REVIEW ARTICLE

The rhizosphere microbiome and biological control of weeds: A review

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Abstract

The productivity of important grain crops wheat, rice and maize is adversely affected by various biotic and abiotic stresses. Weeds and phytopathogens are the major biotic stresses involved in biomass reduction and yield losses of these cereal crops. Various weeds compete with crop plants for natural resources viz. light, moisture, nutrients and space, and cause yield losses to agricultural produce. Weeds also increase harvesting costs and reduce quality of the farm produce. Weed management strategies include crop rotation, mechanical weeding or treatment with different herbicides. Although, sprays of different herbicides control various destructive weeds but their excessive use is environmentally unsafe and uneconomic. Indiscriminate use of these agrochemicals for weed control has resulted into considerable pollution of soil, groundwater and atmosphere. Therefore, effective biological weed management is an attractive approach for achieving the increased crop production to meet the food demands of the escalating global population. Many bacteria and fungi have been identified from the plant rhizospheres, which suppress the growth of weeds. The production of indole acetic acid, aminolevulinic acid, toxins and hydrogen cyanide has been correlated with the growth suppression of various weeds. Interestingly, inoculation with bioherbicides results in creation of biased rhizosphere leading to resource partitioning of nutrients towards growth stimulation of crop plants. Thus, inoculation of plants with bioherbicides has been found to increase germination percentage, seedling vigor, root and shoot growth, seed weight and increased grain, fodder and fruit yields. These environment-friendly biocontrol strategies for management of weeds are highly compatible with the sustainable agriculture.

Introduction

Weeds adversely affect the production of the world's most important food and cash crops. Assessment of yield losses due to weeds were estimated at 26-29% for soybean, wheat and cotton, and 31, 37 and 40% for maize, rice and potatoes, respectively (Oerke, 2006). Significant differences in yield losses were observed between different locations, crops and soil types. For example, Bhan *et al.* (1999) estimated a 31.5% of reduction in yield by weeds, whereas Gharde *et al.* (2018) reported greater variability in yield losses among the different locations (states) in case of direct-seeded rice (15-66%) and maize (18-65%). Soltani *et al.* (2016) estimated average yield loss in corn as 50%, *i.e.*, 148 million tonnes of corn valued at over USD 26.7 billion annually in the United States and Canada.

Weeds are the silent robbers of plant nutrients, soil moisture, solar energy and also occupy the space which would otherwise be available to the main crop. Moreover, weeds harbour insect-pests and disease-causing organisms, exert adverse allelopathic effects,

reduce quality of farm produce and increase the cost of production. Seeds of weeds can stay in the soil for several years until conditions are favorable for their germination. After germination, weed plants grow fast, rapidly establish weed populations and soon reach the flowering phase. They again produce numerous seeds, which are easily dispersed over long distances. Some weeds produce vegetative reproduction organs that help them to survive in soils.

The major prevalent dicot weeds include bathua (*Chenopodium album*), gazari (*Fumaria parviflora*), krishnneel (*Anagallis arvensis*), chetri (*Vicia sativa*), senji (*Melilotus indicus*), matari (*Lathyrus aphaca*) and satyanashi (*Argemone mexicana*). Likewise, monocot weeds viz. kanki/gullidanda/ mandusi (*Phalaris minor*), wild oats (*Avena ludoviciana, Avena fatua*), piazi (*Asphodelus tenuifolius*) etc., impose serious problems in wheat fields. *Avena fatua* is one of the most economically harmful annual grass weed in North America, Europe and Australia especially in grain crops such as barley, oat and wheat. Similarly, *P. minor* is another troublesome weed of wheat in India, Pakistan, USA, Canada, Africa, Australia, France, Iran and Mexico. It may cause 25-80% reduction in wheat yield (Chhokar *et al*., 2009). Herbicides such as isoproturon, clodinafop-propargyl, fenoxaprop, pinoxaden, Accord plus (fenoxaprop + metribuzin), sulfosulfuron and Atlantis (meso + iodosulfuron) are applied for control of common weeds. Nevertheless, the application of chemical herbicides leaves residues that contaminate water, soils and food crops, and in some cases results in the development of herbicide resistance in many weed biotypes. Therefore, it is imperative to explore various biocontrol approaches that are ecofriendly for the control of weeds.

