

Chapter 2

The Management of Soil Quality and Plant Productivity in Stressed Environment with Rhizobacteria

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2.1 Introduction

The urgency of feeding the world's growing population while combating soil pollution, salinization, and desertification has given plant and soil productivity research vital importance. Under such circumstances, it requires suitable biotechnology not only to improve crop productivity but also to improve soil health through interactions of plant roots and soil microorganisms (Lugtenberg et al. 2002). Interest in bacterial fertilizers has increased, as it would substantially reduce the use of chemical fertilizers and pesticides which often contribute to the pollution of soil–water ecosystems. Presently, about 20 biocontrol products based on *Pseudomonas*, *Bacillus*, *Streptomyces*, and *Agrobacterium* strains have been commercialized, but there still is a need to improve the efficacy of these biocontrol products (Copping 2004; Chebotar et al. 2000; Lugtenberg and Kamilova 2004). Soil salinity disturbs the plant–microbe interaction, which is a critical ecological factor to help further plant growth in degraded ecosystems (Paul and Nair 2008). Because plants are under saline or water unbalance stress, they become more vulnerable to diseases caused by pathogenic fungi. The use of specific microbe antagonists which stimulate plant growth and/or are natural enemies of pathogens allows a considerable decrease in the use of agrochemicals which are now being used for plant growth stimulation and control of diseases (Lugtenberg et al. 2001). Development of such a stress-tolerant microbial strain associated with the roots of agronomic crops can lead to improved fertility of salt-affected soils (Mayak et al. 2004; Egamberdieva and Kucharova 2009). The use of beneficial microbes in agricultural production systems started about 60 years ago. The effect of plant growth-promoting bacteria on the growth and nutrient uptake of various

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agricultural crops was well addressed by Kloepper et al. (1980), Lifshitz et al. (1987), Kloepper and Beauchamp (1992), Okon et al. (1998), Lugtenberg et al. (2001), and Glick et al. (2007). Biological control of plant disease by rhizobacteria was also previously reported by other authors (Bloembergen and Lugtenberg 2001; Lugtenberg and Kamilova 2004; Adegemoye et al. 2008). There is now increasing evidence that the use of beneficial microbes can enhance plants' resistance to adverse environmental stresses, e.g., drought, salts, nutrient deficiency, and heavy metal contaminations (Glick et al. 2007).

Understanding the integration of bacterial strains in the rhizosphere of plants and the mechanisms of their interactions are widely recognized as a key to improving the level and reliability of plant growth stimulation by plant growth-promoting rhizobacteria. Most PGPR strains do not have a single mechanism which completely accounts for their beneficial effects on the plant (Burdman et al. 2000; Khalid et al. 2004; Khan 2005; Berg et al. 2005). Some mechanisms by which bacteria are able to stimulate plant growth and to prevent damage caused by plant pathogens include mobilization of nutrients (Lifshitz et al. 1987), production of phytohormones (Frankenberger and Arshad 1995), antagonism (Thomashow and Weller 1996), induction of systemic resistance (van Loon and Glick 2004), and competition for nutrients and niches (Kamilova et al. 2005). However, the interactions among these microbes are still not well understood in field applications under different environments. An understanding of the functions and mechanisms by which bacteria can promote plant growth in stressed environments (e.g., arid region) may provide valuable information on plant-microbe interactions to develop new agricultural technologies that may improve soil ecology and plant development. The objectives of this paper are to discuss recent developments and advances in our understanding of the interactions between the plant and plant growth-promoting rhizobacteria and their mechanism of action under fragile and stressed environments.

2.2 Ecological Factors' Effect on PGPR Performance

Many factors have been discussed that may affect rhizosphere microbial communities and it is likely different soils, varieties, climatic conditions, etc. will effect PGPR performance (Sorensen 1997; Paul and Clark 1989). The abiotic environment has, however, been recognized as the main criterion determining the efficiency of plant growth-promoting bacteria in the plant root. In our previous studies, we observed that the bacterial strains isolated from loamy sand increased the root, shoot length and dry weight of whole plants of peas, wheat, and maize by 45% compared to the control. They were more effective at 16°C as compared to incubation at 26°C. Plant growth was not stimulated by bacterial strains at 26°C temperature (Egamberdiyeva and Höflich 2001).

