PLANT-MICROBES INTERACTIONS IN ENHANCING AGRICULTURAL PRODUCTIVITY: SUCCESS STORIES AND BOTTLENECKS

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Since antiquity, animals as well as plants harbour countless microorganisms as hosts. These microorganisms may be beneficial acting in a synergistic way or play an antagonistic role damaging their hosts as pathogens. Such mutualistic relationships also occur in between microbial communities. Various bacteria and fungi play a significant role in plant growth promotion and such microorganisms are called Plant Growth Promoting Bacteria (PGPBs). Amongst nature, soil acts as the largest reservoir of microbial flora, and various mineral nutrients playing a vital role in the plant's life cycle. Certain beneficial bacteria which reside in the rhizosphere have been known as Plant Growth Promoting Rhizobacteria (PGPR) and we are pioneer in enumerating such host-microbe interactions for the beneficial use of plants by exploiting various enzymes, hormones, metabolites, vitamins, etc for plant growth promotion and biocontrol of pathogenic microorganisms so that they can meet the ever-increasing demand of crop productivity since there has been an enormous increase in the world population since last century. This review is a comprehensive account of our understanding of interactions between plants and their microbial guests. The hurdles faced in achieving the objective have also been discussed in this review.

Keywords: Biocontrol, Bioinoculants, PGPR, Sustainable Plants Growth Promotion

The word 'Agriculture' is derived from the Latin word 'Ager' means Land or field and 'Culture' means cultivation. It means the science and art of producing crops and for economic purposes. Agriculture is an art of raising plant life from the soil for the use of mankind. In countries like India, about sixty-four percent of the total population is dependent on agriculture for their live food. By 2050 it is predicted that there will be between 8.0 and 10.4 billion people on earth, with a median value of 9.1 billion. If all these people are to be fed sufficiently, total food consumption will have to increase by 50–70%. If crop production is not sustainable then it will lead to problems in food security. “Food security exists when all people, at all times, have physical and economic access to sufficient, safe and nutritious food that meets their dietary needs and food preferences for an active and healthy life”.

The rhizosphere is a soiled space of root vicinity wherein microbes establish beneficial or destructive interactions with plants. Thus, the soil is considered a reservoir of microorganisms and nutrients for plant growth and health promotion. Beneficial bacteria profound plant health via inducing growth and mineralizing available nutrient from mother soil. It is, therefore, essential to decode and explore these microbes for successful enhancement of crop productivity. Worldwide, considerable research in this area has proved that below-ground plant-microbe interactions are quite effective to enrich the soil fertility and enhancing crop productivity. Many plant growth-promoting rhizobacteria (PGPR) have been discussed over the last 38 years. In 2010, I proposed to call them as Plant Growth and Health Promoting Bacteria (PGPHB) (Maheshwari 2010). Up to now, more than 72 genera 300 species are considered as PGPR (Maheshwari *et al.* 2015).

In this article, we will review who are beneficial bacteria in the rhizosphere, how they derive their major pathways for plant growth promotion with a little bit elaboration on the application of chemical fertilizers vs. biofertilizers plus a critical commentary on the use of crop rotation and composting. Further, it will address a descriptive account of the various role of plant growth and health-

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promoting bacteria, particularly to the biocontrol. Indeed PGHPR, not only the benefits in one way rather holds multifactor responses towards other traits towards plant for its health promotion. The application of these bacteria in bioformulation on different crops will be a part of a discussion under the plant-microbe interaction.

MAJOR PATHWAY OF PLANT GROWTH AND HEALTH PROMOTION

Recent studies on the rhizosphere ecology have increased awareness to survey soil structure and microbiome to serve in agricultural sustainability. Though PGHPRs are potential to many activities in the rhizosphere we can broadly understand as (i) Directly: by fixing atmospheric nitrogen, synthesizing several plant hormones and enzymes, and solubilizing minerals that can modulate plant hormone levels and (ii) Indirectly by producing certain antibiotics, cell wall-degrading enzymes, siderophore, and hydrocyanic acid, etc. The releases of such metabolites adversely affect the fate of the pathogen. Studying the different parameters via a course of time in different bacteria, several bottlenecks and successes were indeed cheerful.

