Chapter 12
Role of Rhizospheric Bacteria in Disease Suppression During Seedling Formation in Millet

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Abstract Bacteria present in the rhizospheric area of the plant are called rhizospheric bacteria. Rhizospheric bacteria play crucial role in plant development and growth starting from seed germination and also protect the seedlings from fungal phytopathogens. These rhizobacteria are known to produce growth hormones; siderophore; lytic enzymes such as chitinase, lipase, protease, and β-1, 3-glucanase; organic acids; lipopeptides; volatile compounds; and some antibiotics. Some of the common rhizospheric bacteria are *Pseudomonas chlororaphis*, *Bacillus subtilis*, *Bacillus licheniformis*, *Pseudomonas fluorescens*, *Chromobacterium violaceum*, *Bacillus cereus*, and *Bacillus stearothermophilus* which have been found to suppress the growth of fungal pathogens including *Macrophomina phaseolina*, *Magnaporthe grisea*, and *Fusarium oxysporum*. Lytic enzymes such as chitinase, protease, and β-1, 3- glucanase produced by the rhizobacteria degrade the chitin, glucan, and proteins of the fungal cell wall, respectively. Secondary metabolites produced by the rhizobacteria inhibit the growth of pathogenic fungi by reducing the spore germination, swelling in fungal mycelia, making pore formation in hyphae, cytoplasmic leakages from fungal cells, and finally lysis of hyphae. *Pseudomonas* and *Bacillus* are known to induce the induced systemic resistance (ISR) in plants and make them disease resistant against phytopathogens. Millets are group of very important small grain crop which seedling establishment is affected by many soil pathogens. The present chapter is focused on the role of beneficial rhizospheric bacteria in disease suppression in millet crop.

Keywords Rhizospheric bacteria · Pathogenic fungi · Disease suppression · Siderophore · Lytic enzymes

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12.1 Introduction

Narrow region around every plant is colonised by different types of microbes including bacteria and fungi called rhizoshpere, and these microorganism are called rhizospheric microorganism (Hirsch and Mauchline 2012; Darrah 1993; Philippot et al. 2013). Rhizospheric areas directly influence the chemical secretion from roots of the plant (called root exudates) and also determine the growth and distribution of microbes around it. Root exudates contain different types of organic acids, sugars, vitamins, and phenolic compounds, which act as signalling molecules playing important role in the recruitment of microbes; it is also used by microbes as food material (Lugtenberg et al. 2001; Dini-Andreote and van Elsas 2013; Philippot et al. 2013). Microbes present in the rhizospheric zone struggle for nutrition and space; some of the microbes make mutualistic or symbiotic relationships with the roots of the plants (N-fixing bacteria) and improve their growth (Bazin et al. 1990; Lugtenberg et al. 2001). Some of the pathogenic microbes (acting as parasites) harm the plant's health by causing several diseases that affect the growth of the plant (Ahmad et al. 2008). Rhizospheric bacteria play several roles in the growth and development of plants including seed germination and establishment, development of root shoot length, increasing biomass of the plant through plant growth-promoting activities such as the production of auxins, solubilising inorganic phosphate, and increasing nutrient uptake by nitrogen fixation. Such PGPRs (plant growth-promoting rhizobacteria) also control the growth of the plant pathogens in the rhizospheric region by secreting hydrolytic enzymes, hydrogen cyanide, siderophore production, and secreting several types of antimicrobial compounds and also induce systemic resistance inside the plant; rhizospheric bacteria also improve survival of the plant in abiotic stress conditions. *Azotobacter chroococcum*, *Azospirillum lipoferum*, *Bacillus cereus*, *Serratia marcescens*, *Chryseomonas luteola*, *Bacillus subtilis*, *Acinetobacter*, *Pseudomonas fluorescens*, *Acetobacter and Azospirillum*, *Bacillus amyloliquefaciens*, *Burkholderia phytofirmans*, and *Pseudomonas* sp. are reported as rhizospheric bacteria which play an important role in plant growth-promoting activities of the pearl millet, sorghum, foxtail millet, and finger millet (Jogaiah et al. 2007; Idris et al. 2007; Rokhbakhsh-Zamin et al. 2011; Saxena et al. 2013; Khatri et al. 2016; Mounde et al. 2015; Sekar et al. 2018). *Azospirillum* and *Acetobacter* protected the pearl millet against downy mildew (Jogaiah et al. 2007); *Pseudomonas* sp. protects finger millet from the blast disease caused by *Pyricularia grisea* (Sekar et al. 2018). Rhizobacteria including *Pseudomonas migulae*, *Pseudomonas fluorescens*, and *Enterobacter hormaechei* are reported as drought-tolerant bacteria; this might be a reason why some of the millets crop including foxtail millet grow in drought conditions (Niu et al. 2018).