Naturally-occurring rhizosphere microorganisms have the potential to suppress the weed growth through alteration of the rhizosphere ecosystem (Charudattan & Dinoor, 2000; Mohan Babu *et al*., 2003; Adetunji *et al*., 2019). These rhizosphere bacteria colonize the root surface of weed seedlings and suppress the growth of weed plants by reducing weed density, biomass and its seed production (Kremer & Kennedy, 1996). Many rhizobacterial strains including *Pseudomonas aeruginosa*, *Flavobacterium* spp., *Erwinia herbicola*, *Alcaligenes* spp., *Xanthomonas campestris* pv. *poannua*, *Pseudomonas syringae* pv. *tagetis* and *P. syringae* pv. *phaseolicola* have been exploited as foliar bioherbicides, whereas *P. fluorescens*, *Xanthomonas* spp., *Enterobacter* sp and *Erwinia herbicola* have been developed as soil application bioherbicides (Kremer, 2000; Sindhu *et al*., 2018; Adetunji *et al*., 2019). Some deleterious rhizobacteria (DRB) and fungi cause damage to the weed plants through the production of phytotoxins that are absorbed by the plant roots. For example, the AAL toxin produced by the pathogen *Alternaria alternata* f. sp. *lycopersici* has been found to inhibit a range of weed species and has been patented as an herbicide (Abbas *et al*., 1995). Other allelochemicals produced by microorganisms such as indole acetic acid (IAA), δ-aminolevulinic acid (ALA), glycoproteins and mellein have also been reported to reduce the germination and development of weeds (Mejri *et al*., 2010; Adetunji *et al*., 2018; Radhakrishnan *et al*., 2018). Moreover, inoculation of soil with deleterious microorganisms (biocontrol agents) may suppress weed growth by production of hydrogen cyanide (Zeller *et al*., 2007). These rhizosphere microorganisms could be exploited for development of bioherbicides as ecofriendly technology for management of weeds in sustainable agriculture. In addition, in-depth understanding of mechanisms and factors involved in crop-weed competitive interactions is required to develop cost-effective and sustainable weed management strategies (Swanton *et al*., 2015; Adetunji *et al*., 2019).

Rhizosphere and plant microbiome

The rhizosphere is a region of rich microbial diversity, which is influenced by plant roots through rhizodeposition of root exudates, plant mucilage and sloughed cells (Mohanram & Kumar, 2019). Root exudates are the key determinants of rhizosphere microbiome structure. These root exudates contain a variety of compounds, predominately organic acids and sugars, but also contain amino acids, fatty acids, vitamins, growth factors, hormones and antimicrobial compounds (Sindhu *et al*., 2017). The composition of root exudates varies between plant species and cultivars, plant age and the developmental stage. The physico-chemical properties of soils may also directly affect the growth of specific microbes by creating niche environments that benefit certain types of microbes and influence the availability of plant root exudates. For instance, soil pH and nutrient availability (*e.g.* carbon, nitrogen, phosphate) have been found to affect the abundance of crop pathogenic bacteria, fungi and nematodes as well as beneficial microbes (Lareen *et al*., 2016). Recent advances in plant-microbe interactions revealed that plants are able to manipulate their rhizosphere microbiome, when different plant species are grown on the same soil (Berendsen *et al*., 2012; Chaparro *et al*., 2012; Turner *et al*., 2013). Rhizosphere engineering reduce the incidence of plant diseases and invasion of pathogens, the use of chemical inputs and emissions of greenhouse gases resulting in more sustainable agricultural practices for the benefit of the whole ecosystem (Zorner *et al*., 2018). The effect of soil and plants on the composition of rhizosphere

communities has been reviewed recently and the presence or loss of specific microbial hubs under certain environmental distractions could be critical for soil fertility and plant health (Hunter, 2016; Igiehon & Babalola, 2018). Certain microbial hubs in the plant rhizosphere contribute towards improving nutrient uptake or effectiveness of biocontrol agents and mediating defense signals among plants (van der Heijden & Hartmann, 2016) (Fig. 1).

Microorganisms involved in biocontrol of weeds

Various soil microorganisms have been characterized, which increase the nutrient uptake capacity and water use efficiency of crop plants for enhancing food production (Armada *et al*., 2014; Pii *et al*., 2015; Sindhu *et al*., 2019). These microorganisms may be used to enhance soil fertility and plant health without environmental contamination (Sharma & Sindhu, 2019) and are termed as plant growth promoting rhizobacteria (PGPR). These PGPR include bacterial genera such as *Agrobacterium*, *Allorhizobium*, *Arthrobacter*, *Azospirillum*, *Azotobacter*, *Bacillus*, *Bradyrhizobium*, *Burkholderia*, *Chromobacterium*, *Erwinia*, *Mesorhizobium*, *Micrococcus*, *Pseudomonas*, *Rhizobium* and *Serratia*, which either exist in the rhizosphere, on the rhizoplane or in the spaces between the cells of root cortex (Viveros *et al*., 2010; Ahemad & Kibret, 2014). These microbes provide fixed nitrogen, solubilized phosphorus and other nutrients to the plants (Bhattacharyya & Jha, 2012).

Fluorescent and nonfluorescent pseudomonads, *Erwinia herbicola*, *Alcaligenes* spp. and *Flavobacterium* spp., were isolated from seedlings of seven economically important weeds (Kremer *et al*., 1990). Using an *Escherichia coli* indicator bioassay, only 18% of all isolates were found potentially phytopathogenic and 35-65% of the isolates inhibited growth in seedling assays, depending on the weed host. Antibiosis was found most prevalent among isolates of fluorescent *Pseudomonas* spp., the activity of which was due to siderophore production in over 75% of these isolates. Competitive root colonization was reported as another important criterion for development of effective weed biocontrol agents (Kremer *et al*., 1990). In addition, differential colonization of roots may result in selectivity of these allelopathic bacteria in terms of their promotion or growth retardation effects, thereby enabling more targeted control of weeds (Kennedy *et al*., 2001). Differential inhibition of downy brome (*Bromus tectorum*) and winter wheat was reported by screening of 1000 pseudomonad isolates (Kennedy *et al*., 1991). The filtrates of bacteria-free culture (of

8% isolates only) were found to inhibit root growth of downy brome on agar, but did not affect root growth of winter wheat. Under nonsterile soil conditions, only six isolates inhibited the growth of downy brome. Growth of downy brome weed in the field was suppressed by 31 to 53% by spraying (at a population density of 10^8 colony forming units m^{-2}) of only two isolates. Whereas, the spraying of these isolates increased the yield of winter wheat by 18-35%, under field conditions.