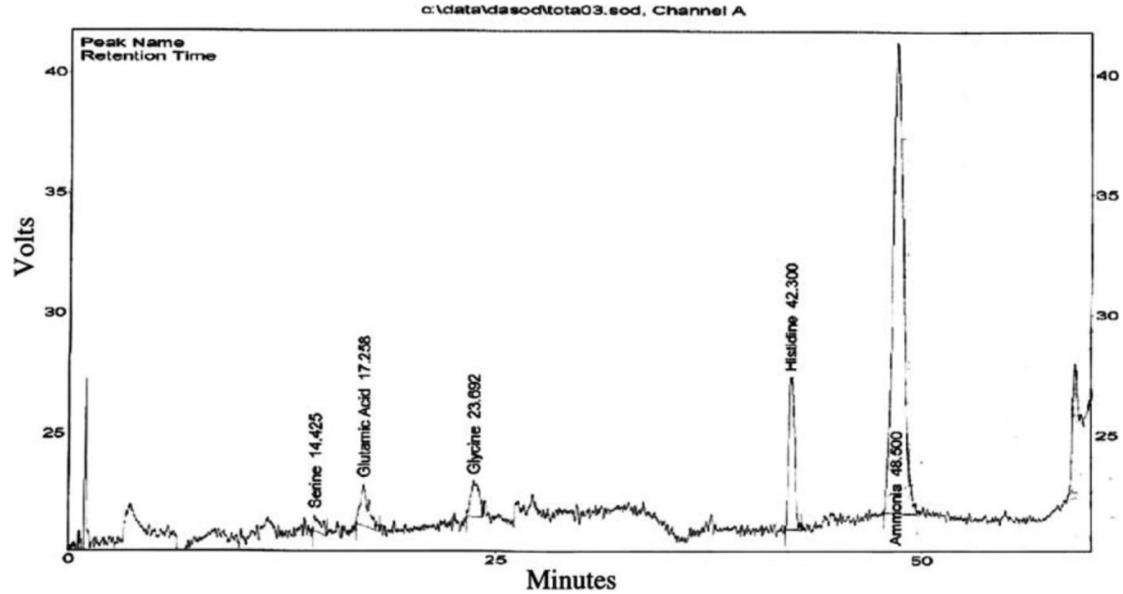
Mineral Solubilisation

For increasing agricultural productivity, mineral nutrition is a deciding factor. When talking about increasing productivity via mineral solubilization, phosphate (P) solubilization is one of the most important mechanisms responsible for the uptake of inorganic phosphorus into available phosphorus. Among the soil-inhabiting bacteria, rhizobia have the greatest phosphorus conversion ability from insoluble phosphorus to phosphates (Aeron *et al.* 2017). Under a field-first strategy for application of Plant Growth Promoting Rhizobacteria (PGPR) in chickpea, the isolates succeeded in the solubilization of Phosphate (P) and potassium (K) so that it can be readily utilized by the crops thus increasing the crop productivity subsequently (Baliyan *et al.* 2018).

A study revealed that buffalo dung can host microorganisms that exhibit better PGP attributes, as they positively enhanced the soil nutrients by solubilizing or oxidizing them. Probably, some microbial oxidation is occurring in dung, resulting in increased plant productivity by providing sulfur (S) and potassium (K) to the plant. Strong PGP activities were observed in a couple of trials (Dhiman *et al.* 2019a, Dhiman *et al.* 2019b, Dhiman *et al.* 2020). In a similar study, the cow dung also proved to be a reservoir of mineral solubilizing microorganisms which successfully solubilized zinc (Zn) and promoted the plant growth (Bhatt and Maheshwari 2019). Availability of Fe^{3+} (Ferric) which is an important macro-nutrient can be achieved via mineral solubilization as it leads to readily available (Fe^{3+}) via iron chelators to be absorbed by plants and therefore siderophore producing microorganisms have proved to be good PGPRs (Kumar *et al.* 2018, Pandey *et al.* 2018).