The effect of soil type that has different nutrient status on the stimulatory efficiency of bacterial inoculants may be important for successful root inoculation and plant growth stimulation. Latour et al. (1996) indicate that the soil types is the dominating factor responsible for the diversity of the bacterial populations

associated with plant roots. Bacterial strains *P. alcaligenes* PsA15, *B. polymyxa* BcP26, and *B. amyloliquefaciens* BcA12 significantly increased the shoot, root dry weight (20–42%) and N, P, and K uptake of pea, wheat and maize in serozem soil better than in loamy sand soil.

The bacterial strains had a much better effect on growth and nutrient uptake of plants in nutrient-deficient saline serozem soil than in relatively rich loamy sand. According to Paula et al. (1992), the magnitude of the plant response to any microbial inoculation can be greatly affected by the soil condition. Inoculation of plants with bacteria only marginally increased yields when tested under ideal climatic situations. The greatest benefits occurred when crops encountered stressful conditions (Lazarovits and Norwak 1997), while nontreated plants by comparison performed poorly under such conditions where high pH make nutrients less available to them.

Similar results were reported by Defreitas and Germida (1992) that in low fertility soil, *Pseudomonas* significantly enhanced early plant growth. Such inoculation could compensate for nutrient deficiency and improve plant development through the production of plant growth regulators by microbes at the root interface, which stimulated root development and resulted in better absorption of water and nutrients from the soil (Kloepper and Beauchamp 1992; Wu et al. 2005).

PGPR may enhance mineral uptake including N, P, K, and microelements more efficiently from the soil, not only as a consequence of the increase in root surface area, but also by stimulating the ion uptake systems (Burdman et al. 2000).

Defreitas and Germida (1992) showed that several PGPB strains increased root hair size and number, and these tubular extensions of root epidermal cells can be involved in mineral uptake capacity in two ways. First, root hairs represent a large surface available for ion uptake and, second, they are believed to play an important role in nutrient uptake.

2.3 Rhizosphere Colonization and Survival

Soil inoculation of beneficial microorganisms will not result in significant effects unless the environment supports growth and survival of the introduced microorganisms (Bull et al. 1991; Devliegher et al. 1995). Survival strategies also depend on the physiological adaptation in the introduced cells, such as adaptation to nutrient-limited conditions and/or other physical chemical conditions, efficient utilization of root-released compounds or specific interactions with plants (Bull et al. 1991; Van Overbeek and Van Elsas 1997; Devliegher et al. 1995). However in the soil, the survival of the inoculated bacteria largely depends on the availability of an empty niche, helping them withstand competition with the often better-adapted native microflora (Rekha et al. 2007).

Earlier reports claim soil salinity has an adverse effect on plant growth-promoting bacterial populations, but members of potentially pathogenic species survive and become enriched in the rhizosphere (Sato and Jiang 1996; Tripathi et al. 2002).

We also observed that bacterial strains isolated directly from the root of wheat grown in saline soil stimulated plant growth but were also human pathogens (Egamberdiyeva et al. 2008). The rhizosphere, which is relatively rich in organic substrates, stimulates microbial growth and also attracts human pathogens which have also evolved to respond to the same signals; thus, the chances to compete effectively with the indigenous microflora in the rhizosphere are high (Roberts et al. 2000; Ji and Wilson 2002; Jablasone et al. 2005).

Continuing with what was reported by Morales et al. (1996) that the survival and colonization of potentially pathogenic human-associated bacteria in the rhizosphere of plants are poor and their persistence and colonization on plants were decreased by coinoculation of pathogens with naturally occurring bacteria (Jablasone et al. 2005), the hypothesis was tested that beneficial bacteria which have been selected as enhanced colonizers (Validov et al. 2006) may be able to outcompete the pathogens, thereby creating a more environmentally friendly agriculture which is healthier for farmers and users.

