

# Microbial Services in Restoration Ecology

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# Microbial Secondary Metabolites: Effectual Armors to Improve Stress Survivability in Crop Plants

IZZAH SHAHID • SAMINA MEHNAZ, PHD

## 4.1 INTRODUCTION

Microbial metabolic products are grouped into two categories based on their functions in microbial reproduction, growth, and development. Primary metabolites are synthesized in trophophase of microbial growth and are vital to fulfill microbe's energy requirements and essential growth compounds, whereas microbial secondary metabolites (SMs) represent valuable organic compounds usually produced during the idiophase of microbial growth and are dispensable for organism's essential functions (Ruiz et al., 2010; Sanchez and Demain, 2009). Production of SMs is controlled by multiple microbial regulatory mechanisms under challenged conditions, and they are acknowledged to provide armor to producing microbe in uncongenial conditions (Singh et al., 2017). SMs improve the organism's potential to withstand extreme environmental conditions; biotic and abiotic stresses, temperature fluctuations, salinity, osmotic, and drought stresses; metallic toxicities, and pathogen attack, despite their production in small amounts (Vimal et al., 2017, 2019). These natural products have significantly contributed to nearly every sphere of agriculture, nutrition, and healthcare for sustainable agriculture practices, biopharmaceuticals, and development of bioprocess technologies (Singh et al., 2011; Gurung et al., 2013).

Distinct groups of organisms including filamentous Actinobacteria, eukaryotic fungi, and unicellular bacteria are the versatile and frequent producers of secondary metabolites. Several endophytic fungal species, imperfect fungi, basidiomycetes, and ascomycetes are the most significant producers of diversified functional secondary metabolites. *Aspergillus*, *Trichoderma*, *Phoma*, *Alternaria*, *Fusarium*, *Penicillium*, *Ganoderma*, *Lactarius*, *Acremonium*, and *Aureobasidium* have shown their tremendous potential as pharmacological, anticancer,

chemopreventive, and immunomodulatory agents (Kelly et al., 2015). Filamentous actinomycetes constitute the 45% of the known microbial bioactive compounds and represent the largest group of SM producers. To date, over 20,000 metabolites have been reported from Actinobacteria, of which 7600 originate from the genus *Streptomyces* (Awad et al., 2012).

Bacterial secondary metabolites constitute 17% of the total bioactive compounds isolated from microorganisms and have shown the tremendous potential in pharmaceutical, agriculture, biomedical, and food industry and acknowledged as "specialized microbial metabolites" (Monciardini et al., 2014). Bacterial natural products were particularly utilized in three diverse ways: direct industrial application of fermentation products in agriculture, biomedical, and other fields; microbiological modifications and derivatization, use of natural compounds as templates in rational drug design (RDD) experiments; and the synthesis of new analogs (Davies, 2013). In the bacterial kingdom, *Pseudomonas* and *Bacillus* species are the most frequent producers of bioactive SMs, and researchers have isolated more than 1700 bioactive compounds from these two genera to date (Demain, 2013; Vimal et al., 2018). Many of the bacilli and pseudomonads are considered key players in agriculture for the suppression of bacterial and fungal phytopathogens, endurance of extreme environmental fluctuations, and successful colonization of internal tissues of plants at high densities (Pierison and Pierson, 2010).

## 4.2 ABIOTIC AND BIOTIC CHALLENGES TO CROP PLANTS

Fluctuating environmental conditions, interacting living organisms, and changing physiological and

edaphic factors that negatively influence plant productivity, growth, survival, and reproduction are called as “stress factors” in plants. These fluctuations are foremost limiting factors for agricultural productivity exacerbated with the increasing human population competing for environmental resources (Bellard et al., 2012; Mickelbart et al., 2015; Vimal, 2018). These confronting factors in plants are broadly divided into two main categories: environmental stresses or abiotic factors, and biological stresses or biotic factors (Rejeb et al., 2014; Singh, 2015).

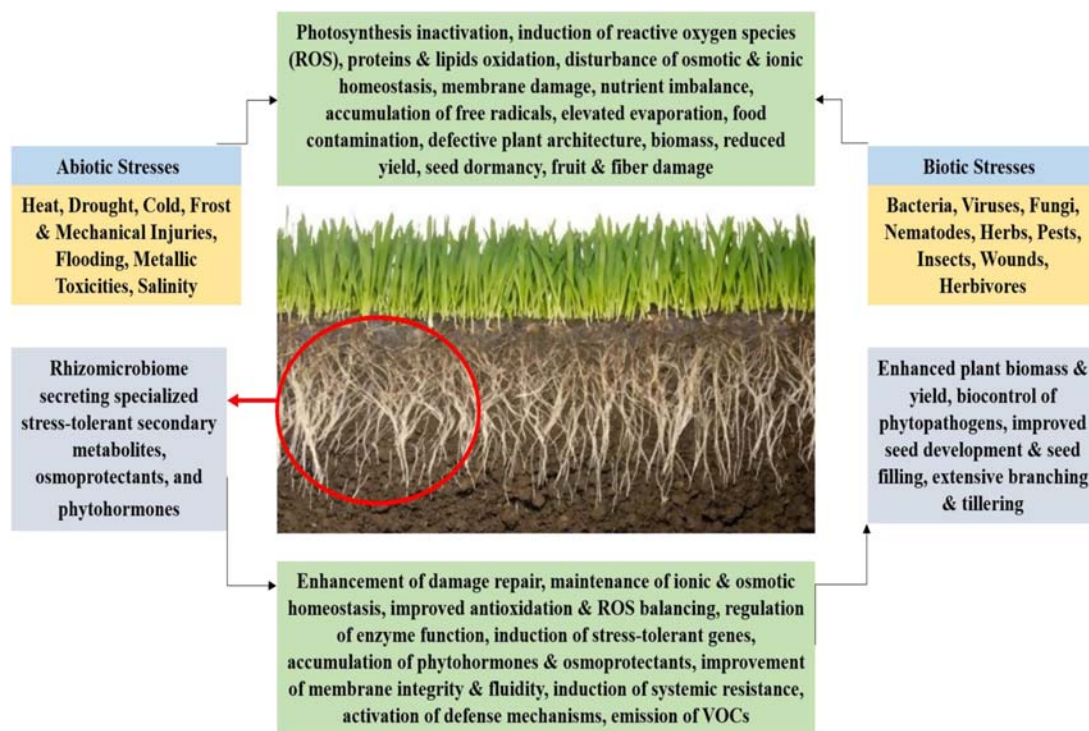
Most commonly noticed abiotic factors include deficiency or excess of water (drought and flooding), fluctuating temperature, excessive and deficient amounts of micro- and macronutrients, extremes of soil pH and irradiance, and exposure to highly saline conditions (Rosenzweig et al., 2014; Vimal and Singh, 2019). Furthermore, several mechanical stresses such as sunscald, freeze, wind, and chemical injuries, wounding, mechanical impedance of root growth in compacted soils, and exposure to xenobiotics also encompass abiotic stresses in plants (Suzuki et al., 2014). According to the Food and Agriculture Organization report, environmental constraints have affected 97% of the global land area, and foremost of these is the drought stress affecting 64% of the global land (Cramer et al., 2011). Anoxia or flooding has affected 13% of the land area, whereas acidic soils and salinity have contributed to 15% and 6% of land deterioration, respectively (Riadh et al., 2010). Similarly, salinity degradation of irrigated lands has been estimated to reach US\$ 27.3 billion, affecting 50% of the total irrigated land. Ever-increasing salinization, soil erosion, and agroecological disturbances have directly affected 3.6 billion ha of dryland agriculture and significantly influenced qualitative and quantitative losses in crop production (Qadir et al., 2014).

Plant problems caused by microbial pathogens, i.e., fungi, bacteria, viruses, pests including nematodes, insects, mites, and herbivores, are categorized as biotic stresses in plants (Bailly and Weisskopf, 2012; Vimal et al., 2017). Biotic stresses are the major constraints to agricultural productivity in developing countries that have fewer resources to combat pre- and postharvest infections and infestations. Association of biotic or abiotic stresses or the combinational effects of biotic stresses were found to aggravate the damage in plants, leading to drastic drop in crop productivity (Atkinson and Urwin, 2012). Biotic stress agents directly reduce plant vigor and deprive their hosts of essential nutrients contributing to annual crop losses. For instance, global yield losses of 20%–40% were

quantified in major cultivated crops of soybean, maize, rice, wheat, coffee, cotton, and barley, due to diseases and pest infestations (van-Ittersum et al., 2013). Moreover, perennial crops experience 26% and 38% of the primary and secondary yield losses, respectively, because of fungal/bacterial diseases and foliar pests (Cerda et al., 2017).