Phytohormone production

Plant growth promotion mainly depends upon phytohormones facilitated by PGPR within the root zone; these hormones stimulate the density and length of root hairs resulting in the enhanced uptake of water and mineral nutrients from the soil. Historically, it was recorded that in the first decade of the 20th century, Starling defined the term phytohormone as "organic substance which is synthesized in minute quantities in one part of the plant body and transported to another part where these influence specific physiological processes" very first. Phytohormones are growth and defense regulatory metabolites of plants including auxin, abscisic acid, cytokinin, gibberellin, and ethylene. A few of semi-synthetic and synthetic phytohormone brassinosteroids, jasmonate, salicylic acid, nitric oxide, and strigolactones have also been added in the majority phytohormones. The most commonly occurring phytohormone is auxin (indole-acetic acid) i.e. IAA also produced by these bacteria via many pathways



Amino acids	Mole (%)	Component ratio (%)
Serine	0.105	1
Glutamic acid	0.308	3
Glycine	0.236	2
Histidine	0.618	6

Figure. 1 Amino acid profiling of siderophore via **(a)** GAS-Chromatograph **(b)** GAS-Chromatography data (Adopted from Pandey *et al.* 2005)

such as indole 3-butyric acid (IBA) 2-methyl-4-chlorophenoxy acetic acid (MCPA), Indole 3-propionic acid (IPA) 2,4-dichlorophenoxy acetic acid (2,4-D) reviewed by our team (Maheshwari *et al.* 2015).

Beneficial group of bacteria is presently dominating by phytohormone producing abilities and acts plant physiology management They can subdue a broad spectrum of symbiosis by root nodules-forming bacteria (Maheshwari and Saraf 1994). Among, plant-growth regulatory hormone, gibberellins (GAs) are involved in many developmental and physiological processes. A study investigates *Bacillus cereus* MEN8 for the constitutive gibberellin production, optimization of abiotic parameters, characterization, and its application on early seed germination parameters and plant growth promotion. The positive root colonization of *B. cereus* MEN8 was a successful strategy for the rhizospheric establishment and opportunity to secret gibberellins, which plants utilize as plant growth metabolite (GAs) and successfully utilizes in its overall growth and health promotion (unpublished from author's lab).

Siderophore production

Other mechanisms of plant growth promotion are known to be mediated by siderophore production. As it is universally known that iron is the fourth most abundant element in the earth's crust and is required for the growth of nearly all forms of life (Emery 1982). However, its availability to the organisms is very limited due to the rapid oxidation of ferrous to the ferric state. Microorganisms have evolved specialized mechanisms for the assimilation of iron in the ferrous state, by the production of low molecular weight iron chelators, known as siderophores. Siderophores have been implicated for both direct and indirect mechanisms of plant growth enhancement by PGPR. Primarily, catecholate, hydroxamate, and pyoverdine type of siderophores can provide an advantage in the survival of both plants and bacteria community by mediating sacked of fungal pathogens and other microbial competitors from the rhizosphere facilitating iron competition and iron-chelating conditions. Our group is nearly the most active and pioneer in India to advance the study of siderophores in the first decade of the millennium. A study in Korean collaboration, root-nodule bacteria, *Rhizobium meliloti* from *Mucuna pruriens* was observed biocontrol agent due to ample siderophore production (Arora *et al.* 2001). In the same year, the effect of metals on the production of siderophore and other proteins was recorded in *Pseudomonas aeruginosa* influences plant growth parameters (Gupta *et al.* 2001). Further, our study led by Pandey *et al.* (2005) suggested the role of siderophore production in *Pseudomonas aeruginosa* GRC1, characteristic for root colonization and rhizospheric competence. Further, in this study amino acid profiling of siderophore strongly suggested the presence of a pyoverdin chromophore. The observed composition appeared to be original and does not correspond to the known amino acid composition of the fluorescent siderophores normally produced by pseudomonads in that era and most probably the first report understanding novel siderophore in *Pseudomonas* (Fig. 1) (Pandey *et al.* 2005). The multifarious roles of siderophore producing *Mesorhizobium loti* MP6 were further observed in biological control (Chandra *et al.* 2007). In the second decade of the 21^{st} century, siderophore production was noticed as an important trait of PGPR in rhizospheric *Bacillus* strains (Kumar *et al.* 2012). Recently, Kumar *et al.* (2018) elaborated the role of siderophore producing rhizobacteria for the all-round plant growth promotion in wheat plant created a newer pedestal to harness the benefits of siderophore production for bioinoculant preparation for sustainable management of agriculture.