Boyetchko (1997) evaluated the efficacy of DRB for biological control of downy brome (*Bromus tectorum*), green foxtail (*Setaria viridis*) and wild oats (*Avena fatua*). Over 100 isolates with ≥80% suppression to root growth of these weeds in laboratory bioassays were selected as potential biological control agents. Kennedy *et al*. (2001) isolated *Pseudomonas fluorescens* strain D7 (*P. f.* D7; NRRL B-18293) that inhibited growth of downy brome (*Bromus tectorum* L. Brote). In the agar plate bioassay, all accessions of downy brome were inhibited by *P. fluorescens* strain D7. Root growth of seven *Bromus* spp. was inhibited on an average of 87% compared with that of controls in the agar plate bioassay. Inhibition in plant–soil bioassays was limited to downy brome, indicating the application of *P. fluorescens* D7 as a biocontrol agent that will not harm nontarget species. Flores-Vargas & O'Hara (2006) isolated bacteria from the rhizosphere, rhizoplane and endorhizosphere of seedlings and mature plants of wild radish (*Raphanus raphanistrum*), annual ryegrass (*Lolium rigidum*) and capeweed (*Arctotheca calendula*) growing in vineyards in the Swan Valley, Western Australia. A total of 442 strains were screened in the glasshouse for deleterious effects on annual ryegrass, wild radish, gra-
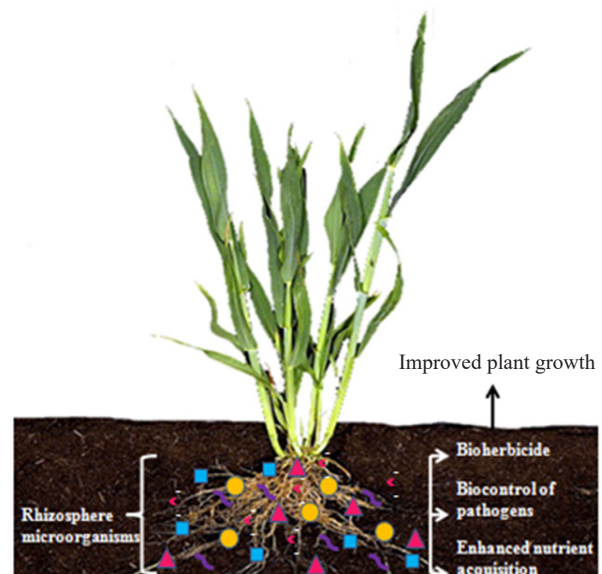

Figure 1. Rhizosphere microorganisms having bioherbicidal activity and plant growth promotion ability.

pevine rootlings (*Vitis vinifera*) and the cover crop subterranean clover (*Trifolium subterraneum*). Three strains specifically inhibited growth of wild radish, but showed no significant deleterious effects on either grapevine rootlings or subterranean clover.

De Luna *et al*. (2011) isolated mycobiota associated with dormant wild oat (*Avena fatua* L.) seeds buried for six months in a no-till wheat field and evaluated their caryopsis decay potential. Of the 118 representative isolates tested, only 15% isolates showed caryopsis decay potential. One isolate of *Fusarium avenaceum* and three isolates of *Fusarium culmorum* completely decayed wild oat caryopses within two weeks. Chen *et al*. (2016) found that culture filtrate of *Streptomyces enissocaesilis* significantly reduced the germination rate of root parasitic weed *Orobanche cumana* (sunflower broomrape) both in the seed germination experiment and the co-culture experiment, with more than 50 and 40% (after cultivation for eight days) growth retardation effect, respectively over the control. In the pot experiment, application of *Streptomyces enissocaesilis* reduced the epigaeous number of *O. cumana* tubercles by 47.5% after 130 days. Abbas *et al*. (2017) recorded the maximum suppression of wild oat due to inoculation with strains L9 and T42 followed by strains O_010, W9, $7O_0$ and others. Inoculation with strains O_010 and $7O_0$ caused maximum inhibition of little seed canary grass, followed by strains L9 and T42. Broad leaved dock was maximally inhibited by strains W9, T42 and L9, followed by strains $7O_0$, O_010, T38 and others. Reduction in germination and growth of the weeds by allelopathic bacteria was attributed to their ability for competitive root colonization and production of phytotoxic metabolites.