Efficient colonizers can be obtained after inoculation of seedlings with a mixture of different bacteria followed by growth of the seedling in a gnotobiotic sand system (Simons et al. 1996). Repeated use of this method yields enhanced root-tip-colonizing wild-type bacteria (Lugtenberg et al. 2001). In our previous work, salt-tolerant enhanced root-colonizing rhizobacteria of wheat were isolated after the third cycle of enrichment for possible use in salinated soil (Egamberdieva and Kucharova 2009). They were nonpathogenic strains, since they do not belong to the risk group 2 (Anonymous 1998).

The subsequent survival and establishment of beneficial microorganisms on the roots is also important for continued plant growth promotion or disease control and root-colonizing indigenous microorganisms. Selected enhanced root tip-colonizing bacteria were able to increase culturable bacterial community in the rhizosphere soil of wheat grown in saline soil (Fig. 2.1).

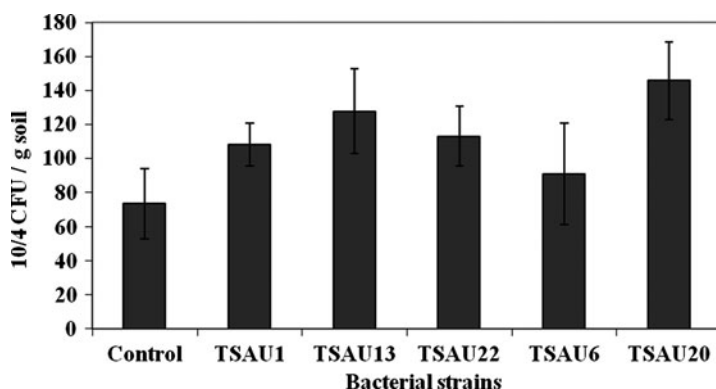


Fig. 2.1 The effect of root-colonizing bacteria *P. putida* TSAU1, *P. chlororaphis* TSAU13, *P. extremorientalis* TSAU20, *P. extremorientalis* TSAU6, and *P. aureantiaca* TSAU22 on total culturable rhizosphere soil bacterial community of wheat in saline soil (10^4 CFU/g soil)

Lugtenberg et al. (2001) have discussed the idea that fast-growing rhizobacteria might out-compete fungal pathogens for carbon and energy sources, and the colonization of large parts of the root system will obviously facilitate biocontrol since colonization can be expected to function as the delivery system for bacterial cells that act as factories of antifungal metabolites. These compounds were shown to be involved in mechanisms through which biocontrol strains can reduce the ability of fungal pathogens to propagate in the soil.

Factors that can influence the survival of microorganisms in soil include soil type, texture, density, pH, temperature, salinity, water potential, organic carbon and inorganic nutrients, as well as the presence of other soil organisms (Van Veen et al. 1997). Information on the effects of different factors on the rhizosphere microflora may help to understand the rhizosphere microbial dynamics in soil. Rifampicin-resistant mutants obtained from bacterial strains *P. chlororaphis* TSAU13 and *P. extremorientalis* TSAU20 were able to survive in the root of wheat and cotton under salt stress. In other experiments, we observed that the total culturable bacteria in the rhizosphere of tomato *P. putida* 1T1, *P. trivialis* 3Re27, *P. extremorientalis* TSAU20 and *S. rhizophila* ep-17 were decreased with increasing salinity level (0–100 mM NaCl) from 5.5 to 5.0 [\log_{10} (CFU/g root)] (Table 2.1).

However, the increase of salinity did not negatively affect root colonization of rifampicin-resistant mutants of *P. putida* 1T1, *P. trivialis* 3Re27, *P. extremorientalis* TSAU20 and *S. rhizophila* ep-17 for tomato. Their numbers were inhibited only at 100 mM NaCl condition (Table 2.2).

Those results showed that in both experiments bacterial strains were able to survive in the root of plants due to their competitiveness and persistence in salinated soil condition (personal communication).

