




Review

Harnessing phytomicrobiome signals for phytopathogenic stress management

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Harnessing the phytomicrobiome offers a great opportunity to improve plant productivity and quality of food. In the recent past, several phytomicrobiome microbes have been explored for their potential involvement in increasing crop yield. This review strategically targets to harness the various dimensions of phytomicrobiome for biotic stress management of crop plants. The tripartite interaction involving plant-microbiome-pathogen has been discussed. Positive interventions in this system so as to achieve disease tolerant plants has been forayed upon. The different signalling molecules sent out by interacting partners of phytomicrobiome have also been analysed. The novel concept of artificial microbial consortium in mitigation of pathogenic stress has also been touched upon. The aim of this review is to explore the hidden potential of phytomicrobiome diversity as a potent tool against phytopathogens, thereby improving crop health and productivity in a sustainable way.

Keywords. Artificial microbial consortium; biotic stress; fungi; microbiome; pathogen-associated molecular patterns; plant growth-promoting rhizobacteria

Abbreviations: AMC, Artificial microbial consortium; AMF, Arbuscular mycorrhizal fungi; BGM, Botrytis grey mould; CAT, Catalase; CSP, Common symbiotic pathway; 2, 4-DAPG, 2, 4-Diacetylphloroglucinol; ET, Ethylene; ETI, Effector-triggered; GPx, Glutathione peroxidase; GR, Glutathione reductase; HMW, High molecular weight; HCN, Hydrogen cyanide; IAA, Indole-3-acetic acid; ISR, Induced systemic resistance; JA, Jasmonate; LCOs, Lipochitooligosaccharides; LMW, Low molecular weight; LysM, Lysin motives; MBCA, Microbial biological control agents; PAMPs, Pathogen-associated molecular patterns; PPPs, Plant protection products; PRPs, Pathogen recognition patterns; PTI, PAMP-triggered immunity; PGPBs, Plant growth promoting bacteria; PGPRs, Plant growth promoting rhizobacteria; PR, Pathogenesis related; ROS, Reactive oxygen species (ROS); SA, Salicylic acid; SOD, Superoxide dismutase; SAR, Systemic acquired resistance.

1. Introduction

Nearly each and every tissue of plants is colonized by specific microbiome, which contributes to the growth, health and fitness of their hosts. Thus, plants and the associated microorganisms establish an intimate mutualistic relationship. The structure and components of the phytomicrobiome are shown in figure 1. Phytomicrobiome members are broadly classified as specialists or generalists based on their jurisdiction of action. As it is evident from the name itself, specialists are species specific and influence plants only after the reception of specific signals, probably produced under conditions of stress or during nodulation. However, generalists affect a larger number of plant species (Lyu *et al.* 2020). Plants provide habitat to microbial communities as rhizosphere, phyllosphere and endosphere. In return, the associated microbes stimulate germination of plants and confer resistance to plants against several infections and stresses. They also assist plants in nitrogen fixation along with increasing the uptake of several immobile nutrients like zinc and phosphorus. The different beneficial traits conferred upon the host plant by the phytomicrobiome community have recently been compiled by Kaul *et al.* (2021). Apart from fulfilling these important functions for the host, the microbiome also forms an indispensable part of the ecosystem (Smith *et al.* 2017; Vandenkoornhuysen *et al.* 2015).

According to Turner *et al.* (2013a) manipulation of plant microbiome can help reduce biotic stresses in

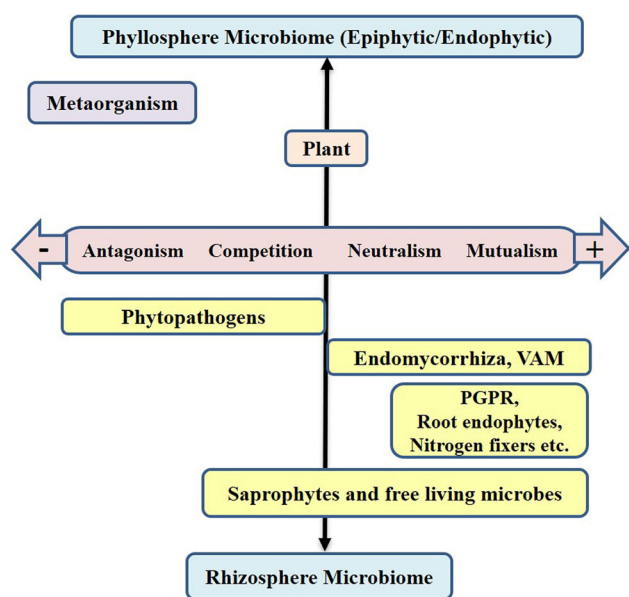


Figure 1. Structure and components of plant-microbiome meta-organism.

plants and increase production. Reduced occurrence of pathogenic diseases also decreases the number of chemical inputs in the fields, thereby, promoting sustainable agriculture. The Irish potato famine of the 1840s, caused by the fungus *Phytophthora infestans*, is one of the many examples of the extent of damage that plant diseases can inflict on food plants (Baker *et al.* 1997). Tapping the potential of the microbiome to counter such epidemics would further avoid indiscriminate use of pesticides, which have tremendous harmful effects on health and environment. French *et al.* (2021) have discussed the various pros and cons of engineering phytomicrobiome for sustainable agriculture. They have also highlighted the current loopholes and the future potentials for the same. Figure 2 shows the various biotic stresses and their effects on plants. Some of the recent reports, wherein the microbiome microbes have been harnessed to control phytopathogens on host plants, are listed in table 1. Although, nearly all plant parts are inhabited by the microbial community, in this review we emphasise on the microbiome-mediated mitigation of biotic stresses pertaining to rhizosphere (area in the vicinity of the root).

Rhizosphere is the thin soil zone which harbours rich microbial diversity and is in immediate contact with plant roots, being directly influenced by the root activities. The composition of this microfauna is influenced by deposition of mucilaginous substances and root exudates (Kent and Triplett 2002). Root exudates not only govern the composition of phytomicrobiome but also determine the physical and chemical properties of soil, prevent herbivory and alleviate symbiotic associations (Ping and Boland 2004; Badri *et al.* 2009; Morel and Castro-Sowinski 2013). Interestingly, Bhatt *et al.* (2020) observed that the microbiome composition of a plant species remains same even if it is grown in diverse soil conditions. This further strengthens the fact that plants can alter and change their surrounding phytomicrobiome very efficiently by the virtue of various chemical signals. Also, enhancement in the rates of photosynthesis in CO₂ rich environment is also known to affect the rhizomicrobiome composition (Berlec 2012; He *et al.* 2017).

Many members of the rhizosphere micro-community can antagonize soil-borne phytopathogens both at primary and secondary stage of infection in the root tissue (Mendes *et al.* 2011). Rhizosphere fungi and bacteria produce metabolic compounds that can inhibit the activity of phytopathogenic microorganisms (Brakhage and Schroeckh 2011). It is thus, imperative to understand the diversity of the

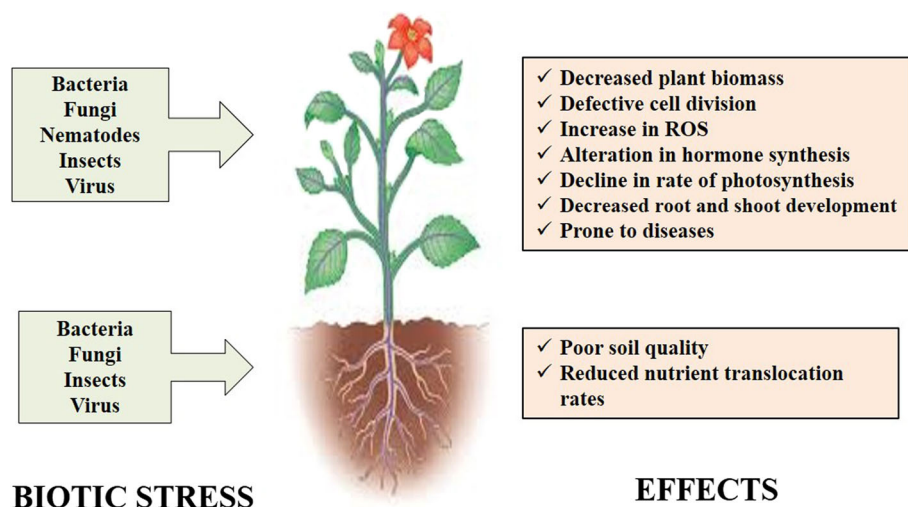


Figure 2. Various biotic stresses and their effect on plants.