### 4.3 MICROBE-MEDIATED STRESS MANAGEMENT IN PLANTS

Biotic and abiotic stresses in plants lead to certain morphological and anatomical changes, and plants respond to these changes by several inherent stress-specific strategies. However, despite possessing a plethora of sophisticated strategies to counteract these stresses, fluctuating environmental conditions and pests could disturb homeostatic metabolism in plants (Massad et al., 2012; Yolcu et al., 2016). In this situation, many times, plants get facilitated by their inhabiting microbiome that helps to reduce the burden of environmental and biotic stresses (Turner et al., 2013; Ngumbi and Kloepper, 2014; Singh et al., 2016b). Plant microbiomes have emerged as the integral part of the crop production system where they not only help in plant growth stimulation through nutrient acquisition but also provide fundamental support in tolerating abiotic stresses and resistance against encountering phytopathogens (Choudhary, 2012; Singh et al., 2014; Nguyen et al., 2016). Plant microbiome refers to the root-associated (rhizosphere) microbial population where microbial count is noticeably high as compared with the other bulk soil. Rhizosphere region creates a microenvironment where plant root secretions or root exudates attract microbial attention and play a vital factor in microbial colonization. Utilization of this rhizosphere microenvironment modulates the role of colonizing microbes as plant growth-promoting rhizobacteria (PGPR) where they can act as biofertilizers, nutrient mobilizers, biocontrol agents, and phytostimulators (Braud et al., 2009; Hayat et al., 2010; Singh, 2013). Microbial metabolic pathways, secondary metabolites, and genetic modulations upon interaction with plants can also evoke certain localized and systemic responses to fight the challenging conditions (Sessitsch et al., 2012). Complete understanding of multilateral rhizosphere plant-microbe interactions have helped to understand multiphasic stress-associated management in microbial communities and how they modulate plant's responses to mitigate abiotic and biotic stress conditions (Fig. 4.1).



**FIG. 4.1** Multilateral rhizosphere plant-microbe interactions to mitigate abiotic and biotic stress conditions in plants.

#### 4.4 SECONDARY METABOLITES IN ALLEVIATION OF ABIOTIC STRESSES IN CROP PLANTS

Microbial-plant interactions are key to alleviate and cope with abiotic stress challenges to crop plants. Microbial secondary metabolites stand at the top in benefiting the plants to manage in stress conditions by modulating plants intrinsic metabolic pathways and induction of systemic resistance. Rhizosphere occupants secrete multitude of secondary metabolites that help the plants to endure drought, salinity, osmolytic, and mechanical injuries.

##### 4.4.1 Salinity Stress

High concentration of  $K^+$ ,  $Ca^{2+}$ ,  $Mg^{2+}$ ,  $Na^+$ , and  $Cl^-$  salts, present in the soil, significantly influence agricultural productivity. Absorption and accumulation of these ions in plants hamper proper working of photosynthetic machinery, damage tissue, and disturb ionic balance of the cells, leading to oxidative stress. Moreover, disturbance in cell elongation and reduction in photosynthesis induces reactive oxygen species (ROS) that negatively affects plant development (Bojórquez-

Quintal et al., 2014; Vimal et al., 2019). Bacteria-induced salinity tolerance has been described for various PGPR genera including *Bacillus*, *Pseudomonas*, *Rhizobium*, *Azotobacter*, *Enterobacter*, and *Burkholderia* spp. (Tiwari et al., 2011; Singh, 2014; Sorty et al., 2016; Vimal et al., 2018, 2019). Secondary metabolites and metabolic by-products of PGPR can modulate plant metabolism helping to withstand extreme salinity conditions. For instance, salinity stress is often correlated with emission of large amounts of ethylene, which is highly lethal to plants. PGPR possess an enzyme 1-aminocyclopropane-1-carboxylate (ACC) deaminase that can reduce ethylene levels by converting it into  $\alpha$ -ketobutyrate and ammonia (Siddiquee et al., 2015). Several ACC deaminase-producing PGPR strains have been used as successful bioinoculants to ameliorate salt tolerance in plants (Singh et al., 2016a; Vimal, 2018). Zhou et al. (2017) reported increased salinity tolerance and decreased stress-induced ethylene production in sugar beet by ACC deaminase-producing halotolerant *Micrococcus* spp., *Planococcus* spp., and *Variovorax paradoxus*-inoculated plants. Likewise, ACC deaminase-producing *Pseudomonas* spp., *Klebsiella*

spp., *Rhizobium* spp., *Marinobacterium*, *B. endophyticus*, *B. tequilensis*, *B. amyloliquefaciens*, *Halobacillus*, *Halomonas*, *Curtobacterium albidum*, and *Pantoea agglomerans* have shown considerable biomass increase, accumulation of osmolytes, salinity tolerance, salt amelioration, and balance of  $\text{Na}^+/\text{K}^+$  ion regulation in maize, peanut, corn, wheat, cucumber, rice, and canola plants (Qin et al., 2014; Sharma et al., 2016; Shukla et al., 2012; Szymańska et al., 2016; Yuan et al., 2016; Zhao et al., 2016; Zhou et al., 2017; Fouda et al., 2018; Vimal et al., 2019).

Emission of volatile organic compounds (VOCs) was first characterized by Ryu et al. (2004), and a number of plant growth-stimulating rhizobacteria were characterized for VOC-mediated homeostasis of root iron uptake and endogenous auxin (Bitas et al., 2013; Farag et al., 2013; Ryu et al., 2003; Zhang et al., 2009). However, more recently documented is the potential of these small organic molecules in salinity amelioration and inducers of disease resistance. VOC-induced stress tolerance allows plants to effectively cope with excessive accumulation of  $\text{Na}^+$  ions, causing osmotic regulation, and helps to accordingly adjust their endogenous metabolism. VOC-mediated salt tolerance facilitates plants via tissue-specific regulation of *HKT1* (xylem parenchyma-expressed  $\text{Na}^+$  transporter) and plant SOS (posttranscriptional activator of the  $\text{H}^+/\text{Na}^+$  antiporter) pathways. One of the latest databases of microbial VOCs indicates the chemical diversity, viability, and success of VOCs in conferring salinity tolerance to crop plants. Volatile organic compounds chemically belonging to alcohols, organic acids, furans, esters, ethers, aromatic compounds, terpenes, ketones, aldehydes, alkanes, and nitrogenous compounds from bacterial phyla *Firmicutes*, and *Proteobacteria*, and *Ascomycetes* fungi have been evaluated for salinity tolerance in maize, soybean, barley, wheat, rice, and model plant *Arabidopsis thaliana* (Gfeller et al., 2013; Hung et al., 2014; Kanchiswamy et al., 2015; Schenkel et al., 2015). Vaishnav et al. (2015) unveiled the role of VOC emissions as activators of proline in plant tissues, which causes reduction in electrolyte leakage and maintenance of water content, leading to salinity and osmotic tolerance. Corn, wheat, rice, chickpea, soybean, and *Arabidopsis* have displayed considerable resistance to salinity when inoculated with proline-expressing *Pseudomonas* spp., *Rhizobium* spp., *Exiguobacterium oxidotolerans*, and *Azospirillum* strains (Vaishnav et al., 2015, 2016). In addition to induced systemic tolerance under high salt concentrations, crop plants treated with halotolerant plant growth-promoting bacteria (PGPB) showed higher levels of

vegetative storage proteins that are known to facilitate plant growth under stress conditions. Besides bacteria, arbuscular mycorrhiza fungi (AMF) are ubiquitous inhabitants of plant rhizosphere and have been widely reported for their mitigation of  $\text{NaCl}$  stress. AMF have been reported to contribute to plant salinity tolerance by accumulating ROS scavengers in plant tissues and homeostatic regulation of several ion channels. Several species of symbiotic fungi have the ability to upregulate glutathione, thiol-dependent peroxidases (APX), glutathione reductases (GR), tocopherol, ascorbates, superoxide dismutases (SOD), and catalases in plants, suppressing salinity stress and contributing to plant growth (Luo et al., 2012; Khan et al., 2013; Guerrero-Galán et al., 2019). Table 4.1 enlists some of the salinity-ameliorating PGPB and AMF and their mode of salinity amelioration in different crop plants.

#### 4.4.2 Drought Stress

Drought stress in plants is characterized as one of the most widespread stresses that broadly affects plants and is responsible for the most fatal losses in agriculture (Vimal et al., 2016). Crop plants face loss of membrane integrity, decreased germination rates, inhibition of photosynthesis, and induction of tissue-damaging ROS. Because of prolonged water stress, plants are subjected to low water potential in their leaves, reduction of leaf size and stomatal opening, reduced seed number, size and viability, suppression of root growth, and delay of flowering and fruiting (Xu et al., 2016). Drought stress is mainly responsible for osmotic stress in plants and is correlated with accumulation of phytohormones and abscisic acid (ABA) that ultimately induce ROS (Mauch-Mani and Mauch, 2005). Plants cope with drought challenges through their diverse inherent mechanisms; however, they often cannot survive the damages of the drought. Herein comes the importance of rhizomicrobiome that facilitates plant growth through water use efficiency (osmotic adjustment, stomatal regulation) and curtails drought tolerance. Several PGPB can biosynthesize antistress biochemicals and activate host stress response system to mitigate the impacts of drought (Waqas et al., 2012).