Similarly, rhizosphere bacteria obtained from different crops were screened for antagonism against *Amaranthus hybridus* L. (pig weed) and *Echinochloa crus-galli* (L.) Beauv. (barnyard grass) using the necrosis assay technique (Adetunji *et al*., 2017). Eight rhizosphere bacterial isolates (B1–B8) produced different degrees of leaf necrosis on target weeds. Isolate B2 showed the highest necrotic activity and was identified as *Pseudomonas aeruginosa* using 16S rRNA sequencing technique. Kennedy (2017) found weed-suppressive *Pseudomonas fluorescens* strains effective for controlling one or more invasive grass weeds consisting of downy brome (*Bromus tectorum* L.), medusa head (*Taeniatherum caput medusae* (L.) Nevski) and jointed goatgrass (*Aegilops cylindrica* L.). Khandelwal *et al*. (2018) reported that four rhizobacterial isolates obtained from the rhizosphere of wheat and mustard showed root growth inhibition of *Chenopodium album* weed and three bacterial isolates caused shoot growth inhibition at both 5th and 10th days of seed germination. Inoculation of bacterial isolate MSA39 resulted in 43-53%

decrease in root dry weight (RDW) and 31-47% decrease in shoot dry weight (SDW) of *Chenopodium album* at 60 and 90 days of plant growth, whereas its inoculation showed 122-144% increase in RDW and 124-205% increase in SDW of wheat under pot house conditions. Inoculation with bacterial isolates WHA82 and WHA100 also decreased root and SDW of *C. album* at both stages of observations.

Recently, inoculation of phytopathogenic strain *Lasiodiplodia pseudotheobromae* showed 56–66% selective inhibition against the *Poaceae* and *Valerianaceae* families (Adetunji *et al*., 2018), whereas *Pseudomonas aeruginosa* strain C1501 showed significant decrease in the dry weight of *Amaranthus hybridus* (pig weed) seedlings (Adetunji *et al*., 2019). ALA-producing *Bacillus flexus* strain JIM24 was reported to cause 92% reduction in root and SDW of *Lathyrus aphaca* weed under pot house conditions (Phour & Sindhu, 2019). Similarly, Lawrancea *et al*. (2019) isolated a rhizospheric bacterium *Pseudomonas aeruginosa* strain H6 from the rhizosphere of *Momordica charantia*. Both, supernatant culture and crude extract of strain H6 showed high inhibition activity in *Pennisetum purpureum*, *Oryza sativa*, *Pisum sativa* and *Amaranthus spinosum*.

Mechanisms involved in bioherbicidal activity

Bioherbicides are natural products derived from either living organisms or their natural metabolites, which are used to control destructive weed species without degrading the environment (Bailey, 2014). Some of the rhizospheric bacteria secrete various plant growth promoting compounds or toxins, which may inhibit seed germination and growth of weed plants (Sindhu *et al*., 2018; Adetunji *et al*., 2019). Various metabolites such as phytotoxins, antibiotics, IAA, ALA and HCN produced by bacterial or fungal cells have been found to retard growth of weeds (Kim & Rhee, 2012; Park *et al*., 2015; Phour *et al*., 2018; Adetunji *et al*., 2018; Radhakrishnan *et al*., 2018; Dahiya *et al*., 2019).

Production of indole acetic acid

Phytohormones are the chemical messengers produced by certain plant-associated bacteria that play crucial role in different plant-microbe interactions (Costacurta & Vanderleyden, 1995; Sindhu *et al*., 2017). Production of different phytohormones like IAA, gibberellic acid and cytokinins by the PGPR strains have been reported to alter root architecture, leading to more adsorption of nutrients and promotion of plant growth (Malik & Sindhu, 2011; Park *et al*., 2015; Sindhu *et al*.,

2017). These phytohormones affect seed growth, time of flowering, senescence of leaves and fruits, gene expression, cellular division and growth. In targeted cells, phytohormones also regulate cellular processes, pattern formation, vegetative and reproductive development and stress responses.

Indole-3-acetic acid is one of the most common and most studied auxins (Spaepen et al., 2007). Plant responses to IAA vary from plant to plant in terms of sensitivity. The capacity to produce IAA is wide spread among plant associated bacteria (Patten & Glick, 1996; Kloepper et al., 2007; Mishra et al., 2010; Malik & Sindhu, 2011) and the numbers of IAA-producing organisms range as high as 80% of total soil bacteria. IAA is also involved in regulating the expression of important compounds in bacteria such as cAMP and amino acids (Katsy, 1997). IAA production may enhance plant growth by enhancing root surface area through which more of the metabolites can be exuded or absorbed as nutrients (Gaudin et al., 1994).