microbiome, especially in the rhizosphere, so as to increase plant productivity. The rhizosphere is one of the most complex ecosystems on earth (Mendes *et al.* 2011; Solanki *et al.* 2020). The microbes of the rhizosphere are part of a complex food web that dwell upon the nutrients released by the plant. Cook *et al.* (1995) postulated that plants might modulate the rhizosphere microbiome for their own benefit by selectively stimulating the growth of beneficial microorganisms. Plants are able to regulate the same by controlling the accumulation of rhizodeposits. The rhizodeposits contribute to complex physiological processes, including cell growth, cell differentiation and suppression of plant pathogenic microbes. They are able to recruit beneficial soil bacteria, called plant growth-promoting rhizobacteria (PGPRs), from a wide range of genera, including *Azospirillum*, *Bacillus*, *Pseudomonas* and *Rhizobium*. These bacteria stimulate plant growth, produce biofertilizers, solubilize phosphorus, suppress pathogens and act as elicitors of tolerance to different abiotic and biotic stresses (Bhattacharyya and Jha 2012; De-la-Peña and Loyola-Vargas 2014; Singh *et al.* 2015; Shameer and Prasad 2018; Gulia *et al.* 2020). Contrary to this, Hartmann *et al.* (2009) reported that, soil microbes can also govern the release of various rhizodeposits. An example is experiment by Zhang *et al.* (2014) using *Bacillus amyloliquefaciens* SQR9 and *B. subtilis* N11 isolated from the rhizosphere of cucumber and banana respectively. The results demonstrated increased rates of bacterial colonisation of the original host. Root exudates of both the plants led to biofilm formation and chemotaxis in the endemic bacteria while only the latter was observed in case of

non-endemic bacteria (Farrar *et al.* 2014). Therefore, studying the variety and differences in root exudation patterns is a promising area of research as it directly affects the growth, development and performance of plants. There are yet many dimensions of phytomicrobiome to unfurl and explore. This review compiles and analyses the recent work done in the field of phytomicrobiome alternations for phytopathogenic stress mitigation in plants.

2. Tripartite interactions involving plant-microbiome-pathogen

The host plant and its micro-colonisers achieve specific and stable microbiomes as they co-evolve. All eukaryotic organisms can be considered meta organisms, comprising of a macroscopic host, living in close association with a diverse community of bacteria, archaea, fungi and protists, which strengthens the idea of holobiont concept. Lynn Margulis coined the term ‘holobiont’ in 1991 in her book *Symbiosis as a source of Evolutionary Innovation: Speciation and Morphogenesis*. A holobiont can be described as an association between the various microorganisms inhabiting in or around a host plant and forming a distinct ecological unit. Also, holobiont is a unit of selection in evolution and thus, forms a promising area of research for plant breeders. In accordance with the term holobiont, hologenome or pan-genome is a term used for the cumulative host and microbial genome (Berendsen *et al.* 2012; Turner *et al.* 2013b; Guerrero *et al.* 2013; Bordenstein and Theis 2015). Dessaux *et al.* (2016) suggested that the plants (and the associated microbes)

Table 1. Recent reports (past 10 years) wherein the phytomicrobiome microbes have been harnessed to control phytopathogens on host plants

S.No.	Microbiome microbe	Host plant	Invading phytopathogen	References
1.	<i>Azotobacter</i> sp., <i>Pseudomonas</i> sp.	<i>Cucumis sativus</i>	<i>Cucumber mosaic virus</i>	El-Borollosy and Oraby (2012)
2.	<i>Bacillus cereus</i> AR156	<i>Arabidopsis thaliana</i>	<i>Pseudomonas syringae</i> pv. tomato	Niu et al. (2016)
3.	<i>Pseudomonas putida</i> CRN-09, <i>Bacillus subtilis</i> CRN-16	<i>Vigna radiata</i>	<i>Macrophomina phaseolina</i>	Sharma et al. (2018)
4.	<i>Paenibacillus</i> sp. P16	<i>Brassica oleracea</i> var. capitata	<i>Xanthomonas campestris</i> pv. campestris	Ghazalibiglar et al. (2016)
5.	<i>Bacillus amyloliquefaciens</i>	<i>Solanum lycopersicum</i>	<i>Ralstonia solanacearum</i>	Li et al. (2017)
6.	<i>Pseudomonas</i> sp. (BaC1–38)	<i>Oryza sativa</i>	<i>Xanthomonas campestris</i>	Lucas et al. (2014)
7.	<i>Bacillus</i> sp. CHEP5	<i>Glycine max</i>	<i>Cercospora sojina</i> Hara	Tonelli and Fabra (2014)
8.	<i>Pseudomonas putida</i> KT2440	<i>Zea mays</i>	<i>Colletotrichum graminicola</i>	Planchamp et al. (2015)
9.	<i>Pseudomonas</i> sp. R41805 in association with <i>Rhizophagus irregularis</i> MUCL 41833	<i>Solanum tuberosum</i>	<i>Rhizoctonia solani</i>	Velivelli et al. (2015)
10.	<i>Pseudomonas fluorescens</i> LBUM223	<i>Solanum tuberosum</i>	<i>Streptomyces</i> sp.	Arseneault et al. (2015)
11.	<i>Bacillus amyloliquifaciens</i> strain HK34	<i>Panax ginseng</i>	<i>Phytophthora cactorum</i>	Song et al. 2015
12.	<i>Funneliformis mosseae</i>	<i>Solanum lycopersicum</i>	<i>Alternaria solani</i> sorauer	Lai et al. (2016)
13.	<i>Bacillus cereus</i>	<i>Zea mays</i>	<i>Cochliobolus heterostrophus</i>	Tonelli et al. (2017)
14.	<i>Bacillus</i> sp. CHEP5 in association with <i>Bradyrhizobium japonicum</i> E109	<i>Glycine max</i>	<i>Cercospora sojina</i>	Tonelli et al. (2017)
15.	<i>Pseudomonas</i> sp. S2 and S4	Vegetables	<i>Salmonella enterica</i>	Hsu and Micallef (2017)
16.	<i>Burkholderia phytofirmans</i> (PsJN)	<i>Arabidopsis thaliana</i>	<i>Pseudomonas syringae</i> pv. Tomato DC3000	Su et al. (2017)
17.	<i>Trichoderma atroviride</i> (TRS25)	<i>Cucumis sativus</i>	<i>Rhizoctonia solani</i>	Nawrocka et al. (2018)
18.	<i>Bacillus</i> sp.	<i>Oryza sativa</i>	<i>Pyricularia oryzae</i>	Rais et al. (2017)
19.	<i>Bacillus</i> sp. (CHEP5 specie) and <i>Bradyrhizobium</i> sp. (SEMIA6144)	<i>Arachis hypogea</i>	<i>Sclerotium rolfsii</i> (the agent that cause plant stem wilt disease)	Figueredo et al. (2017)
20.	<i>Bacillus</i> sp.	<i>Solanum lycopersicum</i> , <i>Piper nigrum</i> , <i>Cucumis sativus</i>	<i>Pseudomonas</i> sp., <i>Xanthomonas</i> , <i>Pythium</i> sp.	Liu et al. (2018)

should no longer be seen as an ‘individual’ but rather as a holobiont. Uroz et al. (2019) further proposed the ‘symbiosis cascade effect’, according to which the plant microbiome is determined by the cumulative effects of the host plant and its symbionts. A positive intervention in this interaction is in demand for sustainable crop management.