Table 2.1 The effect of salinity (NaCl) on total bacterial population in the rhizosphere of tomato *P. putida* 1T1, *P. trivialis* 3Re27, *P. extremorientalis* TSAU20 and *S. rhizophila* ep-17 [\log_{10} (CFU/g root)]

	0	25	50	75	100
Treatments	mM NaCl				
1 T1	5.3 \pm 0.1	5.4 \pm 0.4	5.3 \pm 0.3	5.1 \pm 0.4	5.1 \pm 0.2
3Re27	5.5 \pm 0.2	5.4 \pm 0.1	5.4 \pm 0.3	5.3 \pm 0.3	5.2 \pm 0.1
TSAU20	5.4 \pm 0.2	5.3 \pm 0.3	5.3 \pm 0.3	5.2 \pm 0.1	5.2 \pm 0.1
ep-17	5.5 \pm 0.2	5.4 \pm 0.2	5.3 \pm 0.2	5.2 \pm 0.2	5.0 \pm 0.2

Plants grown in potting soil for 4 weeks with addition of NaCl of 25, 50, 75, and 100 mM, Rif mutants used for inoculation treatments, \log_{10} (CFU/g root)

Table 2.2 The effect of salinity (NaCl) on the survival of rifampicin-resistant mutants of *P. putida* 1T1, *P. trivialis* 3Re27, *P. extremorientalis* TSAU20 and *S. rhizophila* ep-17 in the rhizosphere of tomato [\log_{10} (CFU/g root)]

	0	25	50	75	100
Treatments	mM NaCl				
1 T1	3.6 \pm 0.3	3.6 \pm 0.3	3.6 \pm 0.4	3.6 \pm 0.3	3.4 \pm 0.3
3Re27	3.9 \pm 0.2	3.8 \pm 0.2	3.8 \pm 0.2	3.8 \pm 0.1	3.1 \pm 0.2
TSAU20	3.7 \pm 0.1	3.7 \pm 0.2	3.7 \pm 0.2	3.7 \pm 0.1	3.2 \pm 0.2
ep-17	4.0 \pm 0.1	3.9 \pm 0.4	3.3 \pm 0.5	3.2 \pm 0.3	3.2 \pm 0.2

Plants grown in potting soil for 4 weeks with addition of NaCl of 25, 50, 75, and 100 mM, Rif mutants used for inoculation treatments, \log_{10} (CFU/g root)

Paul and Nair (2008) reported that the root colonization potential of the salt-tolerant *Pseudomonas* strain was not hampered with higher salinity in soil. As a means of salt tolerance, the strain synthesized the osmolytes Ala, Gly, Glu, Ser, Thr, and Asp in their cytosol.

It is suggested the persisting nature of the introduced bacterial inoculants in nutrient limited habitats is closely related to their ability to resist starvation (Madkour et al. 1990). A direct relationship between starvation resistance and the ability of bacterial survival in soil was reported in earlier studies. Salt-tolerant and temperature-resistant characteristics make bacteria able to adapt under extreme environments (Tripathi et al. 2002).

2.4 The Role of Bacterial Phytohormones in Plant Growth Promotion in Saline Soils

Mechanisms by which bacteria can promote plant growth include mobilization of nutrients (Lugtenberg et al. 2002; Lugtenberg and Kamilova 2004) and production of phytohormones (Lifshitz et al. 1987; Frankenberger and Arshad 1995). The microbial synthesis of plant growth regulators is an important factor in soil fertility. Gibberellin and indole acetic acid are secondary metabolites, which are important biotechnological products, obtained commercially from bacteria and fungi for the agricultural and horticultural industry (Patten and Glick 2002).

Indole acetic acid (IAA) is the most common natural auxin found in plants. IAA is involved in physiological processes such as cell elongation and tissue differentiation (Taiz and Zeiger 1991; Frankenberger and Arshad 1995) and has also been associated with the plant growth-promoting effect of numerous rhizospheric microorganisms (Patten and Glick 2002).