Indole-3-acetic acid has been reported to stimulate plant growth in lower concentrations and in contrast, if the concentration becomes higher, the effect is reversed and elongation of root and shoot is inhibited. Natural auxins have modes of action similar to many herbicides that interfere with plant growth such as 2,-4-dichlorophenoxyacetic acid (2,-4-D) and 2,-4,-5-trichlorophenoxyacetic acid (2,-4,-5-T) (Patten & Glick, 1996). Nine strains of *Klebsiella pneumoniae* were isolated from rhizosphere of wheat var. Lokwan (Sachdev et al., 2009) and only six *K. pneumoniae* strains showed *in vitro* IAA production. Inoculation of strains K11 and K42 caused significant gain in root length of inoculated moth beans (~ 92.71%) over the control. Pot experiment results indicated that all the six IAA-producing *Klebsiella* strains significantly increased the root length and shoot height of inoculated wheat seedlings over the control. Serwar & Kremer (1995) reported that auxins produced in high concentrations in the rhizosphere by deleterious rhizobacteria may contribute towards reduced root growth of weeds. For example, an *Enterobacter taylorae* isolate with high auxin-producing potential (72 mg L^{-1} IAA-equivalents) was found to inhibit root growth of field bindweed (*Convolvulus arvensis* L.) by 90.5% when combined with $1 \cdot 10^{-5}$ M L-tryptophan in comparison with non-treated control. Suzuki et al. (2003) isolated an IAA low-producing spontaneous mutant of *P. fluorescens* HP72LI and the colonization ability of strain HP72 on the bentgrass root was found higher than that of mutant HP72LI. Colonization of strain HP72 on the bentgrass root caused root growth reduction, whereas strain HP72LI did not show such growth reduction. The results suggested that IAA production by strain HP72 contribute towards the development of short root systems and take advantage of root colonization.

High amount of IAA production by deleterious rhizobacteria *Bradyrhizobium japonicum* GD3, isolated from soybean rhizosphere, was found to give suppressive effect on growth of morning glory (*Ipomoea* spp.) weed (Kim & Kremer, 2005). Similarly, growth suppressive effect on weed great brome (*Bromus diandrus* Roth.) was observed by inoculation of *Pseudomonas trivialis* strain X33d in a mixture of soil/sand/peat (Mejri et al., 2010). *Bromus diandrus* plants inoculated with rhizobacterial strain X33d showed low root biomass, short root systems and low surface area, volume and number of tips. On the other hand, growth promoting effect was observed on most of the crops, especially durum wheat (*Triticum durum* Desf.) by inoculation of *Pseudomonas trivialis* strain X33d strain. This growth suppression effect on great brome weed and growth promotion effect on durum wheat was attributed to production of IAA by *P. trivialis* strain X33d. Meliani et al. (2017) reported that *Pseudomonas fluorescens* and *Pseudomonas putida* produced IAA *in vitro*, at concentrations of 89 µg mL^{-1} and 116 µg mL^{-1}, respectively. High levels of IAA excretion by *P. putida* gave consistent effects in enhancing the plant growth and vigor index. Recently, bacterial isolates BWA18 and RWA52 with high IAA production ability (53.80 and 19.18 µg mL^{-1}, respectively), were found to cause growth inhibition of *Avena fatua* weed and stimulated the growth of wheat at 25, 50 and 75 days of observations under pot house conditions (Dahiya et al., 2019).

Aminolevulinic acid production

ALA is a key intermediate in the biosynthesis of tetrapyrroles, such as porphyrins, vitamin B12, chlorophyll (bacteriochlorophyll) and heme. ALA is a natural photodynamic compound, which is effective as a biodegradable herbicide (Sasikala et al., 1994; Phour & Sindhu, 2019) and it has been reported to cause a stimulating effect on the growth and photosynthesis of crops and vegetables (Sasaki et al., 1993). In plants, the ALA concentration is strictly controlled at less than 50 nmol g^{-1} fresh weight (Stobart & Ameen-Bukhari, 1984). Herbicidal activity has been reported to increase accumulation of several chlorophyll intermediates, such as protochlorophyllide, protoporphyrin IX and Mg-protoporphyrin IX, when plants are treated with exogenous ALA at relatively high concentrations (5-40 mM). ALA has been applied as a favorable biodegradable herbicide and insecticide, which is harmless to crops, humans and animals (Beck et al., 2007; Bhowmick & Girotti, 2010; Johansson et al., 2010; Kang et al., 2012).

Liu *et al.* (2005) selected, from 36 photosynthetic bacterial strains, seven strains belonging to *Rhodopseudomonas* sp.; among them, '99-28' showed the highest ALA production ability. However, herbicidal activity of ALA on several plants has been reported to differ by the application methods. At low concentrations (0.01-10 mg L^{-1}), ALA showed growth-promoting effects on yield of several crops (Hotta *et al.*, 1997), whereas it suppressed plant growth at higher concentrations (> 2 mM). Zhang *et al.* (2006) reported that ALA at low concentrations of 0.3-3 mg L^{-1} promoted development and growth of potato microtubers *in vitro*, and enhanced protective functions against oxidative stresses, but application of ALA at 30 mg L^{-1} and higher concentrations may induce oxidative damage. Hyun & Song (2007) reported production of IAA and ALA by *Rhodopseudomonas* strains, which promoted the seed germination and growth of tomato plants under axenic conditions. Chaudhary & Sindhu (2016) found that out of 55 rhizobacterial isolates, only six isolates (HCS7, HCS19, HFS7, HFS9, HFS10 and HFS12) showed ALA production varying from 1.3 to 7.0 µg mL^{-1}. Khandelwal *et al.* (2018) reported that 80% of the rhizobacterial isolates from the rhizosphere of wheat and mustard produced ALA. More ALA production (> 11 µg mL^{-1}) was observed in eight bacterial isolates. Other 54 isolates produced ALA ranging from 5 to 11 µg mL^{-1} and nineteen isolates lacked ALA production ability. Phour & Sindhu (2019) reported significant reduction (92%) in RDW and SDW of *Lathyrus aphaca* weed by inoculation of ALA-producing *Bacillus flexus* strain JIM24 under pot house conditions.