Metaorganisms are co-evolved species assemblages. These can be broadly categorized as

mycorrhiza, endophytic fungi and plant growth promoting bacteria. Arbuscular mycorrhiza is the oldest and the most important symbiotic relationship between plants and microorganisms, which dates back to almost 400 million years ago. It is also believed to have played a key role in the evolution of terrestrial plants (Selosse and Le Tacon 1998; Vandenkoornhuysen et al. 2015; Smith et al. 2015b).

Endophytic fungi complete their entire life cycle inside healthy plant tissues. They produce various bioactive substances that provide resistance against several fungal pathogens and insect herbivores along with conferring drought tolerance to the host plant. They are also known to enhance plant growth by producing promoters, such as indole-3-acetic acid (IAA). *Colletotrichum* sp. found in *Artemisia annua* is a relevant example in this regard (Lu *et al.* 2000). The signalling molecules such as IAA, promote siderophore production, fruit development, cell division and elongation, and are involved in the supply and transport of iron back to the microbial cell (Aramsirirujwet *et al.* 2016). Relying on these phytoremediation abilities of fungal endophytes, Farrar *et al.* (2014) carried out successful phytoremediation of land using crops such as *Sorghum* sp., *Salix* sp. and *Populus trichocarpa* inoculated with endophytes. Bamisile (2018) has highlighted the prospects of fungal endophytes, like *Beauveria bassiana* and *Metarhizium anisopliae*, in providing protection to host plants from arthropod pests, diseases and parasitic nematodes as an integral part of pest-management programs. According to Hallmann *et al.* (2001) these fungal endophytes exert their effect on crop plants in two possible ways: (i) by extensive colonization of internal plant tissues and suppression of invading pathogens by niche occupation, antibiosis, or both; and (ii) by colonization of root cortex, where they stimulate general plant defense/resistance mechanisms. In many cases, fungal endophyte infection can also lead to an alteration in the plant biochemistry thereby, making it tolerant against biotic stresses. *Piriformospora indica* is reported to provide enhanced climate resilience to a large number of hosts including Thale grass, *Arabidopsis* sp. and a wide range of cereals. For example, inoculation of *Hordeum* sp. with *P. indica* confers resistance against *Blumeria graminis* and *Fusarium culmorum* (Waller *et al.* 2005).

Alike fungi, bacteria also confer many advantages to plants. These beneficial bacteria are called as plant growth promoting bacteria (PGPBs). The plant growth promoting bacteria may be broadly classified as plant growth promoting rhizobacteria (PGPRs) or plant endophytes. However, a large number of members show transition between these two categories i. e. PGPRs and plant endophytes (Compant *et al.* 2010). *Azospirillum* is such an example and is being commercially used as an inoculant to reduce the dependency on fertilizers and improve plant yields (Baldani *et al.* 1987; Okon and Itzigsohn 1995; Bashan 1998; Hungria *et al.* 2010; Farrar *et al.* 2014). Additionally, certain specific

phytomicrobiome associations with plants like willows also play a crucial role in phytoremediation by allowing them to survive under conditions of soil contamination (Bell *et al.* 2015; Yergeau *et al.* 2015).

Several species of *Pseudomonas*, *Serratia* and *Bacillus* are known to protect plants indirectly through induced systemic resistance (ISR). Plant growth-promoting rhizobacteria (PGPR)-mediated ISR has gained significance in controlling a wide spectrum of fungal diseases affecting crops in an economically viable and environmentally safe manner (Mishra *et al.* 2006). The PGPRs are reported to produce antagonistic metabolites and enhance the immunity of host plant against diverse phytopathogens (Pineda *et al.* 2017; Berendsen *et al.* 2018). Figure 3 depicts the various roles of plant growth promoting microbes (PGPM) and the mechanism of stress alleviation in plants. In a recent review, Backer *et al.* (2018) highlighted various ways to enhance the colonization of rhizosphere using PGPRs. They also highlight the different aspects of commercializing a PGPR-based technology.

Additionally, researchers have articulated various mechanisms which contribute to an increase in the phytomicrobiome concentration in rhizosphere under conditions of biotic stress. These may be further categorized depending on their beneficial or toxic effects to plants. Mechanisms that promote the growth of beneficial soil microbes include the release of certain root exudates under conditions of stress that act as bacterial and fungal attractants (Canarini *et al.* 2019). Rudrappa *et al.* (2008) stated that the roots of *Arabidopsis* sp. release significant proportions of citric acid to sequester the favourable bacterium *Bacillus subtilis* in the rhizosphere upon leaf pathogen strike. Additionally, the nutritional interdependency of one microbial community on the metabolites secreted by the other and vice versa also aids in the harmonious growth of both the species (Frey-Klett *et al.* 2011). Unlike the above stated mechanisms which act as boon for the successful plant rhizosphere colonization, certain microbial associations have detrimental effects on plant growth and development. Seneviratne *et al.* (2008) proposed the benefits of mutualistic associations between bacteria and fungi. While the former aids in fungal spore development and pathogenicity, the latter dispenses nutrients and physical support in the form of biofilms for bacteria (Seneviratne *et al.* 2008; Hoffman *et al.* 2010). For example, *Rhizopus* sp. is dependent on a toxin secreted by its endosymbiont

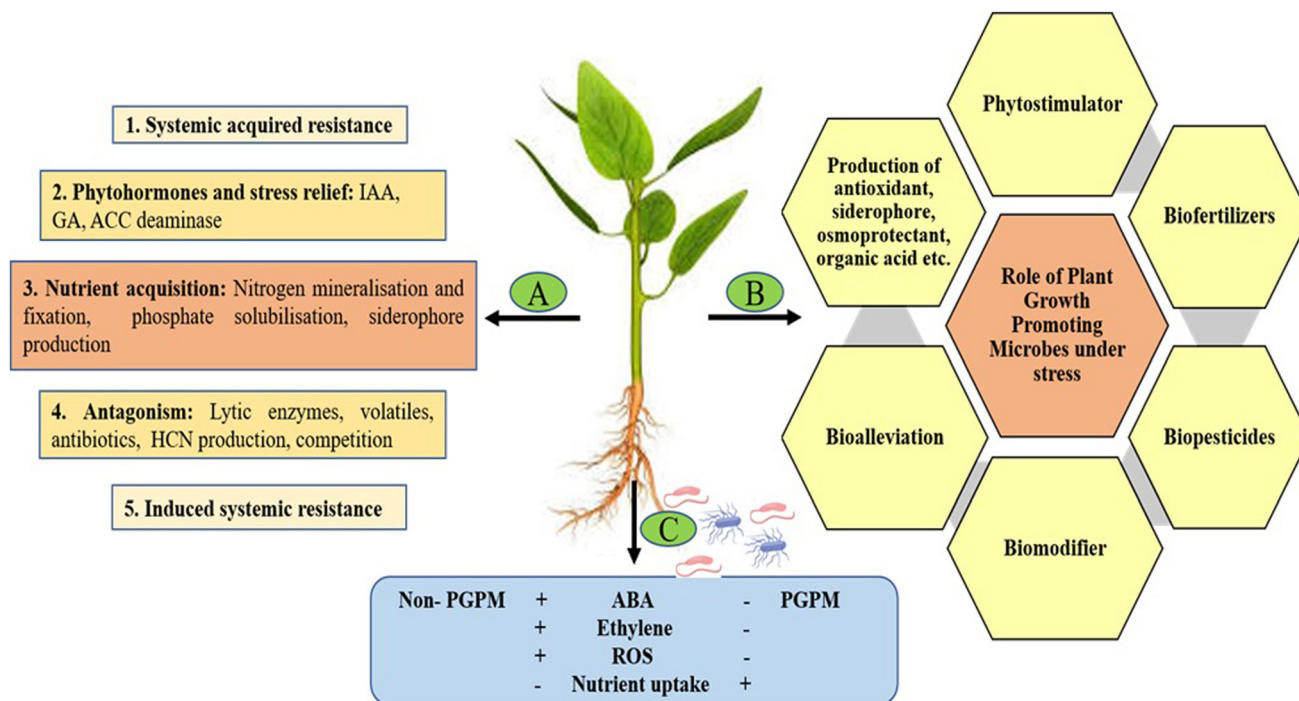


Figure 3. Plant-microbe interaction and mechanism of stress alleviation in plants. (A) Different mechanisms used by PGPM to effect plant growth directly (i.e., phytohormone production and nutrient acquisition) or indirectly (i.e., via, mechanism of SAR/ISR or antagonism). (B) Various roles of PGPM in plant stress management. (C) Mechanisms adopted by PGPM to alleviate stress where Plus (+) indicates increase in effects while minus (−) represents decrease in the same. (SAR - systemic acquired resistance, ISR - induced systemic resistance, PGPM - plant growth promoting microbes).