Several crop plants including rice, dune grass, tomato, soybean, and panic grass have been demonstrated for using less water and increased crop productivity upon inoculation with drought-tolerant PGPB. The possible drought-tolerant mechanism of these PGPB and AMF is attributed to their ability of increasing concentration of solutes, accumulation of SMs, and transcriptional regulation of genes in

**TABLE 4.1**  
**Microbial Strains, Secondary Metabolites and Enzymes in Alleviation of Abiotic Stress in Crop Plants.**

Abiotic Stresses	Microbial Strains	Secondary Metabolites/Enzymes/ Tolerance Strategy	Evaluated Crop	References
Salinity/Salt Stress	<i>Pseudomonas frederiksbergensis</i> OS261	1-Aminocyclopropane-1-carboxylate (ACC) deaminase	<i>Capsicum</i> spp.	Chatterjee et al. (2017)
	<i>Exiguobacterium oxidotolerans</i> , <i>Bacillus pumilus</i> STR2, <i>Halomonas desiderata</i> STR8	Proline	<i>Bacopa monnieri</i> (L.)	Bharti et al. (2013)
	<i>Bacillus amyloliquefaciens</i> RWL-1	Abscisic acid Salicylic acid	<i>Oryza sativa</i>	Shahzad et al. (2017)
	<i>Bacillus subtilis</i> GB03	VOC <sup>a</sup> s, regulation of Na <sup>+</sup> transporter <i>HKT1</i>	<i>Arabidopsis thaliana</i> White clover	Zhang et al. (2008)
	<i>Pseudomonas simiae</i> AU	Proline, 4-nitroguaiacol, quinolone	Soybean	Vaishnav et al. (2015)
	<i>Pseudomonas fluorescens</i> WCS417r	Accumulation of terpenes and phenols	Marigold	Cappilari et al. (2013)
	<i>Azospirillum brasilense</i> Sp7			
	<i>Pseudomonas koreensis</i> AK-1	Proline, stress enzymes	<i>Glycine max</i> L. Merrill	Kasotia et al. (2015)
	<i>Enterobacter cloacae</i> HSNJ4	IAA <sup>a</sup> , ACC deaminase	Canola	Li et al. (2017)
	<i>Sinorhizobium meliloti</i> RD64	IAA, trehalose, proline	<i>Medicago truncatula</i>	Bianco and Defez (2009)
	<i>Scytonema hofmanni</i> , <i>Cyanobacteria</i> spp.	Phytohormones	Wheat, rice	Singh et al. (2014)
	<i>B. amyloliquefaciens</i> IN937a	ISR <sup>a</sup> , acetoin, 2,3-butanediol	—	Ryu et al. (2003)
	<i>Burkholderia cepacia</i> SE4, <i>Promicromonospora</i> sp. SE188, <i>Acinetobacter calcoaceticus</i> SE370	Proline, antioxidants	Cucumber	Kang et al. (2009)
	<i>Acinetobacter</i> sp. ACMS25, <i>Bacillus</i> sp. PVMX4	Antioxidative defense system	<i>Phyllanthus amarus</i>	Joe et al. (2016)
	Arbuscular mycorrhiza fungi	K <sup>+</sup> /Na <sup>+</sup> + homeostasis, osmolytes, antioxidants	Black locust, <i>Ocimum basilicum</i> , <i>Solanum lycopersicum</i> , <i>B. juncea</i> , <i>Panicum turgidum</i>	Sarwat et al. (2016)
	<i>Aspergillus flavus</i> CSH1	Osmolytes, antioxidants, hormones	<i>G. max</i> L.	Lubna et al. (2018)

Continued



**TABLE 4.1**  
**Microbial Strains, Secondary Metabolites and Enzymes in Alleviation of Abiotic Stress in Crop Plants.—cont'd**

Abiotic Stresses	Microbial Strains	Secondary Metabolites/Enzymes/ Tolerance Strategy	Evaluated Crop	References
Cold Stress	<i>P. frederiksbergensis</i> QS261	ACC deaminase	Tomato	Subramanian et al. (2016)
	<i>Pseudomonas vancouverensis</i> OB155-gfp	Reduction in ROS <sup>a</sup>	<i>Solanum lycopersicum</i>	Subramanian et al. (2015)
	<i>Burkholderia phytofirmans</i> PsJN	Proline, starch, phenolic accumulation	Grapevine	Barka et al. (2006); Raheleh et al., (2015)
	<i>Arthrobacter, Flavimonas, Flavobacterium, Massilia, Pedobacter</i> sp.	Proline, starch, phenolic accumulation	Tomato	Subramanian et al. (2016)
	<i>Sphingomonas faeni</i>	Bioactive and osmoprotectant metabolites	Finger and foxtail millet	Srinivasan et al. (2017)
	<i>Pantoea dispersa</i>	HCN <sup>a</sup> , IAA, siderophore	Wheat	Selvakumar et al. (2008)
Drought Stress	<i>Variovorax paradoxus</i> 5C-2	ACC deaminase	<i>Pisum sativum</i>	Belimov et al. (2009)
	<i>B. phytofirmans</i> PsJN	ACC deaminase, siderophores, ECF <sup>a</sup> sigma factors	Potato	Srinivasan et al. (2017)
	<i>Rhizobium tropici</i> (CIAT 899), <i>Paenibacillus polymyxa</i> (DSM 36)	Trehalose	Common bean	Figueiredo et al. (2008)
	<i>Glomus intraradices, Pseudomonas mendocina</i> Palleroni	Proline, antioxidative catalase	Lettuce	Kohler et al. (2008)
	<i>Glomus intraradices Pseudomonas chlororaphis</i> O6	Glutathione, ascorbate 2,3-Butanediol	Lavender	Marulanda et al. (2007)
	<i>B. amyloliquefaciens</i> GB03	WRA <sup>a</sup>	—	Cho et al. (2008)
	<i>Pseudomonas</i> sp. M30-35	VOCs, ISR	<i>Lolium perenne</i> L.	Su et al. (2017)
	<i>B. subtilis</i> GB	VOCs	Ryegrass	He et al. (2018)
	<i>Pseudomonas putida</i> GAP-P45	Choline, glycine betaine	<i>Arabidopsis</i>	Zhang et al. (2010)
	<i>Bacillus thuringiensis</i> AZP2	EPS production	<i>Helianthus annuus</i>	Sandhya et al. (2009)
	<i>B. phytofirmans</i> PsJN, <i>Enterobacter</i> sp. FD17	VOCs	Wheat	Timmusk et al. (2014)
	<i>Serratia</i> sp. XY21, <i>B. subtilis</i> SM21, <i>Bacillus cereus</i> AR156	Increased photosynthesis, auxins	—	Naveed et al. (2014)
	<i>Bacillus licheniformis</i> K11	Proline, antioxidants, monodehydro ascorbate	<i>Zea mays</i>	Wang et al. (2012)
	<i>Trichoderma harzianum</i>	Proteins, VOCs	<i>Cucumis sativa</i>	Lim and Kim (2013)
<i>Phoma glomerata, Penicillium</i> sp.	Proline, VOCs, antioxidants	<i>Capsicum annum</i>	Lim and Kim (2013)	
	Antioxidants	Tomato	Mona et al. (2017)	
	Antioxidants	Cucumber	Waqas et al. (2012)	