12.2 Millets Crop

Millets are small seeded, annual, cereal crops which are grown mostly in developing countries of Asia and Africa (FAO 1972; Sarita and Singh 2016). Millets are favoured due to their productivity and high nutritional values and because they easily grow in dry, low fertility soil condition. Millets include pearl millet, foxtail millet, finger millet, kodo millet, barnyard millet, browntop millet, proso millet, little millet, teff millet, and fonio millet (FAO 1972; Rao 1989; Dendy 1995; Hulse et al. 1980; Doggett 1989). Sorghum, due to their large size grain, is known as great millet (Adeyeye 2008). Millets have high mineral contents including iron, fibre, protein, and calcium. Finger millet has highest calcium content as compared to other millets and other main grains like rice and wheat (Sarita and Singh 2016; Chauhan et al. 2018; Kumar et al. 2018; Ambati and Sucharitha 2019).

12.3 Millets Seedling Disease

Large numbers of pathogenic fungi have been reported which are responsible for causing several diseases in different types of millets during germination of seeds and seedling development. Some seedling diseases are seed rot, seed decay, seedling blight, pre-emergence and post-emergence damping-off, seedling root rot, downy mildew, and blast disease. (Das 2017; Leukel and Martin 1943; Little and Perumal 2019; Nagaraja and Das 2016; Wilson 2000; Raghunathan 1968). Common seedling disease caused by fungal pathogens is listed in Table 12.1.

12.4 Role of Rhizospheric Bacteria in Disease Suppression

Several fungi are known to cause disease in sorghum and other millets at different stages of their life. Production of millets crop has been severely affected due to fungal infection during seedling formation (Das 2017; Wilson 2000). Many rhizospheric bacteria have been reported to play important roles in disease suppression in millet plants. *Macrophomina phaseolina* is responsible for seedling blight and charcoal rot disease in sorghum, and one rhizospheric bacterium *Pseudomonas chlororaphis* SRB127 has shown to suppress the growth of the pathogenic fungus and minimise the severity of charcoal rot disease in sorghum under field conditions (Das et al. 2008). Rhizospheric bacteria including *Bacillus subtilis*, *Bacillus licheniformis*, *Chromobacterium violaceum*, *Bacillus cereus*, and *Bacillus stearothermophilus* have been known to suppress the mycelial growth of *Fusarium oxysporum* and control the root and crown rot disease in sorghum (Idris et al. 2007; Al-Jedabi 2009). *Bacillus subtilis* and *Bacillus cereus* were isolated from rhizospheric regions of sorghum; they significantly suppressed the growth of

Table 12.1 List of diseases caused by pathogenic fungi during seed germination and seedling development

Disease symptoms	Plant host	Pathogens	Reference
Seed rot, damping-off, seedling blight	Sorghum	*Colletotrichum sublineolum* *Bipolaris turcica* *Rhizoctonia bataticola* *Pythium* spp. *Fusarium* spp.	Das (2017) Leukel and Martin (1943) Little and Perumal (2019)
Seedling blight	Sorghum	*Macrophomina phaseolina*	Das (2017)
Reduced germination and seedling death	Sorghum	*Alternaria alternata*	Little and Perumal (2019)
Seedling root rot	Sorghum	*Pythium arrhenomanes*	Leukel and Martin (1943)
Downy mildew	Sorghum	*Peronosclerospora sorghi*	Das (2017)
Downy mildew	Pearl millet	*Sclerospora graminicola*	Das (2017)
Blast	Pearl millet	*Pyricularia grisea*	Nagaraja and Das (2016)
Seed decay, damping-off, stem lesions on seedlings	Pearl millet	*Rhizoctonia solani, Sclerotium rolfsii*	Wilson (2000)
Reduced germination, seedling blight	Pearl millet	*Curvularia penniseti* *Drechslera setariae* *Exserohilum rostratum* *Fusarium moniliforme* *Fusarium solani* *Fusarium equiseti* *Fusarium fusarioides* *Phyllosticta penicillariae*	Wilson (2000)
Blast	Finger millet	*Pyricularia grisea*	Das (2017)
Seedling and leaf blight	Finger millet	*Drechslera nodulosum*	Das (2017)
Damping-off	Finger millet	*Pythium aphanidermatum*	Raghunathan (1968)
Blast	Foxtail millet	*Pyricularia setariae*	Das (2017)
Chlorosis of the seedling leaves	Foxtail millet	*Sclerospora graminicola*	Nagaraja and Das (2016)
Damping-off	Teff millet	*Helminthosporium poae*	Nagaraja and Das (2016)
Seed rotting, coleoptile spot, seedling blight	Proso millet	*Bipolaris panici-miliacei*	Das (2017)
Blast	Barnyard millet	*Pyricularia grisea*	Das (2017)