Burkholderia sp. to parasitise rice (Partida-Martinez et al. 2005). Based on the above stated mechanisms, Liu et al. (2020) furnished a unique ‘Defense Biome’ concept to boost the utilization of microbiome in combating plant biotic stress. They suggested that plants release certain metabolites post stress that act as chemical attractants for Defense Biome. Later, this microbial consortium (Defense Biome) affects salicylic acid and jasmonic acid signalling pathways, thereby unifying with the plant immune system and alleviating stress. They categorized microbes into three divisions depending on their concentration in rhizosphere and roots post stress. These three groups include micro-organisms whose concentration increases, decreases or remains fixed. Liu et al. (2020) further related the microbes whose concentration increases post stress with the ‘cry for help strategy’ (Bakker et al. 2018; Liu et al. 2019). Cry for help strategy relies on the use of chemical signals by stressed plants to attract microbes from soil which further help the plants to dampen the existing stress conditions (Bakker et al. 2018; Carrión et al. 2019). Novel insights into tripartite system would provide cues for phytomicrobiome mediated stress management in crop plants.

3. Cell-to-cell communication and signaling mechanisms in plants during symbiotic association

Pathogen-associated molecular patterns (PAMPs) trigger the immune response in plants by recognizing the chemical signals from the microbes. Such immune response from plants is termed PAMP-triggered immunity (PTI). The plant responses include callose deposition for strengthening of cell walls, reactive oxygen species (ROS) production and activation of signaling- and defense-related genes like pathogenesis related (PR) genes. Some of the PR genes like ethylene responsive gene (*ERF1*) and jasmonate responsive genes (*VSP*, *PDF1.2* and *LOX2*) also act as signalling genes during pathogen invasion (Camehl et al. 2010; Molitor et al. 2011). Pathogens can further impact these responses through secretion of effector molecules which may lead to another type of plant immune response called as effector-triggered immunity (ETI). The ETI is a type of active plant defense and was previously called as ‘gene for gene resistance.’ It is initiated on the recognition of an insect pest or pathogen by a specific class of plant resistance (R) genes (Kaloshian 2004). The R genes initiate a local physiological

response upon pathogen infection which includes expression of PR genes, production and accumulation of nitric oxide and SA, oxidative burst and programmed cell death (Wu *et al.* 2014). In addition, certain molecules that are secreted by the infected cells are transported across the plant through the vascular system and serve as a mobile signal to activate systemic acquired resistance (SAR). Both PTI and ETI activate SAR, which is also called priming. Plants with induced SAR exhibit a higher level of resistance upon subsequent infections, in comparison to the native plants (Ross 1961; Sticher *et al.* 1997; Shah 2009). The SAR is a well-recognized strategy to control plant pathogens because of its evolutionary stability, long-lasting effectiveness and putative trans-generational effect (Nagy *et al.* 2016). Experiments suggest that mobile signals prime the SAR-induced plants to activate faster and elevate transcription of defense-related genes during subsequent infections (Fu and Dong 2013; Xin and He 2013). In a recent review, Enebe and Babalola (2019) have extensively discussed the microbial induction of SAR in response to pathogens and role of endophytes in the activation of plant immunity. They have also provided an informative and extensive list of microbial and chemical elicitors that induce SAR for protection against phytopathogens. The chemical nature of these mobile signals is still elusive and is apparently dependent on the nature of experimental materials and environmental conditions (Dempsey and Klessig 2012). However, many researchers like Ryals (1996); Sticher (1997) and Durrant (2004) suggest that Salicylic Acid (SA) has a significant role in establishing SAR in the remote tissue. While the invading phytopathogens trigger SAR, another type of immune response called as induced systemic resistance (ISR) is the induction of systemic plant resistance by either rhizosphere or endophytic bacteria. A large number of genes are involved in the salicylic acid (SA)- mediated defense signaling networks. It is presumed and proved to a certain extent that SA cross talks with other defense signaling pathways to orchestrate the plant defense (Jalil and Ansari 2018). The ISR is independent of SA accumulation and pathogen-related protein induction (Van Loon *et al.* 1998; Pieterse 1998). Figure 4 highlights the systemic acquired resistance (SAR) and induced systemic resistance (ISR) associated mechanisms of plant defense and the different signalling molecules involved herewith.

The interaction of plants with their immediate biological surroundings takes place by the virtue of

chemical signals. These chemicals originate from rhizodeposits, particularly from the mucilage and root exudates. The different chemical compounds produced by plants can be either primary metabolites (carbohydrates, proteins, organic acids) or secondary metabolites (flavonoids, phenol, phytohormones). Table 2 lists the various metabolites released in plant root exudates and their chemical composition (Narasimhan *et al.* 2003). Plants, under stress, tend to secrete the chemical compounds in excess. The amino acids and carbohydrates present in the rhizodeposits act as chemo attractants for microbes, leading to an increase in the bacterial population in the rhizosphere in comparison to the bulk soil. The root tip mucilage however, releases different antimicrobial compounds, which provide protection to the elongating root cells from pathogenic microbes. The recruitment of chemical signals for establishing mutualistic plant-microbe interactions has been well illustrated for the legume-rhizobia symbiosis (Oldroyd *et al.* 2010; Giles *et al.* 2011). Legumes secrete a specific combination of flavonoids and isoflavonoids, such as methoxychalcone and naringenin, which serve as attractants for the host specific rhizobial community by controlling the rhizobial *nod* gene expression. The rhizobia in turn secrete lipochitooligosaccharides (LCOs) which are identified by the lysine motif receptor like kinases, thereby, establishing a signal common symbiotic pathway for root nodulation (Smith *et al.* 2015a, 2017; Leach *et al.* 2017; Basu and Kumar 2020). These common symbiotic pathway (CSP) signals are widely studied in *Lotus japonicus* and *Medicago truncatula*. The CSP proteins are distributed in the nucleoplasm, nuclear membrane and plasma membrane. While nucleoplasm contains one group of CSP proteins, nuclear membrane hosts three different kinds of CSP proteins i.e., three nucleoporins (NENA, NUP133 and NUP85), two cation channels (Pollux and Castor) and one group which is situated at the core of the nuclear pore. Furthermore, examples of CSP proteins located in the cytoplasm include: two LysM (lysine motifs) receptor kinases, NFR1/LYK3 and NFR5/NFP, a leucine-rich receptor kinase DMI2/SYMRK and the enzyme HMGR1 (HMGR1, 3-hydroxy-3-methylglutaryl-coenzyme A reductase1), (Basu and Kumar 2020). These LCO signals produced by rhizobia are highly specific and thus, constitute the specialist effect (Poustini *et al.* 2007; Clúa *et al.* 2018). However, LCOs not only act as signaling molecules but also improve plant growth under stressful conditions, thereby, constituting the