Hydrogen cyanide production

Cyanide production is considered as a major trait of rhizobacteria for biological control of weeds (Kremer & Souissi, 2001), because of its ability to inhibit root cell metabolism and effective inhibition of the cytochrome oxidase pathway. The HCN production has been found to be a common trait of *Pseudomonas* (88.89%) and *Bacillus* (50%) in the rhizospheric soil and plant root nodules (Ahemad & Khan, 2009). Owen & Zdor (2001) reported that two strains of cyanogenic rhizobacteria (*Pseudomonas putida* and *Acidovorax delafieldii*), though significantly inhibited the growth of velvetleaf (*Abutilon theophrasti*), did not reduce corn growth even in the presence of supplemental glycine. Wani *et al.* (2007) found that most of the rhizosphere isolates produced HCN *in vitro* and stimulated the plant growth. On the other hand, *Pseudomonas entomophila* showed biocontrol properties and pathogenicity due to production of HCN (Ryall *et al.*, 2009). The *Pseudomonas fragi* strain CS11RH1 (MTCC 8984), produced HCN and the seed bacterization with this strain significantly

increased the percentage and rate of germination, plant biomass and nutrient uptake of wheat seedlings (Selvakumar *et al.*, 2009).

Agbodjato *et al.* (2015) identified five rhizobacterial species of *Bacillus* (*B. polymyxa*, *B. pantothenticus*, *B. anthracis*, *B. thuringiensis* and *B. circulans*), three *Pseudomonas* species (*P. cichorii*, *P. putida* and *P. syringae*) and *Serratia marcescens*. Inoculation of these rhizobacteria as biological fertilizers resulted into increased maize production. Nandi *et al.* (2017) found that *Pseudomonas chlororaphis* strain PA23 produced HCN and secreted the antibiotics pyrrolnitrin and phenazine, together with degradative enzymes and siderophores. This strain acted as a biocontrol agent. Similarly, *Pseudomonas aeruginosa* (HM195190) strain KC1 isolated from the rhizosphere of castor plants (*Ricinus communis*) (Lakshmi *et al.*, 2015) was found to produce cyanide (4.78 nmol L^{-1}) and seed bacterization with strain KC1 exhibited significant reduction in root length and shoot length of weed seedlings (*Amaranthus spinosus* and *Portulaca oleracea*) in both laboratory and glasshouse experiments. However, inoculation of strain KC1 was found less inhibitory to the seedlings of *Triticum aestivum* as compared to weed seedlings.

Phytotoxin production

Plant pathogens produce a variety of phytotoxins that interfere with plant metabolism, ranging from subtle effects on gene expression to plant mortality (Walton, 1996). Several bacterial and fungal microorganisms were also found to produce a wide array of phytotoxins with the potential to be used as herbicides (Duke *et al.*, 1991). Two phytotoxic metabolites (prehelminthosporal and dihydropore), were isolated from the cultural filtrates of the fungus *Bipolaris* sp. which showed herbicidal activity against *Sorghum halepense* (L.) Pers. (Parmar & Devkumar, 1993). The AAL-toxin (hydroxylated long-chain alkylamine containing a tricarboxylic acid moiety) produced by *Alternaria alternata* f. sp. *lycopersici* has been found to act as an effective herbicide on a range of crop and weed species. In susceptible varieties of tomatoes, it caused rapid wilting and necrosis (Abbas *et al.*, 1995). Similarly, a phytotoxic metabolite trans-4-aminoproline isolated from culture filtrates of *Ascochyta caulina* was found highly effective in controlling *Chenopodium album* (L.) weed (Evidente *et al.*, 2000).

Evidente *et al.* (2005) isolated a new phytotoxic trisubstituted naphthofuroazepinone from the culture filtrates of *Drechslera siccans*, named drazepinone and characterized as a 3,5,12 a trimethyl- 2,5,5a,12a-tetrahydro-1*H* naphtha [2′,3′:4,5] furo [2,3-*b*] azepin-2-one. The novel metabolite showed broad-spectrum herbicidal properties at 2 µg µL^{-1} solution. Another

mobile phytotoxin mevalocidin, produced by *Fusarium* DA056446 and *Roselliana* DA092917 was reported to act as a broad spectrum post-emergence herbicide against grasses and broad-leaved plants (Gerwik *et al*., 2013). The cyclic tetrapeptide phytotoxin tentoxin produced by *Alternaria alternata* caused phytotoxic damage to both monocot and dicot weeds species and therefore showed the potential to be used as bioherbicide (Saxena, 2014). Rath *et al*. (2018) investigated the role of volatile organic compounds (VOCs) produced by PGPR strains in plant growth promotion. *Bacillus subtilis* and *Bacillus amyloliquefaciens* strains produced VOCs like 3-hydroxy-2-butanone (acetoin) and 2,3-butanediol, which promoted plant growth, whereas other volatiles such as HCN and 3-phenylpropionic acid were found phytotoxic and inhibited the plant growth.