TABLE 4.1

## Microbial Strains, Secondary Metabolites and Enzymes in Alleviation of Abiotic Stress in Crop Plants.—cont'd

Abiotic Stresses	Microbial Strains	Secondary Metabolites/Enzymes/ Tolerance Strategy	Evaluated Crop	References
	<i>Trichoderma hamatum</i> DIS 219b	Peroxidases, catalases, superoxide dismutases	<i>Theobroma cacao</i>	Bae et al. (2009)
	<i>T. harzianum</i> TH-56	Dehydrin, aquaporin upregulation	<i>Oryza sativa</i>	Pandey et al. (2016)
Osmotic Stress	<i>Bacillus megaterium</i>	Increased root expression of osmoprotectants	<i>Z. mays</i>	Aroca et al. (2007)
	<i>Piriformospora indica</i>	ACC oxidase, lipid transfer proteins	<i>C. annuum</i>	Sziderics et al. (2007)
	<i>Glomus intraradices</i> BEG123	Osmoprotectants, active solute transportation	<i>Phaseolus vulgaris</i>	Marulanda et al. (2010)
	<i>Pseudomonas</i> sp.	Glucan, water dikinase, starch degradation	<i>Nicotiana tobaccum</i> , <i>Arabidopsis</i> , <i>Epacrids</i>	Sarma et al. (2011)
Temperature Stress	<i>B. amyloliquefaciens</i> , <i>Azospirillum barsilense</i>	Secondary metabolites production	Wheat	Timmusk et al. (2014)
	<i>Curvularia</i> sp.	Root colonizing metabolites	<i>Solanum</i> sp.	de Zelicourt et al., (2013)
	<i>P. fluorescens</i> PslA12, <i>Pantoea agglomerans</i> 050309 <i>Mycobacterium</i> sp. 44	IAA <sup>a</sup> , ACC deaminase, stress proteins induction	Wheat	Egamberdiyeva and Höflich (2003)
	<i>Pseudomonas</i> sp. AKM-P6	Proline, chlorophyll, sugars, amino acids	Sorghum	Ali et al. (2009)
Metal Toxicity	<i>Streptomyces</i> <i>acidiscabies</i> E13	Siderophores, auxins, coelichelin	Cowpea	Dimkpa et al. (2009)
	<i>Rahnella</i> sp. JN27	ACC deaminase, siderophores	<i>Z. mays</i>	Yuan et al. (2014)
	<i>Pseudomonas</i> <i>koreensis</i> AGB-1	Extracellular sequestration, tolerance to Zn, Cd, As, and Pb	<i>Miscanthus sinensis</i>	Babu et al. (2015)
	<i>Staphylococcus arlettae</i>	Dehydrogenase, phosphatase	<i>Brassica</i>	Srivastava et al. (2013)
	<i>Pseudomonas</i> <i>aeruginosa</i>	ACC deaminase, soluble proteins	Wheat	Islam et al. (2014)
	<i>Bacillus</i> sp. SLS18		<i>Sorghum bicolor</i> , <i>Solanum nigrum</i> , <i>Phytolacca acinosa</i>	Luo et al. (2012)
	<i>Pseudomonas</i> sp., <i>Rhizobium</i> sp.	Metal-chelating metabolites	<i>Brassica</i>	Adediran et al. (2016)
	Arbuscular mycorrhiza fungi	H <sub>2</sub> O <sub>2</sub> , proline	Tomato, <i>Tagetes</i> <i>erecta</i> , <i>Pisum sativum</i> , cotton, <i>Calendula</i>	Hashem et al. (2016), Hristozkova et al. (2016)

<sup>a</sup> ECF, extracytoplasmic function; EPS, exopolysaccharides; IAA, indole-3-acetic acid; ISR, induced systemic resistance; HCN, hydrogen cyanide; ROS, reactive oxygen species; VOC, volatile organic compounds; WRA, water-retaining agents.

inoculated plants as compared with uninoculated control plants. For instance, cacao plants displayed changes in gene expression patterns to withstand drought conditions when inoculated with *Trichoderma* (Bailey et al., 2006).

Microbial VOCs-induced drought tolerance in plants results in accumulation of nitric oxide and H<sub>2</sub>O<sub>2</sub>. In addition to this, drought-stressed plants accumulate choline and other osmoprotectants to trigger the expression of diverse inherent pathways of plants to withstand stress (Zhang et al., 2010). Accumulation of osmoprotective SMs in plant tissues leads to prevention of water loss by increase cellular osmotic pressure to lower the free water potential and contribute to membrane integrity. This phenomenon was highlighted by Zhang et al. (2010) where *B. amyloliquefaciens* GB03—inoculated *Arabidopsis* plants showed higher levels of glycine betaine and choline as compared with uninoculated controls. Likewise, 2,3-butanediol-producing *Pseudomonas chlororaphis* strain O6—inoculated *Arabidopsis* plants showed higher tolerance to dehydration stress in comparison with uninoculated ones (Cho et al., 2008). Microbes can also mitigate drought stress in plants through elevated antioxidant responses besides metabolites accumulation as explained for *Ochrobactrum pseudogregnonense* IP8—inoculated and *Bacillus safensis* W10—inoculated wheat plants. Furthermore, potato plants inoculated with PGPB showed high levels of proline and ROS-scavenging enzymes when exposed to drought stress. Likewise, exopolysaccharides-producing microbes can form biofilms and retain moisture level facilitating water retention in plants (Liu and Zhang, 2015). Table 4.1 enlists some of the successful microbial inoculants to withstand drought stress in plants.

#### 4.4.3 Osmotic Stress

Another damaging abiotic stress for the plants is oxidative stress that significantly reduces chlorophylls content and leaf gaseous exchange capacity. Plants exhibit several metabolic, cellular, and molecular responses against osmotic stress, which can be initiated through diverse array of primary and secondary stress signals including ROS, phytohormones (e.g., ABA, ethylene), and intracellular second messengers (e.g., phospholipids). Chloroplasts serve as the major site for protein degradation during oxidative stress conditions, and resultantly, plant biomass and growth drops to critical levels. According to the investigations, RuBisCo protein accounts for about 90% of the chloroplast's degraded proteins under oxidative stress (Nakano et al., 2006). Oxidative stress damage to the plants can be mitigated

through microbial secondary metabolic products. For instance, osmotolerant *Pseudomonas simiae*—treated seedlings showed maintenance of photosynthetic machinery in plants exposed to oxidative stress. Likewise, upregulation of crucial photosynthetic and chlorophyll accumulator RuBisCo proteins was demonstrated in *Arabidopsis* and rice plants inoculated with VOCs-producing microbes (Agrios, 2005; Kwon et al., 2010). Furthermore, cucumber plants treated with SMs-producing PGP bacterial consortium showed increased chlorophyll content under aggravated osmotic stress (Wang et al., 2012). Moreover, increased expression of RuBisCo large chain precursor was noted in *Pseudomonas fluorescens*—primed rice plants, suggesting plant growth promotion under abiotic stresses (Kandasamy et al., 2009).

Among microbial SMs, proline- and glycine betaine—producing microbes, particularly PGPR, synergistically act to increase osmotic stress tolerance in plants. High levels of proline and glycine betaine accumulation stabilize membrane enzymes and proteins, adjust osmotic pressure in plant tissues, maintain redox homeostasis, and scavenge ROS to fight osmotic stress (Banu et al., 2009). Table 4.1 enlists some of the osmotolerant microbes and their potential mechanisms to increase stress survivability in crop plants.

#### 4.4.4 Cold and Temperature Stress

Erratic global climatic conditions put plants on the challenge to face extreme temperature fluctuations. Temperature fluctuations severely impact plant internal metabolism and disturbance of homeostatic balance, which leads to decreased agricultural productivity. For instance, plants exposed to high temperatures show aggregation and extensive denaturation of cellular proteins that can lead to cell death, whereas cold stress in plants induces alterations in membrane proteins morphology and structure, inhibition of fundamental enzymatic reactions, and impaired metabolic processes and interactions between macromolecules (Theocharis et al., 2012).

Plants respond toward frost injuries and high-temperature stresses through their inherent tolerance mechanisms. Crop plants alleviate frost injuries either through antifreeze proteins or by avoidance of supercooling of plant tissue-water by the process called acclimation displaying short photoperiods. However, recently explored is the facilitation in temperature and freezing stresses to plants by inhabiting plant rhizomicrobiome. Genomic and metagenomic analysis of several cultivable and noncultivable plant microbes reveals mechanisms to cold and high-temperature

adaptations by expressing antifreeze and cold shock proteins, pH homeostasis, and compatible solutes production pathways (Theocharis et al., 2012). Moreover, inoculation with temperature-tolerant PGPR and AMF has shown enhanced nutrient uptake, increased accumulation of osmolytes, and improved photosynthetic capacity and efficacy. For instance, *Dichantheium lanuginosum* (grass) inhabiting Yellowstone National Park can withstand 38–65°C temperatures, and this tolerance is directly attributed because of its root-colonizing fungus *Curvularia protuberata* (Lata et al., 2018). Similarly, entophytic fungi have been shown to induce heat tolerance in wheat and increased plant biomass and grain yield despite the stress (Hubbard et al., 2014). Acclimation processes by these microbes are mainly due to the production of antioxidants that maintain plant's biological activities and extend cold tolerance. This phenomenon was recently witnessed in *Burkholderia phytofirmans* PsJN-inoculated grapevines, which showed long-term chilling stress tolerance (Fernandez et al., 2012). Cold stress-tolerant microbes also regulate carbohydrate mechanism to impart cold acclimation and maintain membrane fluidity conditions. *Saccharomyces cerevisiae*, *Leucosporidium fellii*, *Pseudomonas fragi* P121, and *Mrakia frigida* have shown the high accumulation of glycerol and trehalose to mitigate frost injuries in plants (Subramanian et al., 2016). Likewise, genetically engineered microbial strains have been developed with upregulation of trehalose, proline, phenols, and flavonoids to modulate high temperatures in plants.