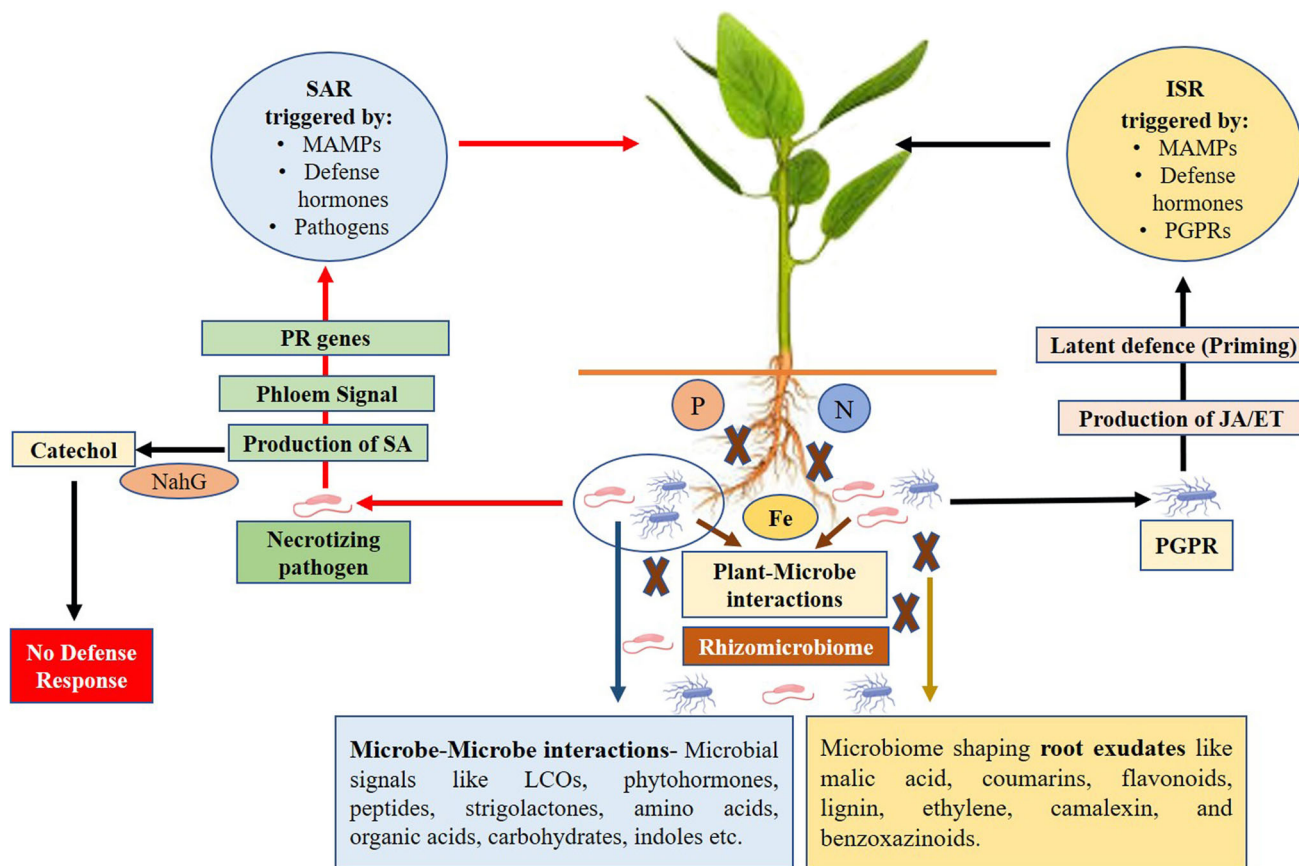


Figure 4. Systemic acquired resistance (SAR) and Induced systemic resistance (ISR) associated mechanisms of plant defense and the different signaling molecules involved herewith. PGPM elicit ISR which requires ET and JA as signaling molecules while necrotizing bacteria elicit SAR which requires endogenous SA. (SA - salicylic acid, JA - Jasmonic acid, ET - ethylene, PR - pathogenesis related, MAMPs - microbe-associated molecular patterns, NahG - salicylate hydroxylase obtained from *Pseudomonas putida* which converts SA to catechol).

generalist effect too (Smith *et al.* 2015a). Interestingly, a microbe can switch over from a specialist to a generalist under specific conditions. For instance, although rhizobia produce LCOs only after the reception of a specific plant signal, they can also be produced in the trancy of living bacteria by the exogenous application of genistein (soy-derived isoflavonoid) to the bacterial culture. These LCOs can then be used to enhance growth in a variety of plants (Smith *et al.* 2015a; Lyu *et al.* 2020). Smith *et al.* (2015a) reported that jasmonate synthesized by certain plants under conditions of stress has the potential to switch on the genes involved in LCO production in rhizobia, thereby, strengthening plant response against stress. The LCOs also have the capacity to induce root nodulation and differentiation even in the absence of rhizobia. Similarly, application of certain isoflavonoids, also called as infection isoflavonoids to rhizobial cultures can switch on the nodulation genes (Liu and Murray 2016).

Signaling via LCOs forms an ancient mode of communication and these molecules are also involved in plant-mycorrhizal associations. Strigolactone, a compound closely related to lactone homoserine is majorly involved in plant-mycorrhizal signaling (Smith *et al.* 2015a). Maymon *et al.* (2015) reported that the cumulative effects of rhizobia and other PGPR resulted in improved plant growth and nodulation. However, the exact mechanism still needs to be elucidated. PGPR secrete a variety of signaling compounds like antibiotics and phytohormones. Thuricin 17 is a small bacteriocin produced by *Bacillus thuringensis* NEB17 which simultaneously enhances plant growth and inhibits the growth of competitors in the nearby surroundings (Subramaniam and Smith 2015; Lyu *et al.* 2020). However, LCOs differ from thuricin 17 in the fact that while they are synthesized in reaction to plant signals, the latter is constitutive in nature (Lyu *et al.* 2020). Similarly, lumichrome, another example of specialist signaling compounds is a plant growth

Table 2. Metabolites released in plant root exudates and their chemical composition (modified from Narasimhan *et al.* 2003)

Metabolite released	Class of released metabolite	Chemical composition of released metabolite	Bacterial diversity supported	Fungal diversity supported
Amino acids	Primary metabolite	l-hydroxyproline, aminobutyric acid, mugineic acid, all 20 proteinogenic amino acids, homoserine	<i>Proteobacteria</i> , <i>Actinobacteria</i> , <i>Acidobacteria</i> ,	Members of families Acaulosporaceae and Gigasporaceae
Organic acids	Primary metabolite	Glutamic acid, l-aspartic acid, piscidic acid, malic acid, l- salicylic acid, gallic acid, citric acid, acetic acid, shikimic acid, caffeic acid, isocitric acid, p-coumaric acid, chorismic acid, mugineic acid, protocatecheuic acid, sinapic acid, p-hydroxybenzoic acid, tartaric acid, ferulic acid, succinic acid, oxalic acid	<i>Chloroflexi</i> , <i>Gemmatimonadetes</i> , <i>Actinobacteria</i>	<i>Funneliformis mosseae</i> , <i>Rhizophagus intraradices</i>
Carbohydrates	Primary metabolite	Pentose, sucrose, arabinose, rhamnose, glucose, xylose, fructose, raffinose, ribose, galactose, mannitol	<i>Actinobacteria</i> , Firmicutes, <i>Proteobacteria</i>	<i>Pythium</i>
Enzymes and proteins	Primary metabolite	Phosphatases, lipase, lectins, hydrolases, proteases, acid peroxidases, PR proteins	<i>Balneimonas</i> , <i>Actinobacteria</i> , <i>Lysobacter</i>	Members of families Gigasporaceae and Zygomycetes
Lignins	Secondary metabolite	Coumaric acid, catechol, nicotinic acid, phloroglucinol, cinnamic acid, ferulic acid, vanillin syringic acid, gallic acid, chlorogenic acid, sinapyl alcohol, sinapoyl aldehyde, quinic acid, benzoic acid, pyroglutamic acid	<i>Bacillus</i> , <i>Actinobacteria</i> , <i>Flavisolibacter</i> ;	<i>Sclerotinia sclerotium</i> , <i>Rhizoctonia solani</i>
Sterols	Primary metabolite	Campesterol, Stigmasterol, sitosterol	<i>Balneimonas</i> , <i>Flavisolibacter</i>	<i>Rhizophagus irregularis</i> , <i>Rhizoctonia solani</i>
Fatty acids	Primary metabolite	Stearic acid, linoleic acid, palmitic acid, oleic acid	<i>Lysobacter</i> , <i>Actinobacteria</i> , <i>Balneimonas</i>	<i>Funneliformis mosseae</i> , <i>Fusarium equiseti</i> , <i>Alternaria solani</i>
Flavanols	Secondary metabolite	Quercitin, naringenin, strigolactone, kaempferol, myricetin, naringin, rutin, genistein	<i>Proteobacteria</i> , <i>Actinobacteria</i>	<i>Rhizophagus irregularis</i> , <i>Funneliformis mosseae</i>
Coumarins	Secondary metabolite	Umbelliferone	<i>Lysobacter</i> , <i>Proteobacteria</i> , <i>Phormidium</i>	Members of family Scutellosporaceae and Ascomycete
Indole compounds	Secondary metabolite	Methyl indole carboxylate, indole-3-acetic acid, brassilexin, camalexin glucoside, brassitin, sinalexin,	<i>Kaistobacter</i> , <i>Actinobacteria</i> , <i>Flavisolibacter</i>	<i>Rhizoctonia solani</i>
Allomones	Secondary metabolite	DIBOA, DIMBOA, jugulone, 5,7,40-trihydroxy-30, sorgoleone, 50-dimethoxyflavone	<i>Chloroflexi</i> , <i>Gemmatimonadetes</i>	<i>Alternaria solani</i> , <i>Verticillium</i> sp.
Glucosinolates	Secondary metabolite	Desulphonapoleiferin, desuphuguconapin, cyclobrassinone, desulphoglucoalyssin, desulphoprogoitrin	<i>Proteobacteria</i> , <i>Actinobacteria</i>	<i>Alternaria solani</i> , <i>Funneliformis mosseae</i> . <i>Rhizophagus intraradices</i>
Aurones	Secondary metabolite	Sinapoyl choline, benzyl aurones synapates,	<i>Actinobacteria</i> , <i>Acidobacteria</i> ,	Members of families Acaulosporaceae and Basidiomycetes