Adetunji *et al*. (2018) isolated an active metabolite mellein (a dihydroisocoumarin) from the broth of phytopathogenic strain *Lasiodiplodia pseudotheobromae* and its structural characterization revealed the compound as (R)-8-hydroxy-3-methylisochroman-1-one. The isolated phytotoxic metabolite from *Lasiodiplodia pseudotheobromae* (at 10 μg μL^{-1} conc.) showed selective inhibition at 56–66% against the *Poaceae* and *Valerianaceae* families. Another bioactive phytotoxin with good herbicidal activity was extracted from *Pseudomonas aeruginosa* strain C1501 and the active compound was identified as a 2-(hydroxymethyl) phenol (Adetunji *et al*., 2019). The C1501 strain showed significant decrease in the dry weight of *Amaranthus hybridus* (pig weed) seedlings. Lawrancea *et al*. (2019) isolated a *Pseudomonas aeruginosa* strain H6 with weedicide efficacy from the rhizosphere of *Momordica charantia*. Metabolite identified from strain H6 showed the presence of antifungal and herbicidal compounds. GC-MS analysis of the distinctive herbicidal metabolites produced by *Pseudomonas aeruginosa* H6 was identified as quinoline derivatives, which were found highly toxic to the target weeds. Both, supernatant culture and crude extract of strain H6 showed high inhibition activity in *Pennisetum purpureum*, *Oryza sativa*, *Pisum sativa* and *Amaranthus spinosum*.

Production of antibiotics

The primary mechanism of biocontrol by rhizobacteria involves production of antibiotics such as 2,4-diacetylphloroglucinol (DAPG), pyoluteorin, pyrrolnitrin, phenazine-1-carboxyclic acid, 2-hydroxyphenazines and phenazine-1-carboxamide. Antibiotics have also been found to act as determinants in triggering induced systemic resistance (ISR) in the plant system and contribute to disease suppression by conferring a competitive advantage to biocontrol agents. Kataryan

& Torgashova (1976) reported that the antibiotic 2,4-DAPG showed phytotoxic activity resembling to the 2,4-D herbicide. Geldanamycin and nigericin, two phytotoxic metabolites, were obtained from a strain of *Streptomyces hygroscopicus* and showed significant pre-emergence activity on proso millet, barnyard grass, garden cress and giant foxtail. A polyketide secondary metabolite, herboxidiene, produced by *Streptomyces chromofuscus*, showed potent and selective herbicidal activity against weeds but not against wheat (Miller-Wideman *et al*., 1992). Secondary metabolites isolated from *Pseudomonas syringae* strain 3366 were found inhibitory to downy brome and these metabolites consisted of phenazine-1-carboxylic acid, 2-aminophenoxazone and 2-aminophenol (Gealy *et al*., 1996). Similarly, phenazine-type antibiotics produced by *Pseudomonas fluorescens* were also reported to inhibit the root growth of downy brome weed (Gealy *et al*., 1996).

Effect of rhizobacterial inoculation on weed and crop plants

Bacterial species inhabiting the crop rhizosphere have been reported to affect plant growth in either a positive or in a negative way. Beneficial effects of rhizosphere bacteria have most often been based on suppression of diseases, increased seedling emergence and stimulation of plant growth along with inhibition of weeds growth (Fig. 2) (Sindhu *et al*., 2014, 2016; Phour & Sindhu, 2019). A large array of bacteria, including species of *Azospirillum*, *Azotobacter*, *Arthrobacter*, *Bacillus*, *Enterobacter*, *Burkholderia*, *Paenibacillus*, *Pseudomonas* and *Rhizobium*, have been reported to enhance plant growth (Wani *et al*., 2008; Khan *et al*., 2009; Sindhu *et al*., 2018). Five bacterial isolates belonging to *Pseudomonas putida* (TSAU1), *Pseudomonas extremorientalis* (TSAU6 and TSAU20), *Pseudomonas chlororaphis* (TSAU13) and *Pseudomonas aurantiaca* (TSAU22) were selected from the rhizosphere of wheat grown in saline soil (Egamberdieva & Kucharova, 2009). These isolates produced IAA and among these four isolates caused significant increase in the shoot, root and dry matter of wheat under saline conditions. Mejri *et al*. (2010) reported significant gain in growth of wheat, barley, oat, pea and chickpea after inoculation with *Pseudomonas trivialis* strain X33d, whereas inoculation of this strain in downy brome weed caused growth inhibition.