#### 4.4.5 Metal Stress

Continuous leaching and contamination of agricultural soils due to addition of agrochemicals leads to metal toxicity and impacts agricultural productivity. Heavy metal stress confers severe difficulties in crop plants interfering their biochemical and physiological processes, rate of photosynthesis, nitrogen and protein metabolism, and nutrient uptake (Zhang et al., 2009; Vimal et al., 2017). Despite possessing an inherent potential to cope up metal toxicity, they often face fatal and permanent damage of their tissues and plant death. Herein, nature comes with its own bugs to debug the plant toxicity and enables plant rhizosphere microbial flora to ease plants to mitigate heavy metals. Microbial secondary metabolites act as an additional arsenal to the host to combat negative effects of metal toxicity. Among these, rhizomicrobiome and tissue-colonizing fungi have been extensively elucidated for their role in reducing metal toxicity (Luo et al., 2012). Fungal endophytes from genera *Microsphaeropsis*, *Mucor*, *Phoma*, *Alternaria*, *Peyronella*, *Steganosporium*, and *Aspergillus*

have shown good growth potential even in contaminated soils and sequestration of metals and salts. Some of the studies also explored the biosorption potential of *Penicillium janthinellum* and *Penicillium simplicissimum* in conferring copper (Cu), cadmium (Cd), lead (Pb), aluminum, and zinc stress tolerance to crops with concomitant increase in plant biomass (Iskandar et al., 2011). Biosorption property of diverse fungal endophytes is attributed to the production of enzymes and bioactive secondary metabolites in these strains, which can convert toxic metals into stable complexes. For example, bioactive gibberellins from *Penicillium funiculosum* can extend tolerance against metal toxicity and damaging NaCl to soybean by their biochemical conversion into stable compounds and reduced levels of metals inside soybean tissues (Khan et al., 2011). Similarly, *Chaetomium globosum* LK4 produces gibberellins and indole-3-acetic acid (IAA), which increase copper stress fitness of *Capsicum annum* L. and rice, suggesting symbiotic fungal endophytes as the best substitutes of synthetic chemicals for bioremediation.

Bacteria can extend metal tolerance to host plants by altering the levels of certain secondary metabolites, active enzymes, and metabolic accumulation of metal stressors. ACC deaminase-producing *Pseudomonas* and *Gigaspora* sp. can enhance elemental tolerance by direct manipulation of plant ethylene levels (Friesen et al., 2011). Luo et al. (2012) reported enhanced metal uptake in crop sweet sorghum inoculated with growth-promoting *Bacillus* sp. SLS18. Likewise, IAA and siderophores producing *Pseudomonas protegens* can effectively bioremediate heavy metal-contaminated agricultural soils and imparts antifungal and insecticidal properties to crops (Bensidhoum et al., 2016). Metal-tolerant *Enterobacter* sp. strain EG16 alleviates toxic metals in *Hibiscus cannabinus* through the production of siderophores (Chen et al., 2016). Moreover, certain metal-tolerant PGPR have been evaluated for their potential of reducing arsenic and cadmium accumulation in vegetable crops. Table 4.1 summarizes some of the metal-tolerant microbes effective in extending metal tolerance to crop plants.

#### 4.5 BIOTIC STRESSES AND ITS MANAGEMENT STRATEGIES

Crop plants are always vulnerable to several bacterial, fungal, viral, and soil-dwelling phytopathogens that can hamper plant growth and cause significant productivity loss. Rhizomicrobiome contributes to provide better plant health through several direct and indirect mechanisms. Colonization of plant host internal

tissues, rhizosphere, and phyllosphere by PGPR enhances plant nutrition via phosphorous, zinc and potassium mobilization, associative nitrogen fixation, phytohormones production, and production of phyto-siderophores (Andrews, 1992; Compant et al., 2010; Drogue et al., 2013; Vacheron et al., 2013). However, the most celebrated aspect of PGPR is the inhibition of phytoparasites and microbial pathogens, which is done by bacterial and fungal SMs (Beneduzi et al., 2012; Shahid et al., 2017). Bioactive microbial SMs can suppress the growth of invading pathogens and parasites through competitive antagonism or by eliciting plant defense mechanisms such as induced systemic resistance (Pierson and Pierson, 2010).

Bacterial SMs have been extensively explored in the past two decades for the development of biofertilizers and biofungicides. Biodegradability, effectiveness against large spectrum of fungal, bacterial, and parasitic pathogens of crop plants, sustainability, and substitution of synthetic nonbiodegradable agrochemicals have resulted in significant rise of bacterial metabolites market. Bioactive secondary metabolites of *Pseudomonas* spp. constitute an incredible array of exquisite chemical structures with versatile biological functions and varying degree of fungitoxicity. These antimicrobials constitute different classes on the basis of structural similarities and differences. Some of the major antagonistic metabolites of *Pseudomonas* spp. include phenazines, pyrrolnitrin, pyoluteorin, rhizoxin, cyclic lipopeptides (CLPs), acetaminophen, polyketides, phloroglucinol, diketopiperazines, and volatile antimicrobial compounds (Mehnaz et al., 2013). *Pseudomonas* spp. SMs can help crop plants with phytotoxic, nematocidal, antimicrobial, herbicidal, antimutagenic, and anthelmintic activities against pathogenic nematodes, bacteria, fungi, and yield-affecting herbs (Shahid et al., 2018). Owing to effective biocontrol and biofertilizer properties, several pseudomonad species have been marketed as commercial products. For instance, an Indian biofungicide based on *P. fluorescens* is available with diverse trade names including ABTEC Pseudo, Biomonas, Esvin Pseudo, Sudo, Phalada 104 PF, Sun Agro Monus, and Bio-cure-B, to control plant soilborne infections (O'Callaghan, 2016). *P. chlororaphis* 63–28—based “At-Eze” can effectively fight soil- and seedborne fungi (Fravel, 2005). “Spot-Less” is based on *P. aureofaciens* Tx-1, whereas “Proradix” comprising *Pseudomonas* sp. DSMZ 13134 can effectively inhibit turf fungal diseases and root rots (Hardebeck et al., 2004). *P. fluorescens* A506—based “Blightban A506” (NuFarm Inc., United States)

can efficiently protect almond, apple, apricot, blueberry, cherry, peach, pear, strawberry, tomato, and potato against *Erwinia amylovora* infection, frost injury, and russet-inducing bacteria. A biopesticide “Mycolytin” contains *Pseudomonas aurantiaca* M-518 (Elkins et al., 2005). “Cedomon and Cerall” (BioAgri AB, Sweden) are effective inhibitors of *Pyrenophora teres*, *Pyrenophora graminea*, *Tilletia caries*, *Septoria nodorum*, and *Fusarium* spp. and are based on *P. chlororaphis* strain (O'Callaghan, 2016).

Phenazines constitute the class of over 150 redox-active secondary metabolites, produced by many bacteria and archaeal *Methanosarcina* species, particularly from fluorescent pseudomonads. These heterocyclic, pyrazine-ring aromatic metabolites are characterized for the production of brightly colored compounds that act as broad-specificity antibiotics (Guttenberger et al., 2017). Many of the fluorescent pseudomonad species are bestowed with the tremendous capacity to simultaneously produce different phenazine derivatives (Beneduzi et al., 2012; Naik and Sakhivel, 2006). Most abundant phenazine derivatives include pyocyanin (PYO), 2-hydroxyphenazine (2-OH-Phz), phenazine-1-carboxamide (PCN), phenazine-1-carboxylic acid (PCA), and 2-hydroxyphenazine-1-carboxylic acid (2-OH-Phz-1-COOH) are most commonly produced by *Pseudomonas* spp. (Pathma et al., 2010). PCA and 2-hydroxyphenazine-1-carboxylic acid (2-OH-PCA) produced by *P. chlororaphis* 30-84, *Pseudomonas putida* P-15, *P. aurantiaca* FS-2, ARS-38, PB-St2, *P. chlororaphis* RP-4, and *Pseudomonas aeruginosa* PA14 were characterized for the mycelial inhibition of phytopathogenic fungi *Gaeumannomyces graminis* var. *tritici* (causative agent of wheat take-all disease) *F. oxysporum*, *F. moniliforme*, *F. solani*, *Rhizoctonia solani*, *Alternaria alternata*, and *C. falcatum* (Wang et al., 2016a,b). Phenazine-1,6-dicarboxylic acid (Phz-1,6-di-COOH) from *P. fluorescens* 2–79, PCN from *P. aeruginosa* MML2212, and PYO from *P. aeruginosa* PA14, B0097, and B094 exhibited broad-specificity biocontrol against causal agents of root rot, seedling blight, red and stem rots in sugarcane, rice, wheat, chickpea, cotton, soybean, and okra (Al-Hinai et al., 2010; Djavaheri et al., 2012; Shanmugaiah et al., 2010; Liu et al., 2016).

Polyketides from *Pseudomonas* spp., *Burkholderia rhizoxina*, and *Rhizopus microspores* including mupirocin or pseudomonic acid, phytotoxin coronatine (COR), 2,4-diacetylphloroglucinol (DAPG), pyoluteorin (PLT), and rhizoxin successfully inhibited *Botrytis cinerea* and *Phytophthora ramorum* and were recently evaluated for insect toxicity against fruit fly *Drosophila melanogaster*

(Loper et al., 2008, 2016). Additionally, pyrrolnitrin-producing *P. fluorescens* Pf1TZ competitively inhibited plant pathogen *B. cinerea* in in vitro experiments conducted on vine plantlets and was also shown to be herbicidal against several field herbs (Kilani et al., 2010). Many of the plant-associated species of fluorescent pseudomonads produce a phenolic polyketide with diverse ecological and biocatalytic functions named as 2,4-diacetylphloroglucinol (Meyer et al., 2009). A strong inhibitor of many plant-pathogenic fungi including *Penicillium digitatum*, *Penicillium italicum*, *R. solani*, *A. alternata*, *F. moniliforme*, and *Aspergillus flavus*, 2,4 DAPG, is also toxic to many plant-parasitic and bacterial-feeding nematodes. These include *Heterodera glycines*, *Pratylenchus scribneri*, *Pristionchus pacificus*, *Caenorhabditis elegans*, and *Rhabditis rainai* (Gong et al., 2016). Phylogenomic analysis of 2,4-DAPG-producing *Pseudomonas* spp. endophytes with antiglycation ability was evaluated for their inhibitory activities through 2,4-DAPG and its derivatives (Gutiérrez-García et al., 2017).