Table 2 (continued)

Metabolite released	Class of released metabolite	Chemical composition of released metabolite	Bacterial diversity supported	Fungal diversity supported
Anthocyanins	Secondary metabolite	Delphinidin, pelargonidin, cyanidin	<i>Actinobacteria</i> , <i>Acidobacteria</i>	<i>Rhizophagus intraradices</i> , <i>R. irregularis</i> , <i>Fusarium equiseti</i>

promoting compound produced by certain specific bacteria like *Sinorhizobium meliloti* (Phillips *et al.* 1999) and *Pseudomonas* (Yanagita and Foster 1956) upon degradation of riboflavin. It also functions in stress alleviation (Rovira and Harris 1961; Sierra *et al.* 1999; Dakora *et al.* 2015). Additionally, the compound canavanine, a structural analogue of arginine is released by the root mucilage of some legumes and is toxic to majority of soil bacteria. However, a few rhizobial strains are specialized to detoxify canavanine. These specific rhizobium strains have an edge over other bacteria for root colonization and symbiosis (Cai *et al.* 2009; Farrar *et al.* 2014). Interestingly, Behm *et al.* (2020) reported the similarity in signals used in legume-rhizobia and the only non-legume, *Parasponia* and rhizobia symbiosis. The same set of signals are also said to govern symbiosis in *Frankia*, the exact mechanism of which is still being under cover (Cissoko *et al.* 2018; Lyu *et al.* 2020). Lyu *et al.* (2020) have made an interesting revelation as to how certain signaling molecules are activated only on the reception of a specific plant-to-microbe signal by the rhizobacteria particularly under specific stress conditions. This is referred to as the positive regulation. On the contrary, signaling molecules that are synthesized without any specific signal form the basis of the negative regulation. Table 3 details about the different signaling molecules released by plants along with their chemical interactions with the rhizomicrobia. These microbial signals are perceived by the plants using internal and external receptors present on the interior and exterior of the cell respectively (Oldroyd *et al.* 2013). Pattern recognition receptors (PRPs) can recognize the microbial cells and thus, control the functioning of the external receptors. Upon activation, these receptors initiate a signalling cascade ultimately synthesizing the essential molecules required for microbial biofilm formation (Dang *et al.* 2013; Bhatt *et al.* 2020). In spite of all this existing information, our current knowledge about the signalling molecules used by plants is very bleak. According to Singh *et al.* (2017) the primary reasons responsible for this lack of information are the low

concentrations of these molecules in bacterial films and root exudates supplemented by our inability to characterize them using the available technology.

4. Multilateral interactions on plant performance under pathogenic stress

In nature, association of plants with microbiome promotes plant growth and reduces the damage caused by environmental stresses during multilateral interactions with pathogens (Solanki *et al.* 2020). The interaction between plant and its microbiome activates many local and systemic responses in the host. These responses modulate the cellular, biochemical and metabolic status of plants, which finally confers immunity to the plants. The beneficial micro-organisms growing in the proximity of plants sometimes release antagonistic chemicals that may act against phytopathogenic organisms, for example, the bacterial colonizer, *Pseudomonas* species, synthesizes an antifungal compound 2,4-diacetylphloroglucinol, which acts against the fungus *Gaeumannomyces graminis* (Raaijmakers and Weller 1998). *Pseudomonas aeruginosa* inhabits diverse plant species and aids in boosting their immunity. For instance, *P. aeruginosa* increases not only the plant height and root-shoot biomass, but also induces resistance against stunt virus in soybean (Khalimi and Suprata 2011). Several other factors, such as phytohormonal activity, release of volatile compounds, accumulation of osmolytes, exopolysaccharide production, changes in reactive oxygen species production and activation of antioxidant enzyme machinery are also involved in stress tolerance.

For example, in the tripartite interaction of *P. indica*, *Botrytis cinerea* and chickpea, plants are better protected against pathogens because of their association with microorganisms (Narayan *et al.* 2017). *B. cinerea* is a necrotrophic fungus causing Botrytis Grey Mould (BGM) disease in many crop plants, including chickpea. Plants induce different types of anti-oxidative enzymes like catalase (CAT), superoxide dismutase

Table 3. Signaling molecules released by plants along with their chemical interactions with rhizomicrobia

Plant		Microorganism		Signaling molecule	References
Class	Species	Group	Species		
Monocot	<i>Oryza sativa</i>	Bacteria	<i>Pseudomonas aeruginosa</i>	Rhamnolipids, I-Hydroxy-phenazine, pyochelin, lahorenoic acid, pyocyanin	Yasmin <i>et al.</i> (2017)
Monocot	<i>Oryza sativa</i>	Bacteria	<i>Pseudomonas</i> sp. CMR12	Phenazine, sessilins, orfamides	Ma <i>et al.</i> (2016)
Monocot	<i>Sorghum</i> sp.	Fungus	<i>Glomus intraradices</i>	Phenazine	León-Martínez <i>et al.</i> (2012)
Monocot	<i>Lolium</i> sp.	Fungus	<i>Glomus intraradices</i>	Phenazine	León-Martínez <i>et al.</i> (2012)
Eudicot	<i>Lotus japonicus</i>	Fungus	<i>Gigaspora margarita</i>	Strigolactone	Akiyama <i>et al.</i> (2005)
Dicot	<i>Arabidopsis thaliana</i>	Fungus	<i>Pseudomonas fluorescens</i>	Polyketide antibiotic 2,4-diacetylphloroglucinol	Weller <i>et al.</i> (2012)
Dicot	<i>Arabidopsis</i> sp.	Fungus	<i>Laccaria bicolor</i>	Benzothiadiazole	Martin <i>et al.</i> (2016)
Dicot	<i>Orobancha</i> sp.	Fungus	AM fungi	Sesquiterpene lactones	Akiyama <i>et al.</i> (2005)
Dicot	<i>Lycopersicon esculentum</i>	Bacteria	<i>Pseudomonas syringae</i> pv. tomato	Benzothiadiazole	Herman <i>et al.</i> (2008)
Dicot	<i>Lycopersicon esculentum</i>	Bacteria	<i>Pseudomonas aeruginosa</i>	Pyocyanin, pyochelin, salicylic acid	Audenaert <i>et al.</i> (2002)
Dicot	<i>Lycopersicon esculentum</i>	Bacteria	<i>Pseudomonas aeruginosa</i>	Phenazine	Munhoz <i>et al.</i> (2017)
Dicot	<i>Phaseolus vulgaris</i>	Bacteria	<i>Pseudomonas aeruginosa</i>	Pyochelin, pyoverdine, salicylic acid	De Meyer <i>et al.</i> (1997)
Dicot	<i>Phaseolus vulgaris</i>	Bacteria	<i>Pseudomonas</i> sp. CMR12	Phenazine, sessilins, orfamides	Ma <i>et al.</i> (2016)
Dicot	<i>Solanum tuberosum</i>	Bacteria	<i>Pseudomonas</i> sp. LBUM223	Phenazine	Arseneault <i>et al.</i> (2013)
Dicot	<i>Helianthus</i> sp.	Fungus	<i>Glomus</i> sp.	Benzothiadiazole	Bán <i>et al.</i> (2017)
Dicot	<i>Vigna radiata</i>	Bacteria	<i>Agrobacterium tumefaciens</i>	N-Acyl-homoserine-lactones	Siddiqui <i>et al.</i> (2012)

