growth promoting rhizobacteria and Rhizobium on nodulation and nitrogen fixation by pigeonpea (Cajanus cajan). Europ J Soil Sci 57: 67–71.

Tsavkelova EA, Cherdyntseva TA, Klimova S, Shestakov AI, Botina SG, Netrusov AI (2007) Orchid-associated bacteria produce indole-3-acetic acid, promote seed germination, and increase their microbial yield in response to exogenous auxin. Arch Micro 188: 655–664.

UNEP (2008) In dead water. Merging of climate change with pollution, over-harvest, and infestations in the world’s fishing grounds. UNEP/GRID-Arendal, Arendal, Norway. Available at: http://www.grida.no/_res/site/file/publications/InDeadWater_LR.pdf [accessed 28 June 2014]

UNEP (2009) The environmental food crisis: The environment’s role in averting future food crises. A UNEP rapid response assessment. Nellemann C, MacDevette M, Manders T, et al. (eds). United Nations Environment Programme/GRID-Arendal. Available at: http://www.grida.no

Upadhyay SK, Singh JS, Singh D P (2011) Exopolysaccharide-producing plant growth-promoting rhizobacteria under salinity condition. Pedosphere 2: 214–222.

Vádez V, Krishnamurthy L, Serraj R, et al. (2007) Large variation in salinity tolerance in chickpea is explained by differences in sensitivity at the reproductive stage. Field Crops Res 104: 123–129.

Van Hoom JW, Katerji N, Handy A, Mastrorilli M (2001) Effect of salinity on yield and nitrogen uptake of four grain legumes and on biological nitrogen contribution from the soil. Agr Water Man 51: 87–98.

Wei GH, Yang XY, Zhang ZX, Yang YZ, Lindstrom K (2008) Strain Mesorhizobium sp. CCNWGX035; a stress tolerant isolate from Glycyrrhiza glabra displaying a wide host range of nodulation. Pedosphere 18: 102–112.

Yang J, Kloeper JW, Ryu C-M (2009) Rhizosphere bacteria help plants tolerate abiotic stress. Trends Plant Sci 14: 1–4.

Zafar-ul-Hye M, Ahmad M, Shahzad SM (2013) Synergistic effect of rhizobia and plant growth promoting rhizobacteria on the growth and nodulation of lentil seedlings under axenic conditions. Soil Env 32: 79–86.

Zahir ZA, Munir A, Asghar HN, Shahroona B, Arshad M (2008) Effectiveness of rhizobacteria containing ACC deaminase for growth promotion of peas (Pisum sativum) under drought conditions. J Micr Biot 18: 958–963.

Zahir ZA, Zafar-ul-Hye M, Sajjad S, Naveed M (2011) Comparative effectiveness of Pseudomonas and Serratia sp. containing ACC-deaminase for coinoculation with Rhizobium leguminosarum to improve growth, nodulation, and yield of lentil. Biol Fert Soils 47: 457–465.

Zahran HH (1999) Rhizobium-legume symbiosis and nitrogen fixation under severe conditions and in an arid climate. Microbiol Mol Biol Rev 63: 968–989.

Zahran HH, Sprent JI (1986) Effects of sodium chloride and polyethylene glycol on root-hair infection and nodulation of Vicia faba L. plants by Rhizobium leguminosarum. Planta 167: 303–309.

Zou N, Dort PJ, Marcar NE (1995) Interaction of salinity and rhizobial strains on growth and N\textsubscript{2} fixation by Acacia amiclpes. Soil Biol Bioch 27: 409–413.