Loper et al. (2008) first discovered orfamides from biocontrol strain *P. protegens* Pf-5 and demonstrated these compounds for strong antifungal activities against plant pathogens. Later on, orfamide A from *P. protegens* F6 was evaluated for decrease in surface tension value of water, insecticidal role, and was inimical to green peach aphid displaying dose-dependent mortality (Jang et al., 2013). Manipulation of orfamide-producing *Pseudomonas* sp. CMR12a to yield biosynthetic mutants evaluated structural dynamics and functional synergism with sessilin-type CLPs and phenazine groups to antagonize root rot causing *R. solani* (Olorunleke et al., 2017). Orfamides blocked appressorium formation in *M. oryzae*, leading to reduction in blast severity, and zoospore lysis of *Phytophthora* and *Pythium* was observed when exposed to orfamides of *Pseudomonas* sp. CMR5c (Ma et al., 2016).

Relatively new and among the novel class of CLPs, xantholysins were first characterized from *P. putida* strain BW11M1 demonstrating inhibition of pathogenic *Xanthomonas* sp. In addition to antifungal activity and toxicity against gram-positive bacteria, supportive roles of xantholysins were determined in biofilm formation, surface colonization through swarming, and inhibition of several gram-negative bacteria (Li et al., 2013). Later on, bioassay-guided insecticidal assays from extracted metabolites (xantholysins A and B) of *Pseudomonas* sp. strain DJ15 showed 50% mortality of insect plant pest *Myzus persicae* (Lim et al., 2017). Moreover, role of bio-surfactant viscosin in increasing the efficiency of *P. fluorescens* SBW25 in surface spreading onto the plant roots, bacterial swarming, protection of germinating

seedlings, and inhibition of plant pathogen *Pythium* was highlighted (Alsohim et al., 2014). Massetolides from biocontrol strain *P. fluorescens* SS101 showed successful inhibition of *Phytophthora infestans*, causative agent of late blight in many plant species (Tran et al., 2007). *Pseudomonas poae* RE\* 1-1-14 is a sugar beet isolate reported for the production of rare CLP metabolite; poaeamide caused the in vitro and in-field suppression of *Phytophthora capsici*, *P. infestans*, *Pythium ultimum*, and *R. solani* (Zachow et al., 2015). Moreover, sessilin-type cyclic lipopeptides produced by *Pseudomonas* sp. CMR12a successfully inhibited the damping-off disease on Chinese cabbage and root rot disease on beans, caused by ubiquitous pathogen *R. solani* species (Olorunleke et al., 2015). Likewise, adding to pyrrolnitrin's role as an antifungal secondary metabolite, its significance as repellent of *C. elegans* grazing was highlighted by Burlinson et al. (2013). *P. fluorescens* NZ17 effectually repelled grazing by bacterivore *C. elegans* naturally present in mushroom farms. Furthermore, nematocidal activity of pyrrolnitrin-producing *P. chlororaphis* biocontrol strain PA23 was also investigated against *C. elegans* (Nandi et al., 2015).

Among the most active classes of bioactive compounds produced by the *Bacillus*, three families of CLPs, namely, surfactin, iturin, and fengycin have been well characterized for their bioactivities. In addition to their functions as antagonistic and cytotoxic compounds, these CLPs are pivotal in root colonization of *Bacillus* (Bionda et al., 2013). Furthermore, ability of surfactins to defend plants in response of pathogen attack has been demonstrated by many research studies. A surfactin-like CLP from *B. amyloliquefaciens* B014 exhibited successful bactericidal activity for the control of bacterial blight-causing *Xanthomonas oryzae* pv. *oryzae* (Li et al., 2016). Similarly, *B. amyloliquefaciens* surfactins induced systemic resistance in *Beta vulgaris* and significantly reduced infection by the rhizomania disease vector *Polymyxa betae* in sugar beet (Desoignies et al., 2013). Recently, *B. methylotrophicus* strain XT1 CECT 8661 was explored for its antifungal potential in the suppression of necrotrophic plant pathogen *B. cinerea* (Toral et al., 2018). Likewise, a model bacterium and a commercial biofertilizer and biocontrol strain *B. amyloliquefaciens* subsp. *plantarum* FZB42 can efficiently antagonize *R. solani* (Chowdhury et al., 2015). Biocontrol efficiency of *Bacillus mojavensis* A21 for its application as natural biofungicide was expressed against *Fusarium* spp. for plant disease treatment (Ayed et al., 2018). Antifungal effects of surfactin-producing *B. subtilis* were characterized against wheat pathogen *Zymoseptoria tritici*, which is one of the main

wheat pathogens and causes significant reduction in yield (Mejri et al., 2017). Biocontrol strain *B. subtilis* strain BJ-1 caused significant reduction in rice blast fungus *Magnaporthe oryzae*, and its antifungal activity was due to CLP surfactin (He et al., 2019). Moreover, antibacterial activities of surfactins-producing bacilli including *B. pseudomycooides* strain NBRC 101232, *B. anthracis* strain ATCC 14578, *B. toyonensis* strain BCT-7112 were evaluated against bacterial wilt causing *Ralstonia solanacearum* (Yanti et al., 2017).

Iturins demonstrate strong *in vivo* and *in vitro* antifungal abilities and participate in plant protection by means of suppressing growth of invasive strains and membrane permeability. For instance, iturin A has shown broad-spectrum fungitoxicity against *Aspergillus*, *Fusarium*, *Rhizoctonia*, and *Pyricularia* spp. and other fungal pathogens (Pyoung et al., 2010).

*Bacillus* spp. strains (P5 and C3) isolated from Puba have shown strong antifungal potential against plant pathogens *F.oxysporum* f.sp. *lycopersici* and *A. flavus* (Perez et al., 2017). Likewise, a cotton endophyte of *Bacillus B. amyloliquefaciens* 41B-1, demonstrated over 50% biocontrol efficacy against verticillium wilt-causing fungus *Verticillium dahlia* (Han et al., 2015). Similarly, biological control agents (BCAs) from cell-free culture filtrates of *B. subtilis* and *B. amyloliquefaciens* displayed strong fungi toxicities against *A. alternate*, hence reducing 68%–81% lesion sizes and frequencies *ex vivo* (Ali et al., 2016). *Colletotrichum acutatum* is the causative agent of fungal infections in many crop plants worldwide and hence significantly contributes to yield reduction. Recent reports investigated the efficacy of *Bacillus* spp. for the biocontrol of anthracnose in Andean lupin caused by *C. acutatum* (Yáñez-Mendizábal and Falconí, 2018). *B. subtilis* CMB32 showed successful inhibition of anthracnose disease caused by *C. gloeosporioides* due to the production of CLP fengycin (Kim et al., 2010).

Similarly, CLP profile of plant growth-promoting endophytic *B. subtilis* HC8 showed the production of heterogeneous mixture of fengycin homologs with varying degrees of fungitoxicity (Malfanova et al., 2012). CLP-enriched extracts from *B. subtilis* M4 were tested for fungicidal effects against causative agents of damping-off of bean seedlings (*P. ultimum*) and gray mold of apple in different pathosystems. In addition to provide strong antagonism against pathogens, root preinoculation with M4 strain allowed hosts to fight more efficiently with fungal pathogens, hence reducing leave infections (Ongena et al., 2005). *Mycosphaerella fijiensis* is a global pathogen of banana causing significant fruit loss. *B. subtilis* EA-CB0015 was evaluated for

the production of a new fengycin isoform, fengycin C, and inhibited *M. fijiensis* by  $89 \pm 1\%$  (Villegas-Escobar et al., 2013). Chromatin condensation and the production of ROS was observed by marine bacterium *B. subtilis* BS155 for the biocontrol of rice blast-causing *Magnaporthe grisea* (Zhang and Sun, 2018). Biocontrol of cotton seedling damping-off disease caused by *R. solani* has also been evaluated by *B. subtilis* NCD-2 that utilizes fengycins for the suppression of pathogen (Guo et al., 2014). Antibacterial broad-specificity diffidicin was reported from *B. amyloliquefaciens* strains FZB42 and GA1 (Arguelles-Arias et al., 2009). Recent studies demonstrated its promising potential in inhibition of necrotrophic fire blight disease causing *E. amylovora*. Similarly, macrolactins are complex polyketide with diversified structures and were reported for suppression of gram-positive bacterial pathogens (Romero-Tabarez et al., 2006).