Kennedy *et al*. (2001) reported stimulation of oilseed rape growth due to application of *P. fluorescens* strain D7, which aggressively reduced the growth of downy brome. Similarly, Li & Kremer (2006) reported increase in growth of soybean and wheat due to application of
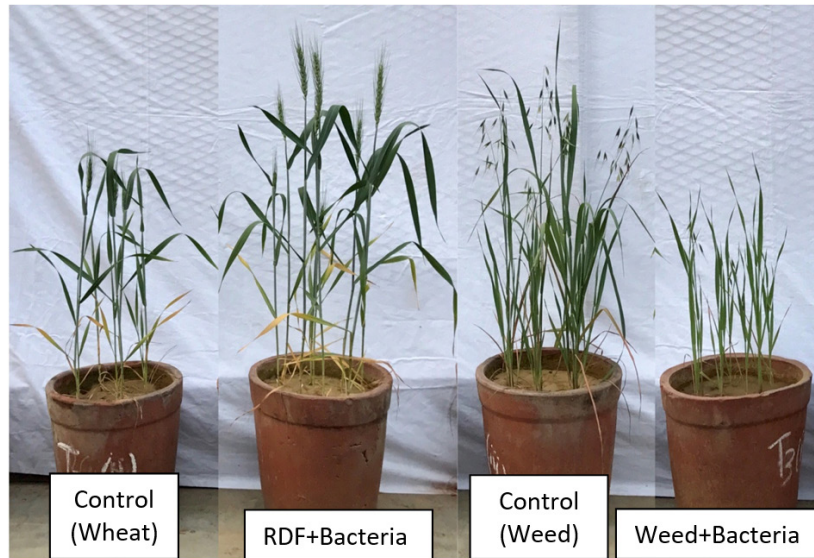
Figure 2. Inoculation effect of rhizobacterial isolates on growth of wheat and weed (*Avena fatua*) plants under pot house conditions at 60 days of plant growth. RDF denotes application of recommended doses of fertilizers in the soil for growth of wheat crop.

P. fluorescens strain G2-11. Previously, this strain showed suppressive effect on the growth of several weeds (barnyard grass, green foxtail and morning glory). Certain rhizosphere bacterial strains T42, L9, $7O_0$, $O_0 10$ and W9 were found to be advantageous under field conditions by causing weed suppression and also improved the competitive ability of the crop against weeds (Abbas *et al*., 2017). Thus, those rhizospheric bacterial isolates that specifically colonize and inhibit growth of weeds but not that of crop plants, may be used as biological control agents. This may benefit agriculture by contributing to increased crop yields, by reducing weed competition and reducing the use of chemical herbicides (Patil, 2014).

Twelve rhizobacterial isolates were tested for their effect on growth of wheat and weed under pot house conditions. Rhizobacterial isolates SYB101, CPS67 and HWM11 were found to stimulate growth of wheat and inhibited the growth of *Phalaris minor* (Phour, 2012). Khandelwal (2016) reported that inoculation of bacterial isolate WHA87 caused 94-182% increase in RDW and 30-340% increase in SDW of wheat, whereas its inoculation showed 21-81% decrease in RDW and 33-43% decrease in SDW of *Chenopodium album* at 30, 60 and 90 days of plant growth under pot house conditions. In case of *Asphodelus tenuifolius*, inoculation of bacterial isolate MSA56 showed 231% increase in RDW and 225% increase in SDW of wheat, whereas its inoculation caused 40-85.7% decrease in RDW and 53-54.3% decrease in SDW of *A. tenuifolius*. Rhizobacterial isolates WHA87, MSA39, MHA75

and MSA56 were found to stimulate growth of wheat, whereas isolates MSA39 and WHA87 inhibited the growth of *C. album* and isolates MHA75, MHA93 and MSA56 inhibited the growth of *A. tenuifolius*.

In another study, rhizobacterial isolates HMM76, HMM92, JMM24, JMM35 and SYB101 were found to stimulate growth of mustard and inhibited the growth of *Lathyrus aphaca* under pot house conditions (Phour, 2016). At 75 days after sowing, inoculation of the two bacterial isolates HMM92 and JMM24 showed 54 to 191% increase in RDW and SDW of mustard, whereas they caused 36 to 92% decrease in RDW and SDW of *Lathyrus aphaca*. These rhizobacterial isolates may be further tested for suppression of weed growth under field conditions for their subsequent application as bioherbicides. A better understanding of the molecular biology of plant-microbe interactions may be useful for designing of strategies in which specific microorganisms may act as PGPR for the cereal and legume crops along with suppressive effects on the growth of weeds.

Conclusion and future prospects

Plant rhizosphere is a rich source of nutrients for different microorganisms in the soil (Wen *et al*., 2017; Mohanram & Kumar, 2019). These microorganisms in turn, provide different nutrients and hormones for the plant growth, and some of the microbes produce the metabolites which suppress the growth of weeds (Sindhu *et al*., 2018). The interactions among microbial

population in the rhizosphere, plant and environment are responsible for the variability observed in growth retardation effects on weeds and in stimulation of plant growth. However, the establishment, persistence and survival of biocontrol agents/bioherbicides in the soil is also a major constraint to their widespread use in commercial agriculture. The continual development of novel molecular methods to investigate soil microbial ecology and the soil microbial community will certainly affect weed ecosystem dynamics, diversity, function and populations. Owing to serious problems of environmental pollution, energy crisis, climate change and an increasing demand of sustainable agriculture, more sincere efforts are required for application of PGPR in weed management to optimize ecofriendly biocontrol strategies. Thus, application of microbial strains having better colonization ability, capability to suppress the growth of weeds and the ability to promote the growth of crops will provide the pesticide-free food to ever-expanding human population (Sehrawat & Sindhu, 2019). Therefore, more emphasis is required on the development of bioherbicides for their application in sustainable agriculture.

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