(SOD), glutathione reductase (GR) and glutathione peroxidase (GPx), to sequester the reactive oxygen species (ROS) that are generated during the fungal attack. The tolerance shown by *P. indica*-associated chickpea plants against *B. cinerea* is also because of overexpression of antioxidative enzymes. The *P. indica* might also participate in promoting plant growth by keeping the ROS levels below a critical threshold. Since *P. indica* is free living, it can be cultivated along with many hosts, including bryophytes, pteridophytes and gymnosperms. It promotes nutrient uptake from the soil, leading to enhanced growth and biomass production. In addition, co-culture of plants with *P. indica* offers tolerance against biotic and abiotic stresses (Gill *et al.* 2016). The colonization of *P. indica* restricts disease development caused by the pathogen

Verticillium dahlia and *Fusarium* in the model plant *Arabidopsis* and economically important maize respectively (Kumar 2009; Sun *et al.* 2014). In addition, colonization of *P. indica* with barley plants has been reported to provide resistance against *B. graminis* infection (Waller *et al.* 2005; Deshmukh and Kogel 2007).

On similar lines, *Trichoderma* sp., the mycoparasites of several soil-borne plant pathogens also provide tolerance against various biotic stresses to plants. The fungus synthesizes a wide array of volatile and non-volatile antibiotics and enzymes that are antagonistic to phytopathogenic fungi and nematodes. Kumar *et al.* (2017) reported *Trichoderma* sp. to be effective against various root-related diseases, such as root-rot, foot rot and damping off disease. Therefore, *Trichoderma*

species are being widely used against plant pathogens such as fungal species *Rhizoctonia solani* whose hyphae are directly parasitized by *Trichoderma* sp. (Grosch et al. 2006). Rivera-Varas et al. (2007) reported that *Acremonium strictum* isolated from *Dactylis glomerata* L. can also act as a mycoparasite of the potato pathogen, *Helminthosporium solani*. Therefore, it may be envisaged that the interaction between plant and its microbiome modulate the cellular, biochemical and metabolic status of plants, which finally confers immunity to the plants. This immunity may be due to activation of many local and systemic responses in the host.

5. Phytomicrobiome-mediated mitigation of biotic stresses in plants

Phytopathogenic microbes are the main threat to sustainable agricultural production. Chemical control methods against pathogens are not only expensive but also degrade soil quality and contaminate ground water, consequently impairing human health (Chouhan et al. 2021). On the contrary, plant-friendly microbes are beneficial organisms. They can contribute towards an environment-friendly approach to acquire sustainable fertility of the soil and plant growth indirectly. Plant growth-promoting microbiome could be redirected using traditional techniques of plant breeding as well as advanced cultural practices. The methods used for redirecting microbiomes may involve favoring antagonistic plant pathogens by modification of cultural practices, followed by their introduction into the soil or inoculation of the seeds, planting material or plant. Finally, the plants are inoculated with incompatible or hypo-virulent strains of the phytopathogens. This technique is functionally quite similar to the process of vaccination, which also involves the inoculation of dead or attenuated microorganisms inside the bodies of the host. It therefore, confers the host with an inherent resistance against the inoculated microorganisms.

For instance, cultural practices to stimulate antagonists or competitors of *Verticillium dahlia*, a pathogen of potato, include crop rotation, solarization and infestation of seedlings or soil with species of a nematophagous fungus, *Dactyella*. Chestnut blight, caused by the fungal pathogen *Cryphonectria parasitica*, can be controlled by inoculating the plants with hypo-virulent strains of the same pathogen (Anagnostakis and Hillman 1992). Some breeders have even considered traits related to rhizosphere and root

exudates to enhance beneficial soil microbiome in their breeding programs (Smith et al. 1999; Rengel 2002; Wissuwa et al. 2009). Sharma et al. (2020) reported impaired growth of *Listeria monocytogenes* in presence of beneficial microbes *Azotobacter chroococcum*, *Bacillus megaterium*, and *Pseudomonas fluorescens* in *Cajanus cajan* and *Festuca* plants. In another recent experiment, Lau et al. (2020) reported that inoculation of black pepper plant with *Bacillus subtilis*, *Bacillus siamensis*, *Brevibacillus gelatini*, *Pseudomonas geniculata*, *Pseudomonas beteli*, *Burkholderia ubonensis*, and *Burkholderia territorii*, antagonises the soil borne phytopathogen *Fusarium solani*.

Genetics behind the plant-rhizobacteria interactions has been widely studied. In a field study, the differences between the variants of rhizospheric bacteria and their relative abundance between bulk soil and the maize rhizosphere, as well as between fields was observed in 27 maize inbreds lines (Peiffer et al. 2013). A minor but noteworthy fraction of genetic variation in the total bacterial population across fields was observed in the rhizosphere from maize inbreds. It was also observed that in *Boechera stricta*, host genes regulate the microbiome only in leaves but not in roots (Wagner et al. 2016). These studies indicate that genotype-by-environment interactions play an important role in complexity of microbial communities. Thus, this kind of research should be expanded on other crops too to identify robust heritable host-microbe interactions at the level of individual polymorphisms. This information can ultimately be useful in breeding agriculturally important crop plants. Collins et al. (2008) suggested that quantitative trait loci (QTLs) can regulate the physiological factors affecting biomass production and its partitioning along with controlling heritable variability in plants.

The exploitation of fungi for the control of plant diseases is an exciting and rapidly evolving research field with promising results. Some fungal species, such as *Phlebia gigantean*, *Pichia guillermondii* and *Gliocladium virens* have been used to control diseases of conifers, citrus, peach and cotton crops. *Trichoderma harzianum* is a potential biocontrol agent against *Fusarium* stalk rot caused by *Fusarium graminearum* (Saravanakumar et al. 2017). On the other hand, various studies have demonstrated the efficacy of PGPRs as biocontrol agents, including *Pseudomonas fluorescens*, *Pseudomonas putida* and *Azotobacter chroococcum* under field conditions (Gupta et al. 2015). The production of antibiotics by PGPRs against phytopathogens is considered to be one of the most efficient and widely studied biocontrol mechanisms