ACC-deaminase

Another bacterial mechanism that beneficially influences plant growth both directly and indirectly in the production of the enzyme 1-aminocyclopropane-1-carboxylate (ACC) deaminase. PGPR producing ACC-deaminase hydrolyzed endogenous ACC into ammonia and α-ketobutyrate instead of ethylene. This enzyme plays a significant role in the regulation of the plant hormone, ethylene. The accumulation of ethylene in root tissues is known to be detrimental to root growth and development. Bacterial strains bearing ACC deaminase activity alleviate the stress-induced ethylene mediated negative impact on plants. Like many other abiotic and biotic factors, accelerated ethylene production occurs under high and chilling temperatures both in plant tissues and microbial species in the rhizosphere. Plants with ACC deaminase expression also cope with this unfavorable situation by lowering the ethylene level. Considering the role of ethylene in stress physiology, it is postulated that much more effort is needed to decipher the role of ACC deaminase producing bacterial strains in plant growth promotion under abiotic stress conditions of cold temperature conditions. Bacterial members of family Rhizobiaceae infect the root tissues of compatible host causing the formation of nitrogen-fixing nodules. The plant growth regulator - ethylene known to inhibit nodulation, is produced in higher amounts under stress affecting rhizobia-legume symbiosis. Therefore, it is desired to score rhizobia with mechanisms that help to facilitate the reduction of endogenous ethylene in plants. 1-amino-cyclopropane-1 carboxylate

(ACC) deaminase catalyzes the cleavage of ACC to alpha-ketobutyrate and ammonia, thus, decrease in ethylene production in host roots, and in turn enhanced root nodulation. Following the discovery of the role of ACC deaminase in plant growth promotion (Glick *et al.* 1998), we were experimenting with ACC deaminase positive rhizobacteria in North India. We were the first group from India to report a beta class of Proteobacteria as rhizobia, identified as *Burkholderia* sp. having ACC deaminase activity (Pandey *et al.* 2005). We reported the role of *Bacillus* sp. with ACC deaminase production ability and other symbionts such as *Sinorhizobium meliloti* bear *acdS* gene conferring ACC deaminase (Kumar *et al.* 2012, Maheshwari *et al.* 2014, Aeron *et al.* 2017). In our continued study on ACC-deaminase, *acdS* in different classes of rhizobia, associated with crop-legumes, *Pisum sativam*, *Glycine max,* and *Cajanus cajan* (Unpublished data from the author's lab).

Biocontrol

PGPR of multifarious PGP traits may improve plant growth and development (Maheshwari 2011). Exclusion of the pathogen through competition for limited resources, production of antibiotics or other inhibitory molecules, predation and parasitism, and induction of plant host defense pathways are few major mechanisms of biocontrol. The widely recognized mechanisms of biocontrol mediated by PGPR are competition for an ecological niche or a substrate, production of inhibitory allelochemicals, and ISR in host plants to a broad spectrum of pathogens and/or abiotic stresses.

While working on a biocontrol agent to combat phytopathogens namely *Fusarium udum, Fusarium oxysporum, Fusarium solani, Rhizoctonia solani, Sclerotinia sclerotiorum, Phytophthora capsici, Macrophomina phaseolina* etc. causing diseases in different crops such as *Cajanus cajan* (pigeon pea), *Cicer aerietinum* (chick pea), *Seasamum indicum* (seasame), *Phaseolus vulgaris* (common bean), *Macrotyloma uniflorum* (horse gram), *Mucuna pruriens* (velvet bean) *Brassica campestris* (Mustard), *Pinus roxburghii* (Pinus), etc. using hundred plus bio-control strains collected from rhizospheric soil (Table 1,2 and 3). Among these some are chemotactic (Pandey *et al.* 2005, Kumar *et al.* 2009). Some efficient in consortia to combat *Macrophomina phaseolina, Fusarium oxysporum,* and *Rhizoctonia solani* (Pandey and Maheshwari 2007a, b). In concern of bio-control studies, pot and field trials were carried out by seed bacterization (Maheshwari 2011, Maheshwari and Dubey 2002) monitoring bacterial populations using green fluorescent protein (GFP) tagging technology. Large scale field trials have been carried out by using carrier-based formulations (Arora *et al.* 2008, Aeron *et al.* 2014) to deliver the inoculant in good physiological conditions to subsistence farmland.