It is thought that the repressive effect of salinity on germination could be related to a decline in endogenous levels of plant growth hormones or phytohormones (Zholkevich and Pustovoytova 1993; Jackson 1997; Debez et al. 2001). It has been reported previously that salt stress reduces the supply of cytokinin from root to shoot and also the recovery of diffusible auxin from maize coleoptile tips (Itai et al. 1968). Indeed, the exogenous application of plant growth regulators (PGRs), e.g., gibberellins (Prakash and Parthapasenan 1990; Afzal et al. 2005), auxins (Gul et al. 2000; Khan et al. 2001, 2004), and cytokinins (Dhingra and Varghese 1985; Khan and Weber 1986; Gul et al. 2000) produced some benefit in alleviating the adverse effects of salt stress and they also improve germination, growth, fruit setting, fresh vegetable and seed yields and yield quality (Saimbhi 1993). Other authors also reported that presowing wheat seeds with plant growth regulators such as IAA and gibberellins alleviated the growth-inhibiting effect of salt stress (Singh and Dara 1971; Datta et al. 1998; Sastry and Shekhawa 2001; Afzal et al. 2005).

Sakhabutdinova et al. (2003) also reported that salinity resulted in a progressive decline in the level of IAA in the root system of plants. In this condition, soaking

seeds with plant growth regulators and applying additional natural phytohormones supplied sufficient hormones for normal plant development and growth in saline conditions (Kabar 1987; Afzal et al. 2005).

It is also suggested that root-colonizing bacteria which produce phytohormones, when bound to the seed coat of a developing seedling, may act as a mechanism for plant growth stimulation and these organisms can prevent the deleterious effects of stresses from the environment (Lindberg et al. 1985; Frankenberger and Arshad 1995). Salt-tolerant IAA-producing bacterial strains *P. aureantiaca* TSAU22 and *P. extremorientalis* TSAU20 alleviated quite successfully the reductive effect of salt stress on percentage of germination (up to 79%), probably through their ability to produce IAA (Egamberdieva 2009). They were able to produce indole-3-acetic acid (IAA) in saline conditions as well. Hasnain and Sabri (1996) showed that inoculation of wheat with *Pseudomonas* sp. stimulated plant growth by reducing plant uptake of toxic ions and increasing the auxin content.

Also, several workers have demonstrated the production of phytohormones by plant growth-promoting bacteria (Zimmer et al. 1995) and which may have pronounced effects on plant growth and development (Frankenberger and Arshad 1995).

They may supply additional phytohormone to the plants, and thus may help stimulate root growth and reverse the growth inhibiting effect of salt stress to a certain extent in both the shoot and the root (Egamberdieva 2009). Such results suggest recommending root-colonizing bacteria that produce phytohormone to alleviate the salt stress of wheat grown under conditions of soil salinity, without any genetic manipulation of the plant. These organisms should therefore be considered as a seed dressing in field trials to improve growth and yield of wheat in farms where soil salinity is high.

2.5 Alleviation of Salt Stress in Plants by PGPR

Inhibition of plant growth by salinity is considered to be due to the toxic effects of NaCl, to the ability of the root system to control entry of ions to the shoot and to slowing down water uptake of plants (Hajibagheri et al. 1989). Jamil et al. (2006) reported that salt stress decreased germination and also delayed the emergence of seeds in four vegetable species.

Plant stress can be reduced by 1-aminocyclopropane-carboxylate (ACC) deaminase-producing bacteria (Glick et al. 1997). The plant hormone ethylene has previously been found to be an inhibitor of plant root elongation (Abeles et al. 1992), and its production in plants is highly dependent on the endogenous levels of ACC. The ACC deaminase enzyme can cleave the ethylene precursor ACC to α -ketobutyrate and ammonium and thereby lower the level of ethylene in developing or stressed plants (Glick 1995; Glick et al. 1998). Thus, plant growth-promoting bacteria contain the enzyme ACC deaminase and colonize the seed coat of a developing seedling, and may decrease the ethylene level so that it does not

become too high to limit root growth (Glick et al. 1998; Hontzeas et al. 2004). Furthermore, by removing ACC, the bacteria reduce the deleterious effect of ethylene, ameliorating plant stress and promoting plant growth (Shah et al. 1997; Glick et al. 2007). These bacteria may enhance the survival of some seedlings, especially during the first few days after the seeds are planted. In our previous study, only strain *P. trivialis* 3Re27 could utilize ACC as the sole N source (Egamberdieva and Kucharova 2009) and showed high stimulatory effect on the growth of plants in saline soils.