Pythium ultimum and also controlled the root rot in sorghum (Idris et al. 2008). *Pseudomonas fluorescens* having chitinase activity was shown to suppress the growth of *Magnaporthe grisea* and control the blast disease in finger millet/ragi (Negi et al. 2017). Downy mildew is a very damaging disease caused by *Sclerospora graminicola* in pearl millet. Treatment of seeds with *Pseudomonas fluorescens*, *Acetobacter*, *Azospirillum* strain, *Bacillus subtilis*, and *Bacillus pumilus* reduced the downy mildew disease in pearl millets (Raj et al. 2003; Jogaiah et al. 2007). Smut disease is caused by *Ustilago crameri* in foxtail millet, and a research found that rhizospheric bacterial community plays significant role in minimising disease occurrence and loss of productivity in fox tail millet (Han et al. 2017).

12.5 Mechanism of Disease Suppression

Rhizobacteria control the growth of fungal phytopathogens directly by producing antifungal antibiotics, siderophores, volatile compounds, antifungal lipopeptides, and lytic enzymes and indirectly by induced systemic resistance in the crop plants and protect the crops from fungal infections (Duffy and Défago 1999; Bhattacharyya and Jha 2012; Lugtenberg and Kamilova 2009; Glick 2012; Negi et al. 2017). These rhizospheric bacteria are considered as better prospect for eco-friendly cultivation.

12.6 Lytic Enzymes

The cell wall of fungi is made up mainly of chitin, glucans, and glycoproteins. Chitin provides rigidity and structural support to the cell wall. Several hydrolytic enzymes including chitinase, glucanase, protease, lipases, and cellulase production have been reported from plant growth-promoting bacteria including *Serratia marcescens*, *Paenibacillus*, *Streptomyces* spp., *Bacillus cepacia*, *Lysobacter antibioticus*, *Bacillus licheniformis*, *Bacillus cereus*, *Bacillus circulans*, *Bacillus thuringiensis*, *Enterobacter agglomerans*, *Stenotrophomonas maltophilia*, *Pseudomonas aeruginosa*, *Pseudomonas fluorescens*, *S. plymuthica*, *Pseudomonas stutzeri*, *Paenibacillus ehimensis*, etc. which play important roles in several fungal disease control (Dunne et al. 1997; Neiendam Nielsen and Sørensen 1999; Sadfi et al. 2001; Xiao-Jing et al. 2005; Compant et al. 2005; Radjacommare et al. 2010; Sekar and Prabavathy 2014; Negi et al. 2017; Tariq et al. 2017). Chitinase enzymes degrade the chitin by breaking the β-1, 4 glycosidic bonds in between the two *N*-acetyl-D-glycosamines (Fleuri et al. 2009; Kim et al. 2003; Webster and Weber 2007; Jadhav et al. 2017). The β-1,3-glucanase enzymes break the β-1,3 glucosidic bonds in β-1,3-glucans (Gupta et al. 2013; Jadhav et al. 2017). Protease plays important role in the breakdown of the membrane integrity in the cell wall of fungi by hydrolysing the proteins into small peptide chains through the breaking of the peptide bond (Jadhav et al. 2017). During interaction with fungi, plant growth-