Root colonization

The rhizosphere is a narrow zone of soil directly surrounding the root system. This is an extremely important and active area for root activity and metabolism (Aeron *et al.* 2019). Root colonization can be defined as the ability of certain rhizospheric microorganisms to colonize plant roots. Root colonization also helps in the replacement of chemical fertilizers by 1. Increasing plant growth-promoting traits 2. Biocontrol actions against pathogens. The role of active motility in the root colonization has been shown for strains *B. endophyticus* TSH42 and *B. cereus* TSH77 in *Curcuma longa* L. by chemotaxis for biocontrol against root rot disease caused by *F. solani* (Chauhan *et al.* 2016). It has been shown that *Burkholderia sp.* RHT8 and *Burkholderia sp.* RHT12 showed effective root colonization of fenugreek (Kumar *et al.* 2017) in a consortium and thus provide a better alternative for chemical fertilizers by promoting plant growth parameters as well as fight with the pathogens. Replacement of chemical fertilizers also alleviates the soil stress and thus assimilation of nutrients is well documented as in a study by (Arya *et al.* 2020) where *S. fredii* SSR1 and *A.*

Table 1: List of PGPRs showing percentage fungal inhibition concerning its mode of action

PGPR	Causal Agent	Fungal Inhibition (%)	Factors involved	Reference
***Pseudomonas putida* CRN-09** ***Bacillus subtilis* CRN-16**	*M. phaseolina*	ISR	peroxidase (PO), polyphenol oxidase (PPO), phenylalanine ammonia lyase (PAL), β- 1,3 glucanase, chitinase	(Sharma *et al.* 2018)
***Bacillus spp.* BS-58**	*R. solani* *F. oxysporum*	73 65	IAA, phosphate solubilisation, siderophore production	(Pandey *et al.* 2017)
***B. pumilus* MSUA3**	*R. solani* *F. oxysporum*	72 65	Chitinase, surfactin	(Agarwal *et al.* 2017)
***Pseudomonas* sp. PPR8**	*M. phaseolina* *F. oxysporum*	65 67	extracellular chitinase, β-1,3-glucanase, β-1,4-glucanase and oxalate oxidase	(Kumar *et al.* 2016)
***Bacillus* spp.**	*F. solani*	70	Chitinase 1,3-glucanase, surfactins	(Chauhan *et al.* 2016)
***P. aeruginosa* KRP1**	*S. sclerotiorum* *F. oxysporum*	81 79	HCN	(Maheshwari *et al.* 2015)
***B. licheniformis* KRB1**	*S. sclerotiorum* *F. oxysporum*	76 77	HCN	(Maheshwari *et al.* 2015)
***B. subtilis* BSK17**	*F. oxysporum*	78	Chitinase production	(Dubey *et al.* 2014)
***Bacillus* sp. BPR7**	*M. Phaseolina* *F. oyxsporum* *F. solani* *S. sclerotiorum* *R. solani*	62.10 65.91 64.38 55.59 54.86	Chitinase, β-1,3 glucanase β-1,4 glucanase	(Kumar *et al.* 2012)
***Azotobacter chroococcum* TRA2**	*M. phaseolina*	65.3	Chitinase and β-1,3 glucanase	(Maheshwari *et al.*2012)
***Pseudomonas fluorescens* PS1**	*Sclerotinia sclerotiorum*	72	β-1,3 glucanase, Chitinase, HCN, Oxalate oxidase	(Aeron *et al.* 2011)
***Rhizobium leguminosarum* TR2**	*F. oxysporum*	69	β-1,3 glucanase, Siderophore,	(Kumar *et al.* 2011)
***Pseudomonas aeruginosa* PN1**	*M. phaseolina*	69	β-1,3 glucanase, Chitinase, Siderophore, HCN	(Singh *et al.* 2010)
***Pseudomonas aeruginosa* PGC2**	*Rhizoctonia solani* *Phytophthora capsici*	53 39.6	β-1,3 glucanase, Chitinase	(Arora *et al.* 2008)
***Bacillus subtilis* BN1**	*M. phaseolina*	74	Siderophore, Chitinase, β-1,3 glucanase	(Singh *et al.* 2008)
***Mesorhizobium loti* MP6**	*S. sclerotiorum*	75	Siderophore, HCN	(Chandra *et al.* 2007)
***Pseudomonas aeruginosa* GRC2**	*Macrophomina phaseolina*	80	Siderophore	(Joshi *et al.* 2006)
***Pseudomonas aeruginosa* GRC1**	*S. sclerotiorum*	80	Siderophore	(Gupta *et al.* 2006)
***Pseudomonas aeruginosa* PE10**	*Fusarium Oxysporum*	60	Siderophore HCN, Antibiotics	(Kumar *et al.* 2005)
***Bradyrhizobium* (Arachis) AHR2**	*M. phaseolina*	72	Siderophore	(Deshwal *et al.* 2003)
***Pseudomonas aeruginosa* GRC2**	*M. phaseolina*	74.1	HCN, Siderophore	(Gupta *et al.* 2002)