(Shilev 2013). Soils enriched in gamma proteobacteria and beta proteobacteria suppressed *Rhizoctonia solani* infection in sugar beet (Mendes *et al.* 2011). Many of the bacteria, such as *Bacillus*, *Streptomyces* and *Stenotrophomonas sp.*, produce antibiotics that can inhibit the growth of plant pathogens (Compant *et al.* 2005). One of the antibiotics, 2, 4-diacetylphloroglucinol (2, 4-DAPG), which is produced by *Pseudomonas sp.*, is effective against wheat fungus, *Gaeumanomyces graminis* var. *tritici* (De Souza *et al.* 2003). Similarly, phenazine-1-carboxylic acid, produced by *P. fluorescens*, is useful as a biocontrol agent against all diseases of wheat (De Souza *et al.* 2003). However, extensive dependence on antibiotic-producing PGPRs as biocontrol agents can lead to development of antibiotic-resistance among phytopathogens. To prevent this action, scientists have been using biocontrol strains that can produce more than one antibiotic. The production of antibiotics DAPG and hydrogen cyanide (HCN) by *Pseudomonas sp.* contributed towards controlling bacterial canker of tomato (Lanteigne *et al.* 2012). The PGPRs showing typical enzymatic activities have emerged as a means to protect plants from biotic and abiotic stresses by inhibiting the proliferation of pathogenic fungi, such as *Botrytis cinerea*, *Sclerotium rolfisii*, *Fusarium oxysporum*, *Phytophthora sp.*, *Rhizoctonia solani* and *Pythium ultimum* (Hayat *et al.* 2010; Nadeem *et al.* 2013). Likewise, viral biopesticides are being widely used for the control of vegetable and field crop pests globally and are effective against plant-chewing insects. However, they have a narrow host spectrum range and a short life span. Beneficial nematodes (*Steinernema feltiae*, *Steinernema carpocapsae* and *Heterorhabditis bacteriophora*) are another group of microorganisms that can be used for the control and management of various soil pests (Lacey and Georigis 2012). It is thus, safe to presume that the practice of microbial inoculation to enhance disease resistance continues to make significant contributions to the global crop production in an environment-friendly way.

Badri and Vivanco (2009) suggested that gene mutations influence not only the intrinsic plant physiology but also the rhizosphere community. They observed that the root exudate composition of *Arabidopsis thaliana* ABC transporter mutants was different from the wild type. The root exudate profiles differed among the different mutants too. The mutant abcg30 was the most variant amongst the wild types, which showed enhanced secretion of phenolic compounds and less secretion of sugars. The exudates of mutant abcg30 could potentially harbour a rich

community of plant-growth-promoting rhizobacteria and nitrogen fixers. Simultaneously, the root exudates of mutant abcg30 were also rich in bacteria responsible for heavy metal remediation.

A tomato mapping population, segregating for disease resistance to *Pythium torulosum*, suppressed by *Bacillus cereus*, indicated the presence of QTLs, which can be used to mitigate biotic stresses (Smith 1999). Thus, indirect manipulation of QTLs can aid plant breeders to better analyze the genetic basis of plant growth under conditions of biotic stress and thereby, grow plant varieties better suited to cope up with such biotic constraints (Collins *et al.* 2008). More advances in genome-based analyses have made it possible to understand the microbial communities living in the rhizosphere and their interactions with plants (Sorensen *et al.* 2009; Guttman *et al.* 2014).

Turner *et al.* (2013a) compared the active rhizosphere microbiomes in bulk soil with three different plant species (wheat, oat and peas) and avenacin antifungal compound-deficient mutant of oat, *sad1*. Rhizospheres of oat and pea were enriched with eukaryotes, indicating the differences in rhizosphere microbiome composition between bulk soil and plant species. There were significant differences between the rhizosphere microbiomes of legumes and cereals. The non-fungal eukaryotic rhizosphere microbial community was intensely different from the fungal community in *sad1* mutant, suggesting a broader role of avenacin *in vivo* than just providing protection from fungal pathogens.

Some other studies have shown that plants can secrete specific signaling molecules to converse with the microbes present in the rhizosphere (Lareen *et al.* 2016). Some specific chemical compounds released from the plants have been shown to restrict the bacterial quorum (Bauer and Teplitski 2001; Gao *et al.* 2003). Quorum sensing is also a relatively newer field of science which deals with the understanding of interactions between bacterial cells using various chemical signals. Overexpression of lactonase gene that can interfere with bacterial quorum sensing in potato plants confers tolerance to a pathogenic bacterium *Pectobacterium carotovorum* (Dong *et al.* 2001). These signaling molecules are reported to be highly specific in different microbes, for example, cis-11-methyl-2-dodecanoic acid in *Xanthomonas sp.*, N-acyl-homoserine lactones in Proteobacteria, oligopeptides in Gram-positive microorganisms and gamma butyrolactones in *Streptomyces sp.* (Danhorn and Fuqua 2007; Jalil and Ansari 2018). Therefore, understanding and modeling of the host-associated

communities are crucial steps to understand the function of microbes and will thus, open the doors for manipulating them to combat diseases.

6. Use of artificial microbial consortia in mitigating biotic stress

Artificial microbial consortium (AMC), also known as synthetic microbial consortium is a relatively newer concept that lays its foundation on the concept of synthetic biology. It can be used to remodel the plant microbiome by altering its function and structure to maximize benefits to plants (Arif *et al.* 2020). The major steps required to compose an effective AMC include determining the microbial origin, procuring and cultivating the required micro-organisms, enhancing the microbial associations based on their affinity and finally monitoring the effectiveness of the constructed consortia (Kong *et al.* 2018). Owing to the capacity of plant microbiome to affect plant growth and development by releasing certain phytohormones (Stringlis *et al.* 2018), Tsolakidou *et al.* (2019) constructed two AMC comprising of ACC deaminase exhibiting bacterial strains. Employment of these bacterial groups on tomato plants resulted in increased tolerance against *Fusarium oxysporum* f. sp. *lycopersici*. Thus, to conclude, AMC can prove to be an ideal option in enhancing growth rates in plants along with alleviating both biotic and abiotic stresses. They can also fill up the lacunae in the use of conventional microbial biofertilizers by solving the problems of maladjustment with surroundings, host incongruity and futile competitiveness with local micro-organisms (Hart *et al.* 2018). Also, various microorganisms like *Trichoderma* spp., are categorized as Microbial Biological Control Agents (MBCA) and enlisted as Plant Protection Products (PPPs; Woo *et al.* 2014). Additionally, many of these microorganisms though being listed as biopesticides also have the potential to promote plant growth and development (Lorito and Woo 2015). Similarly, arbuscular mycorrhizal fungi (AMF) that are commonly known to function as biostimulants can also protect plants from disease or pathogen attack by inducing ISR (Cameron *et al.* 2013; Roupael *et al.* 2015). These examples significantly highlight the urgent need of preparing a new registration track of microbial consortia which confer more than one benefit to plants like PGPM and MBCA. This will help in boosting the efficient use of microbes that are 'all inclusive (e.g., biopesticide, biofertilizer, biostimulant; Woo and Pepe 2018).

7. Conclusion

Focus on an in-depth study pertaining to identification, trait characterization, compatibility assessment, delivery methods and impact of application of microbes isolated from diverse environments would help in mitigation of environmental stresses in crop plants. The correct identification of signaling molecules and its correlation with plant communication networks at the field scale is recommended. To comprehend the complex mechanisms of biocontrol agents-mediated stress tolerance, it is imperative to investigate omics-based data generation, followed by integrated approaches that encompass genomics, metagenomics, proteomics, metabolomics and comparatively new culturotomics on specific tripartite/multilateral interactions. New technologies, such as genome editing, could be deployed for targeted alternations in phytomicrobiome by modifying the root exudates. *In situ* microbiome engineering and synthetic biology if exploited fully also have the potential to revolutionize the agricultural system by devising predictable yet novel mechanisms to control microbiome in the desired way. The integration of novel technologies with the current, traditional knowledge of plant breeding, genetics, plant and microbial eco-physiology is the key to harness the microbiome in complete sense. The obtained results can also be supplemented with sensor-based technologies and remote sensing to widen the scope of research. However, there are lacunae in this field which need to be addressed, such as host specificity, quorum sensing, biofilm formation, signaling pathways, bacterial motility, commercial formulations and inconsistency under field conditions. Several newer approaches have been opted for improving field success deploying microbial inoculants, such as, designing smart microbial consortia, selection of agricultural management practices favoring beneficial microbiota or a new generation of plant breeding approaches for improved field applications.

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