promoting bacteria release these hydrolytic enzymes in the interaction zone and inhibit the growth of pathogenic fungi around that. Due to lytic enzymes, several changes are observed in fungal structure like swelling in a fungal hyphae or lysis of hyphae, deformed mycelia, pore formation in the tips of hyphae, and leakage of cytoplasmic material. Lytic enzymes are also known to retard the growth of fungal pathogens by reducing the spore germination and suppressing the elongation of germ tubes (Budi et al. 2000; Kim et al. 2003; Negi et al. 2017). Chitinases produced by fluorescent *Pseudomonas* showed antifungal activity against *Colletotrichum falcatum* which is responsible for red rot disease in sugarcane (Viswanathan and Samiyappan 2000). Rhizobacteria that belong to *Serratia* genus produce hydrolytic enzymes such as chitinases and β-1,3-glucanases which showed greater antagonism against *Verticillium dahliae*, *Rhizoctonia solani*, and *Sclerotinia sclerotiorum* causing diseases of oilseed rape (Kalbe et al. 1996). *Paenibacillus ehimensis* IB-X-b secretes both glucanase and chitinase, which are responsible for the cell wall degradation of fungi (Aktuganov et al. 2008). Rhizobacteria *Stenotrophomonas maltophilia* strain W81 suppresses the growth of *Pythium ultimum* by producing protease enzyme and protects the sugar beet from damping-off (Dunne et al. 1997). *Bacillus subtilis* and *Pseudomonas fluorescens* produce chitinase and inhibit the growth of root rot causal fungal pathogens such as *Rhizoctonia solani* and *Fusarium solani* (El-Mougy et al. 2011). Chitinolytic enzymes produced by *Serratia plymuthica* HRO-C48 was shown to retard the growth of phytopathogens *Botrytis cinerea* by inhibiting spore germination and elongation of germ tube (Frankowski et al. 2001). Rhizobacteria *Serratia marcescens* suppressed the mycelial growth of *Sclerotium rolfsii* by producing chitinase (Ordentlich et al. 1988). Lytic enzymes including chitinase, β-1,3-glucanase, lipase, and protease are produced by *Lysobacter antibioticus* HS124 and are known to inhibit the growth of *Phytophthora capsici* by partial swelling or lysis of fungal hyphae (Ko et al. 2009).

12.7 Antibiotics

Antibiotics produced by several PGPRs including *Pseudomonas* spp., *Bacillus subtilis*, and *Bacillus cereus* are known to suppress the growth of pathogenic fungi and finally protect the crop from fungal infections (Idris et al. 2008; Das et al. 2008; Sekar et al. 2018). Antibiotics produced by rhizobacteria reduce the spore formation, lyse the fungal hyphae, make pore formation at the tips of hyphae, and increase vacuolisation in the fungal cells (Das et al. 2008; Sekar et al. 2018). Antibiotics produced by *Bacillus subtilis* and *Bacillus cereus* played a major role in disease suppression caused by *Pythium ultimum* in sorghum root (Idris et al. 2008). Volatile compounds, siderophore, and antibiotics produced by *Pseudomonas chlororaphis* SRB127 inhibited the growth of *Macrophomina phaseolina* by inhibiting the growth of mycelia and reduced microsclerotia and spore germination and control the charcoal rot disease in sorghum (Das et al. 2008). 2, 4-DAPG, chitinase, and protease produced by *Pseudomonas* spp. inhibited the growth of *Erwinia persicina*,

Pyricularia grisea, *Xanthomonas campestris*, *Gaeumannomyces graminis*, and *Fusarium oxysporum* (Sekar and Prabavathy 2014). *Pseudomonas* sp. MSSRFD41 isolated from the rhizospheric region of the finger millet has been reported to produce several antifungal compounds such as derivatives of 2,4-DAPG, pyrrolo [1, 2-a]pyrazine-1, 4-dione, octasiloxane, 2, 5-piperazinedione, 1, 2 benzenedicarboxylic acid, pyran, 2-propenoic acid and dasycarpidan-1-methanol, n-hexadecanoic acid, 1, 2-benzenedicarboxylic acid, and 9-octadecenoic acid and also produce lytic enzymes such as chitinase, protease, and lipase; these above activities are responsible for suppressing the growth of *Pyricularia grisea*. Antifungal compounds and lytic enzymes make the changes in structures of *Pyricularia grisea* like abnormal mycelia, loss of smoothness, and unusual bulges in the fungal hyphae then suppress the growth of fungi (Sekar et al. 2018).