Table 2 List of PGPRs showing crop disease protection

PGPR	Crop	Disease	Causal Agent	Disease incidence reduction (%)	Reference
***Aneurinibacillus aneurinilyticus* WBC1 *Aeromonas sp.* WBC4, *Pseudomonas sp.* WBC10**	Wheat	Fusarium foot rot	*F. solani*	62 56 65	(Kumar *et al.* 2018)
***Sinorhizobium meliloti* RMP66 *Bradyrhizobium diazoefficiens* BMP17**	*Mucuna pruriens*	Charcoal Rot	*M. phaseolina*	80 71	(Aeron *et al.* 2017)
***P. aeruginosa* KRP1**	Mustard	White rot Wilt disease	*Sclerotinia sclerotiorum* *Fusarium oxysporum*	30	(Maheshwari *et al.* 2015)
***B. licheniformis* KRB1**	Mustard	White rot Wilt disease	*Sclerotinia sclerotiorum* *Fusarium oxysporum*	40	(Maheshwari *et al.* 2015)
***P. aeruginosa* EKi**	Chickpea	Charcoal rot	*M. phaseolina*	67.65	(Khare *et al.* 2011)
***Bacillus subtilis* BN1**	Chir-pine	Root Rot	*M. phaseolina*	96	(Singh *et al.* 2008)
***Mesorhizobium loti* MP6**	Mustard	White Rot	*Sclerotinia sclerotiorum*	99	(Chandra *et al.* 2007)
***P. aeruginosa* GRC1**	Ground Nut	Stem Rot	*S. Sclerotiorum*	48	(Gupta *et al.* 2006)
***P. aeruginosa* PE10**	Tomato	Wilt disease	*Fusarium Oxysporum*	96	(Kumar *et al.* 2005)
***Pseudomonas aeruginosa* GRC2**	Ground Nut	Charcoal Rot	*M. phaseolina*	99	(Gupta *et al.* 2002)
***Rhizobium meliloti* RMP5**	Ground Nut	Charcoal Rot	*M. phaseolina*	96.2	(Arora *et al.* 2001)

valerianellae CCR1, with the low portions of Urea, DAP, MOP, and gypsum (120 DAS), effectively colonized the *C. cajan* roots. These additionally colonized the rhizosphere of *C. cajan* as shown by 6.8 and 6.9 log10 CFU of SSR1 and CCR1, individually. Interestingly, when *A. valerianellae* was utilized as inoculants, the knob number expanded, albeit segregated from knobs it has not been demonstrated to re-nodulate any vegetable plant. Truth be told, the quantity of nodulation was most noteworthy with HDCF in consortia with *S. fredii* which was measurably huge over control thereby reducing the farmer's dependability on chemical fertilizers.