Bacterial QS network also regulates the production of versatile iron-scavenging molecules known as siderophores. Microbial siderophores sequester iron molecules under Fe-limited conditions and make it unavailable for the use of phytopathogens, thereby suppressing their growth. Pyoverdines, pyochelin, quinolobactin, achromobactin, and pseudomonine are the commonly known microbial siderophores since long, and their biosynthesis pathways were unveiled by researchers (Zhang and Rainey, 2013). Other than diffusible SMs, production of volatile SMs is an important aspect of bacterial secondary metabolism. VOCs constitute the group of structurally diverse, low-molecular-weight, and high-vapor-pressure chemical compounds considered to be the products of certain catabolic pathways such as lipolysis, proteolysis, and glycolysis (Murthy et al., 2014). These compounds not only can induce systemic resistance in plants against several pathogens but also have been reported to exhibit antimicrobial and nematocidal activities (Audrain et al., 2015). For instance, VOCs produced by the strain *P. fluorescens* UM270 were reported for antifungal and plant growth-promoting potential and efficiently repressed *R. solanacearum*, a causal agent of tomato wilt (Seleim et al., 2011). Similarly, cyanogenesis or the production of cyanide compounds including hydrogen cyanide (HCN) has been reported from many strains of fluorescent pseudomonads that exhibit toxicity against plant pathogens by the inhibition of cytochrome-C oxidase (Nandi et al., 2017). *P. fluorescens* was evaluated for the production of VOCs such as 2-decanol, 2-tridecanol, 1-undecanol, 1-nonene, dodecane, m-xylene, and ethyl-benzene and demonstrated concentration-dependent bacteriostatic effect on the

**TABLE 4.2**  
**Microbial Secondary Metabolites and Bioactive Compounds in Alleviating Biotic Stresses in Crop Plants.**

Secondary Metabolites	Producer Strains	Evaluated Crops	Bioactivities	References
Hydrogen cyanide	<i>Pseudomonas aeruginosa</i> PAO1, <i>Pseudomonas aurantiaca</i> PB-St2, FS-2, ARS-38, <i>Pseudomonas chlororaphis</i> RP-4	Wheat, rice, tomato, sugarcane	<sup>a</sup> Anti- <i>b</i> , <sup>a</sup> Anti- <i>f</i> , <sup>a</sup> <i>Phtytox</i> , <sup>a</sup> <i>nema</i>	Shahid et al. (2017), Wells (2017)
Albuterol 1,3-Propanediol	<i>Bacillus subtilis</i> SYST2	Tomato	Anti- <i>f</i> , <sup>a</sup> PGP	Tahir et al. (2017)
2,3-Butanediol acetoin Dimethyl disulfide (DMDS) 1-Undecene 2-Undecanone 4,7-Dimethylundecane 2-Methanethiol (MT)	<i>Pseudomonas fluorescens</i> WR-1 <i>Pseudomonas tolaasii</i> (NCPB2192, USB1, USB66), <i>Pseudomonas</i> spp., <i>Achromobacter</i> sp. MM1, <i>Serratia</i> sp. DM1	Mushrooms, potato	Anti- <i>f</i>	Raza et al. (2016), Lo Cantore et al. (2015), De Vrieze et al. (2015)
Hexadecane, 2,3- dimethoxybenzamide, <i>O</i> - anisaldehyde	<i>Bacillus atrophaeus</i> CAB-1, <i>Burkholderia</i> <i>ambifaria</i>	Tomato, chilli, rice, soybean, banana	Anti- <i>f</i>	Kanchiswamy et al. (2015)
1,3,5-Trichloro-2-methoxy benzene	<i>Streptomyces</i> strains W47, W214	—	Anti- <i>f</i>	Cordovez et al. (2015)
Isoamyl acetate, 2-methyl butanol, isobutyric acid	<i>Muscodor albus</i>	Banana	Anti- <i>f</i>	Strobel et al. (2011)
β-Elementene, β-caryophyllene	<i>Trichoderma virens</i>	<i>Arabidopsis</i>	Anti- <i>f</i>	Contreras-Cornejo et al. (2014)
Peptaibiotics, gliotoxin, gliovirin, pyrones, isocyanide, epidithiodioxopiperazines, dioxolanones	<i>Trichoderma</i> <i>harzianum</i>			Contreras-Cornejo et al. (2014)
Phenazine	<i>P. chlororaphis</i> 30-84	Wheat	<sup>a</sup> Anti- <i>f</i> , PGP	Pierson and Pierson (2010), Kerr (2000)
2-Acetamidophenol	<i>P. fluorescens</i> 2–79	Wheat	Anti- <i>f</i>	Slininge et al. (2000)
<sup>b</sup> PCA	<i>P. chlororaphis</i> 30-84 <i>P. aurantiaca</i> PB-St2, <i>Pseudomonas putida</i> P-15, <i>P. aurantiaca</i> FS-2, <i>P. chlororaphis</i> RP-4	Wheat, rice, corn	<sup>a</sup> Anti- <i>b</i> , Anti- <i>f</i>	Pathma et al. (2010), Shahid et al. (2017), Mehnaz et al. (2013)
Phenazine carboxamide	<i>P. aeruginosa</i> MML2212	Rice	Anti- <i>f</i>	Shanmugaiah et al. (2010)
Pyocyanin	<i>P. aeruginosa</i> PA14, B007, B094	—	Anti- <i>b</i> , Anti- <i>f</i>	Cezairliyan et al. (2013), Al-Hinai et al. (2010), Djavaheri et al. (2012)

Continued



**TABLE 4.2**  
**Microbial Secondary Metabolites and Bioactive Compounds in Alleviating Biotic Stresses in Crop Plants.—cont'd**

Secondary Metabolites	Producer Strains	Evaluated Crops	Bioactivities	References
<sup>b</sup> 2,8-di-OH-Phz	<i>P. aurantiaca</i> PB-St2	Wheat	Anti- <i>b</i>	Mehnaz et al. (2013)
<sup>b</sup> 2-OH-Phz-1-COOH	<i>P. chlororaphis</i> 30-84 <i>P. aurantiaca</i> PB-St2	Wheat, rice	Anti- <i>f</i>	Wang et al. (2016a,b), Mehnaz et al. (2013)
<sup>b</sup> Phz-1,6-di-COOH	<i>P. fluorescens</i> 2–79	Wheat	Anti- <i>f</i>	Kerr (2000)
<sup>b</sup> 6-Methyl-Phz-1-COOH or 5-methyl-Phz-1-COOH	<i>P. putida</i> PUW5	—	Anti- <i>f</i>	Kennedy et al. (2015)
<sup>b</sup> 2-OH-Phz	<i>P. aeruginosa</i> BRp3, <i>P. chlororaphis</i> GP72, RP-4, <i>P. aurantiaca</i> FS-2, ARS-38, <i>P. aeruginosa</i> PA14	Rice, wheat, cotton	Anti- <i>f</i> , <sup>a</sup> <i>nema</i>	Yasmin et al. (2017), Liu et al. (2016), Shahid et al. (2017), Cezairliyan et al. (2013)
Pyrrrolnitrin, oxypyrrrolnitrin	<i>Pseudomonas</i> sp., <i>P. chlororaphis</i> PA23	<i>Brassica napus</i>	Anti- <i>f</i> , <i>nema</i>	Hashimoto and Hattori (1966), Nandi et al. (2015)
Pyoluteorin	<i>P. fluorescens</i> Pf-5	Cotton, maize, millet, potato	Anti- <i>f</i> , <sup>a</sup> <i>herbi</i>	Kidarsa et al. (2011)
Rhizoxin, Rhizoxin D	<i>P. fluorescens</i> Pf-5	Cotton, maize, millet, potato	<i>Phytox</i> , Anti- <i>f</i> ,	Loper et al. (2008)
Mupirocin	<i>P. fluorescens</i> NCIMB 10586	—	Anti- <i>b</i>	Gao et al. (2014)
Iturin Bacilysin Bacillomycin Ssurfactin Subtilin Subtilosin	<i>Bacillus amyloliquefaciens</i> VB7, <i>B. subtilis</i> JKK238, <i>B. amyloliquefaciens</i> B014, <i>B. methylotrophicus</i> XT1 CECT 8661, <i>B. amyloliquefaciens</i> subsp. <i>plantarum</i> FZB42, <i>B. mojavensis</i> A21	Carnation, arugula, wheat, rice, soybean, potato, chilli, tomato	Anti- <i>f</i> , <sup>a</sup> <i>biosurf</i> , Anti- <i>b</i> , <sup>a</sup> Anti- <i>v</i>	Kim et al. (2007), Li et al., (2016), Toral et al., (2018), Chowdhury et al., (2015), Ayed et al., (2018), Vinodkumar et al., (2017)
Viscosin/viscosinamide	<i>P. fluorescens</i> SBW25	Pine	<i>nema</i> , Anti- <i>f</i> , <sup>a</sup> <i>biosurf</i>	Bonnichsen et al. (2015)
<sup>b</sup> WLIP, massetolides	<i>P. aurantiaca</i> PB-St2 <i>Pseudomonas reactans</i> NCPPB1311, <i>P. fluorescens</i> SS101	Wheat, tomato, <sup>a</sup> <i>bf</i> , <sup>a</sup> <i>S.m</i>	Anti- <i>f</i>	de Bruijn et al. (2008), Mehnaz et al. (2013), Coraiola et al. (2006)
Tensin	<i>P. fluorescens</i> 96.578	Sugar beet	Anti- <i>f</i>	Henriksen et al. (2000)
Amphicin	<i>Pseudomonas</i> sp. DSS73	Mushroom, sugar beet	Anti- <i>f</i>	Sørensen et al. (2002)