12.8 Volatile Organic Compounds (VOCs)

Bacillus subtilis by producing several VOCs such as acetophenone, aniline, benzothiazole, 5-methyl-2-hexanone, 6-methyl-2-heptanone, m-tolunitrile, and 2-ethylhexanol inhibited the growth of *Alternaria solani*. Similarly, volatile organic compounds produced by *Bacillus subtilis* is shown to reduce the conidia germination, penetrate the fungal hyphae, and decompose the cell wall, resulting in inhibition of the fungal growth (Zhang et al. 2020). VOCs such as acetic acid and 2-nonanone were produced by *Pseudomonas* spp. which caused changes in the structure of fungal mycelia and partial lysis of fungal hyphae and degraded the cell wall, and finally leakages of cytoplasm material reduced the growth of *Sclerotinia sclerotium* (Giorgio et al. 2015).

12.9 Siderophore

Siderophore is a low-molecular-weight iron-chelating agent that plays important role in antagonistic activity against fungi by reducing iron contents in the rhizospheric region. Generally, iron is present in the soil as insoluble ferric ion; some of the bacteria chelate the ferric ions from soils by secreting siderophore. Siderophore has a high affinity toward the ferric form of iron so siderophore makes a complex with ferric ion called ferric-siderophore complex, and this complex is taken up by the cell membrane. After reaching in cell cytoplasm, ferric ion is reduced into ferrous ion and siderophore dissociates from the complex due to its low affinity toward ferrous ion. As a result, the availability of iron in the soil is reduced due to which fungal spore germination is inhibited (Beneduzi et al. 2012; Ali and Vidhale 2013; Patil et al. 2014; Dimkpa 2016). In a study by producing siderophore, *Pseudomonas aeruginosa* FP6 suppressed the growth of *Rhizoctonia solani* by 72.25% in the absence of ferric chloride and by 12% in the presence of ferric chloride indicating

that siderophores play important role in antagonistic activity against fungal pathogens (Sasirekha and Srividya 2016).

12.10 Lipopeptides

By producing lipopeptides such as surfactin, fengycin, and iturin, rhizobacteria play important role in the suppression of growth of fungal phytopathogens (Ongena and Jacques 2008). Rhizobacteria *Bacillus velezensis* produces lipopeptides that retard the growth of *Fusarium oxysporum* by inhibiting the spore germination (Cao et al. 2018). WH1fungin, a new surfactin produced by *Bacillus amyloliquefaciens*, inhibited the growth of fungal pathogens. Low level of WH1fungin induces apoptosis process in fungi, but when treated with a high dose of WH1fungin, it creates pores in the cell membrane. WH1fungin also stops the synthesis of glucan part of the cell wall by inhibiting the activity of glucan synthase. When *Rhizoctonia solani* was treated with WH1fungin, then pores in the cell membrane and leakage of the cytoplasm from the pores were observed which ultimately caused to cell death in fungi (Qi et al. 2010).

12.11 Induced Systemic Resistance

Beneficial rhizobacteria play important role in inducing disease resistance in plants toward pathogens called induced systemic resistance (ISR) (Van Loon et al. 1998; Ramamoorthy et al. 2001). *P. fluorescens* strain WCS417 protected the *Dianthus caryophyllus* plant by induced systemic resistance against *F. oxysporum* (Van Peer et al. 1991). Many species of rhizobacteria belonging to the genus of *Pseudomonas* and *Bacillus* are known to induce systemic resistance in plants by inducing defence gene expressions (Van Peer et al. 1991; Kloepper et al. 2004; Van Wees et al. 2008). Both jasmonic acid and ethylene signalling pathways play major role in enhancement of the induced systemic resistance in plants (Pieterse et al. 1998; Beneduzi et al. 2012).

12.12 Conclusion

Numerous reports on rhizospheric microbes of millets have suggested the potential of rhizospheric bacteria in biocontrol of phytopathogenic fungi through the production of lytic enzymes, VOCs, siderophores, antibiotics, etc. However, majority of the studies have been confined to controlled experiments in sterilised soil and in pots. Field trials must be conducted regularly in order to justify the true biocontrol potential of PGPRs. Development of an effective microbial consortia against a

wide range of phytopathogens can do wonders in the field of biofertilisers and pesticides. Further, lack of interest of commercial players in the biocontrol of phytopathogens by rhizospheric microorganisms is also a limiting factor.

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