OTHER ALTERNATIVES

Composting under a variety of applications is quite important for farming with interesting aspects of large cultivation of aquatic plants and it's composting to generate an animal feed, soil amendments, and other energy sources. Compost of both plant residues is entirely suitable as organic manure which, offset the cost of fertilizers in the farming system. The addition of compost corroborates nutrients, micronutrients, and organic matter availability to soil and favors growth/activity of symbiotic bacteria resulting in improved biomass. The immense importance of organic manure/compost in the form of humus-rich with plant nutrients increases the fertility of several kinds of soil. Though chemical fertilizers are thought of as the only way to increase soil fertility, several affect soil-fertility too. So, in this scenario, an urgent need

Table 3 List of PGPRs showing net increase percentage in crop yield

PGPR	Crop	Increase Yield	Successful mechanisms	Reference
Bacillus **spp.**	Ragi	38%	IAA, P solubilization, Siderophore Secretion HCN	(Dheeman *et al.* 2019)
P. mirabilis	Saunf	55%	IAA production, HCN, P solubilization, Phytase production	(Dhiman *et al.* 2019)
Bacillus altitudinis **MRN-16** ***Pseudomonas chlororaphis*** **MRN-52**	Chickpea	14%	IAA, P solubilization, K solubilization, Siderophore Secretion, HCN	(Baliyan *et al.* 2018)
Bacillus endophyticus **TSH42** ***Bacillus cereus*** **TSH77**	Turmeric	18%	Chemotaxis, IAA	(Chauhan *et al.* 2017)
Burkholderia sp. **RHT8** ***Burkholderia sp.*** **RHT12**	Fenugreek	40%	IAA, Siderophore, solubilized insoluble phosphate	(Kumar *et al.* 2017)
Pseudomonas aeruginosa **KRP1**	Mustard	33%	IAA, PS, SID, HCN and BC (Fo, Sc)	(Maheshwari *et al.* 2015)
Bacillus licheniformis **KRB1**	Mustard	31%	IAA, PS, SID, HCN and BC (Fo, Sc)	(Maheshwari *et al.* 2015)
Bacillus subtilis **BSK17**	Chickpea	47%	IAA, PS, HCN, and Chi	(Dubey *et al.* 2014)
Rhizobium leguminosarum **PCC2** ***Ensifer meliloti*** **PCC7**	Psorlia corylifia	55% 57%	IAA, SID, HCN and Chi	(Prabha *et al.* 2013)
Ensifer meliloti **TR1** ***Rhizobium leguminosarum*** **TR2**	Fenugreek	35% 36%	IAA, SID, HCN, PS, ACC, Chi, Glu, BC (Fo)	(Kumar *et al.* 2011)
Pseudomonas **sp. EKi**	Chickpea	25%	Salt tolerant, IAA, HCN, BC (Fo)	(Khare *et al.* 2011)
Pseudomonas fluorescence	Mustard	42%	SID, HCN, BC (Ss)	(Aeron *et al.* 2011)
Pseudomonas **sp. RMP1** ***Pseudomonas aeruginosa*** **GRC_2**	*B. juncea*	26% 27%	Chemoadaptive strain, Synergistic, Chemotactic and Root competent	(Maheshwari *et al.* 2010)
S. fredii **KCC5** ***Pseudomoans fluorescence***	*C. cajan*	26% 26%	IAA, PS, SID, HCN, Chi, Glu, BC (Fu)	(Kumar *et al.* 2010)
Pseudomonas aeruginosa **GRC_1** ***Pseudomonas aeruginosa*** **PS2** ***Pseudomonas aeruginosa*** **PSII** ***Pseudomonas aeruginosa*** **LES4** ***Pseudomonas aeruginosa*** **PRS4** ***Pseudomonas aeruginosa*** **PS15**	*S. indicum*	38% 32% 33% 36% 35% 44%	Indigenous and Non-indigenous nature	(Aeron *et al.* 2010)
Pseudomonas aeruginosa **LPT3** ***Pseudomonas aeruginosa*** **LPT5**	*S. indicum*	20% 21%	IAA, SID, PS, HCN, Chi, Glu	(Kumar *et al.* 2009b)
Pseudomonas aeruginosa **LES4**	*S indicum*	41%	IAA, PS, HCN, Chi, Glu, BC (Mp, Fo)	(Kumar *et al.* 2009a)
Pseudomonas aeruginosa **PS1** ***Pseudomonas aeruginosa*** **PS2**	Ground nut	27% 35%	SID, HCN, IAA, PS, BC (Mp)	(Bhatia *et al.* 2008)
Mesorhizobium loti **MP6**	Mustard	52%	SID, IAA, HCN, PS, BC (Ss) and Rhizospheric competent	(Chandra *et al.* 2007)
Burkholderia **sp. MSSP** ***Sinorhizobum meliloti*** **PP3**	*C. cajan*	32% 38%	IAA, PS	(Pandey and Maheshwari 2007)
Pseudomonas aeruginosa **GRC_2** ***Azotobacter chroococcum*** **AC_1**	*B. juncea*	22% 20%	IAA, PS, SID, N_2 fixation and Rhizospheric competent	(Joshi *et al.* 2006)
Pseudomonas aeruginosa **GRC_1**	Peanut	36%	IAA, SID, BC (Mp)	(Gupta *et al.* 2006)
****Pseudomonas aeruginosa*** **GRC_1**	Mustard (2000) Mustard (2001) Mustard (2002)	18% 11% 13%	Rhizospheric competent SID	(Deshwal *et al.* 2006)
Pseudomonas **sp. PE10**	Tomato	46%	IAA, SID, HCN, BC	(Kumar *et al.* 2005)
Pseudomonas aeruginosa **GRC_1**	Peanut	33%	Rhizospheric competent IAA, SID, HCN, BC (Mp)	(Gupta *et al.* 2002)