Soil salinity particularly disturbs the symbiotic interaction between legumes and rhizobia. Numerous studies have shown that soil salinity causes decrease in nodulation and reduces dramatically N₂ fixation and nitrogenase activity of nodulated legumes such as soybean (Singleton and Bohlool 1984), common bean, and faba bean (Rabie et al. 2005).

Other authors reported a decrease of rhizobial colonization and shrinkage of root hairs of soybean, common bean, and chickpea in salt stress (Zahran and Sprent 1986; Singleton and Bohlool 1984; Elsheikh and Wood 1990).

The study of Marcar et al. (1991) indicated that symbiotic properties were more sensitive to salinity than plant growth. Thus, the development of salt-tolerant symbioses is an absolute necessity to enable cultivation of leguminous crops in salt-affected soils (Yousef and Sprent 1988; Lauter et al. 1981; Velagaleti and Marsh 1989).

In the rhizosphere, the synergism between various bacterial genera, such as between *Bacillus*, *Pseudomonas*, and *Rhizobium* has been demonstrated to promote plant growth and development (Bolton et al. 1990; Halverson et al. 1993). The coinoculation with *Pseudomonas* spp. and *Rhizobium* spp. had enhanced nodulation and nitrogen fixation, plant biomass, and grain yield in various leguminous species including alfalfa (Bolton et al. 1990), soybean (Dashti et al. 1998), chickpea (Goel et al. 2002), and pea (Tilak et al. 2006). We have also observed that root-colonizing *Pseudomonas* strains improve rhizobia–legume interactions. Combined inoculations could be an option to improve plant growth and increase nodule numbers and N content of galega species (personal communications).

Plant growth-promoting bacteria can prevent the deleterious effects of stressors from the environment (Lugtenberg et al. 2001; Egamberdieva 2009). Hasnain and Sabri (1996) reported that inoculation of plants with *Pseudomonas* sp. stimulated plant growth by reduction of toxic ion uptake and increases in auxin contents.

Another explanation for enhancement of nodule formation by the rhizobia in legumes might be the production of hydrolytic enzymes such as cellulases by root-colonizing *Pseudomonas* strains, which could make penetration of rhizobia into root hairs or intercellular spaces of root cells easier, leading to increased numbers of nodules (Sindhu and Dadarwal 2001).

Under drought stress, coinoculation of bean (*Phaseolus vulgaris* L.) with *Rhizobium tropici* and two strains of *P. polymyxa* resulted in augmented plant height, shoot dry weight, and nodule number. Coinoculation of lettuce (*Lactuca sativa* L.) with PGPR *Pseudomonas mendocina* and arbuscular mycorrhizal fungi (*Glomus intraradices* or *G. mosseae*) augmented an antioxidant catalase under severe

drought conditions, suggesting that they can be used in inoculants to alleviate the oxidative damage elicited by drought (Tain et al. 2004; Yang et al. 2009).

2.6 Concluding Remarks

As discussed in this review, ecological factors such as temperature and soil nutritional condition affect the performance of plant growth-promoting rhizobacteria. The bacterial inoculation has a much better stimulatory effect on plant growth and nutrient uptake in nutrient-deficient soil than in nutrient-rich soil. The screening and application of the enhanced potential root-colonizing rhizobacteria is essential for developing sound strategies to manage the rhizosphere in such a way that it becomes more difficult for pathogens to colonize the same. Thus, these beneficial bacteria can engineer positive interactions in the rhizosphere and stimulate plant growth, nutrient uptake, and symbiotic performance of *Rhizobium* under saline conditions.

The phytohormone auxin produced by root-colonizing bacteria plays an important role in alleviating salt stress in plants and these organisms should therefore be considered as a seed dressing in field trials to improve growth and yield of crop plants in farms where soil salinity is high. To further understand the highly complex nature of microbial adaptation and their response to alterations in the biological, chemical, and physical environment of the rhizosphere remains a significant challenge. Hopefully, new research will provide farmers with novel control strategies for the development of microbial strains that are more effective and have longer shelf-lives as a “plant growth stimulators” and “biocontrol” to supplement and/or complement chemical fertilizers and pesticides in agriculture.

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