**TABLE 4.2**  
**Microbial Secondary Metabolites and Bioactive Compounds in Alleviating Biotic Stresses in Crop Plants.—cont'd**

Secondary Metabolites	Producer Strains	Evaluated Crops	Bioactivities	References
Orfamide A	<i>Pseudomonas</i> sp. CMR5c	Rice	Anti- <i>f</i> , <sup>a</sup> <i>insect</i>	Ma et al. (2016)
Xantholysin A	<i>P. putida</i> BW11M1	—	Anti- <i>b</i>	Li et al. (2013)
2,4-Diacetylphloroglucinol	<i>P. fluorescens</i> Pf-5, PFM2, F113, CHAO	Rice, wheat, chilli, potato	<sup>a</sup> Anti- <i>f</i> , <sup>a</sup> Anti- <i>b</i> , <sup>a</sup> <i>herbi</i> , <sup>a</sup> <i>Anthel</i>	Gutiérrez-García et al. (2017), Meyer et al. (2009)
Lahorenoic acids A–C	<i>P. aurantiaca</i> PB-St2, GS-1, GS-3, GS-4, GS-6, GS-7, FS-2, ARS-38, <i>P. chlororaphis</i> RP-4	—	<sup>a</sup> ND Anti- <i>b</i> ND	Mehnaz et al. (2013), Shahid et al. (2017)
Pyoverdine	<i>P. fluorescens</i> 2–79, <i>P. fluorescens</i> SBW25, BBc6R8	—	Fe <sup>++</sup> scavenger	Zhang and Rainey (2013), Deveau et al. (2016)
Pyochelin	<i>P. fluorescens</i> BBc6R8	—	Fe <sup>++</sup> scavenger	Deveau et al. (2016)
Quinolobactin	<i>P. fluorescens</i> ATCC 17400	—	Anti- <i>f</i>	Matthijs et al. (2004)
Achromobactin	<i>P. chlororaphis</i> 30-84, PCL1606	—	Fe <sup>++</sup> scavenger	Berti and Thomas (2009)
Maculosin <sup>b</sup> Cyclo-L-Pro-Val <sup>b</sup> Cyclo-L-Pro-Met <sup>b</sup> C6-HSL <sup>b</sup> 3-oxo-C6-HSL <sup>b</sup> 3-OH-C6-HSL <sup>b</sup> 3-OH-C8-HSL <sup>b</sup> PQS <sup>b</sup> 2-octyl-3-OH-4(1H)-Q <sup>b</sup> Hexahydro-Q-1,4-dioxide <sup>b</sup> HHQ <sup>b</sup> QSS 2,3,4-tri-OH-2-alkylquinolines 1,2,3,4-tetra-OH-2-alkylquinolines	<i>P. aurantiaca</i> PB-St2, <i>Pseudomonas stutzeri</i> ST1302, <i>P. aeruginosa</i> PAO1	Rice	Anti- <i>b</i> , Anti- <i>f</i>	Mehnaz et al. (2013), Thongsri et al. (2014), Vazquez et al. (2015), Yasmin et al. (2017)

<sup>a</sup> Anti-*f*, antifungal; Anti-*b*, antibacterial; *nema*, nematocidal, *Antimi*, antimicrobial; *herbi*, herbicidal, *Phytox*, phytotoxic; *biosurf*, biosurfactants; ND, not detected; *Anthel*, anthelmintics; Anti-*v*, antiviral; *insec*, insecticidal; PGP, plant growth-promoting.

<sup>b</sup> PCA, phenazine-1-carboxylic acid; 2,8-di-OH-Phz, 2,8-dihydroxyphenazine; 2-OH-Phz-1-COOH, 2-hydroxyphenazine-1-carboxylic acid; Phz-1,6-di-COOH, phenazine-1,6-dicarboxylic acid; 2-OH-Phz, 2-hydroxyphenazine; 6-methyl-Phz-1-COOH, 6-methylphenazine-1-carboxylic acid; WLIP, white line-inducing principle; Cyclo-L-Pro-Val, cyclo(prolyl-valyl); Cyclo-L-Pro-Met, Cyclo-Met-Pro-diketopiperazine; C6-HSL, N-hexanoyl-L-homoserine lactone; 3-oxo-C6-HSL, N-(3-oxohexanoyl)-L-homoserine lactone; 3-OH-C6-HSL, 3-Hydroxy-hexanoyl-L-homoserine lactone; 3-OH-C8-HSL, N-3-hydroxyoctanoyl-L-homoserine lactone; 3-OH-C10-HSL, N-3-hydroxydecanoyl-L-homoserine lactone; PQS, *Pseudomonas* quorum sensing signals, 2-heptyl-3-hydroxy-4(1H)-quinolone, 2-octyl-3-OH-4(1H)-Q, 2-octyl-3-hydroxy-4(1H)-quinolone; hexahydro-Q-1,4-dioxide, hexahydro-quinoxaline-1,4-dioxide, HHQ, 4-hydroxy-2-heptyl-quinolone; QSS, 2-nonyl-3-hydroxy-4-quinolone.

growth of *R. solanacearum* (Raza et al., 2016). Moreover, HCN from *P. chlororaphis* strain PA23 strain was reported for nematicidal and repellent activity against *C. elegans* (Nandi et al., 2015).

Bacterial blight in leek (*Allium porrum*) caused by *Pseudomonas syringae* pv. *porri* results in severe damage to the crop yield and lacks concrete control measures to counter this pathogen. One of the recent reports to control this pathogenic stress to plants suggests phage therapy as an effective biocontrol mechanism. Five novel bacteriophages belonging to *Felixounalikevirus* genus were classified as “KIL-like viruses” and complemented with selected host-displayed stability and lytic potential against bacterial pathogen *P. syringae* pv. *porri* (Rombouts et al., 2016).

Similarly, endophytic and root-colonizing fungi serve as the novel reservoir of bioactive secondary metabolites reducing the biotic stresses in crop plants. Fungal endophytes constitute 51% of the total bioactive compounds and have been screened for the production of peptides, alkaloids, terpenoids, lignans, steroids, flavonoids, and peptides that enhance the survival and fitness of crop plants against invading pathogens (Schulz et al., 2002; Kusari et al., 2012). Among these, gibberellins (GAs) comprise a huge group of structurally related phytohormones that modulate plant response during biotic stress and elicit fundamental metabolic functions necessary for stem elongation, flowering, gametes expression, seed germination, fruiting, and senescence. To date, more than 140 GAs have been characterized from various fungal endophytes including *Basidiomycetes*, *Piriformospora indica*, and *Scolecobasidium tshawytschae* (Hilbert et al., 2012). *Paecilomyces formosus* LHL10, *Exophiala* sp. LHL08, *Penicillium commune*, and *Aspergillus fumigatus* LH02 have been characterized for enhanced production of certain classes of GAs, isoflavones, and IAA and improve stress survivability in soybean and *Cucumis sativus* (Kusari et al., 2012). Fungal-based bioherbicides comprising *Sclerotinia*, *Colletotrichum*, and *Phoma* open the new avenues to replace nonbiodegradable chemical herbicides. Table 4.2 highlights some of the important microbial SMs evaluated for bioactivities against plant pathogens.

## 4.6 CONCLUSIONS

Microbe-mediated stress tolerance to improve survivability in plants has been in limelight since the past two decades. To date, hundreds of bacterial and fungal strains with a plethora of SMs have been characterized for their potential role as phyto-stimulators, agents of disease suppression, and nutrient mobilizers. Long-

term viability, eco-friendliness, biodegradability, and cost-effectiveness gained the attention of the world as substitutes of chemical fertilizers and fungicides. Based on the existing knowledge, many of the stress-tolerant microbial strains have been commercialized as bio-fungicides and biofertilizers. However, their successful filed applications are still hampered because of insufficient knowledge of their interrelated metabolic pathways and incomplete understanding of metabolites selectively inhibiting pathogens. To overcome this issue, naturally competent, genetically amenable, excessive, and rapid colonizers of rhizosphere with broad specificity must be selected and tested against an array of crop plants. Moreover, bacterial consortia with broad-spectrum activities against pathogens and environmental stresses must be developed for their potential agricultural applications.

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