***** Residual effect; Abbreviation: Mp: *Macrophomina phaseolina* for use of composting for agricultural benefits is the need of the hour to help in the reclamation of wastelands. Composting is another effective way for stepping out agricultural production and extension of area for cultivation through the reclamation of wastelands. Millions of farmers in developing countries need adequate resources for augmenting the crop productivity and ensuring continued maintenance and building up of the soil fertility for greater productivity from agricultural waste residues.

The influence of microorganisms significantly contributes to the process of compost formation as they multiply and decompose the biomass residue under aerobic conditions for composting. The community of microorganisms alters the composting process due to variation in temperature, moisture, nutrient levels, etc. The initial decomposition accelerates with heat generation through oxidation and respiratory activity that leads to a further increase in the decomposition process of compost formation resulting production of uniform fermented dark-coloured material called humus or compost.

The immense importance of organic manure/compost in the form of humus-rich with plant nutrients increases the fertility of several kinds of soil. Extensively, chemical fertilizer thought is the only way to increase soil fertility, but fertilizer on soil under long term use leads the several harmful effects, in this scenario, an urgent need for use of composting for agricultural benefits is the need of today as it also helps in the reclamation of wastelands. Organic materials are available as by-products from the plant (aquatic and terrestrial) and animal origin is considered as the immense source of crop productivity. The enormous importance of organic manure/compost is the need of today as it also helps in the reclamation of wastelands. Wastelands formed due to indiscriminate and overutilization of forest produce standing over the area, unscientific land management by putting the area to improper land use, and sometimes even as an unintended side effect of the very process of development.

CHEMICAL FERTILIZERS VS. BIOFERTILIZERS

A sustainable agroecosystem is vital in today's world because agriculture contributes a major share of national income and export commodity in many developing countries while ensuring food security and employment. One of the finest success stories of the post-independent era is the Green revolutions in the 1960s, which transformed the country from “begging bowl” to “breadbasket.” This has been possible because of the use of chemical fertilizers and hybrid crops. Nonetheless, the chemical fertilizers also pollute the soil environment and exert direct and indirect effects on the microbial community causing a reduction in microbial diversity and eventual extinction of species, and in turn, may cause a catastrophic loss in function and reduced ability of crop ecosystems to withstand unexpected disturbance and periods of stress. The challenges of meeting the food requirements of the burgeoning population and plateauing productivity of agricultural lands can only be met by a second green revolution or evergreen revolution. Some of the strategies that can be channelled to the second green revolution include micro-irrigation system, organic farming, precision farming, green agriculture, eco-agriculture, white agriculture, straw revolution, and use of PGPR in the combination of integrated low doses of fertilizers in term of Integrated Nutrient Management (INM). I have attempted to focus on the above problems relating to our agriculture because it is now possible to achieve economic development in an eco-friendly manner. Given above, it seems imperative to re-asses the agricultural practices and modification of below-ground interactions under specific plants and microbe's communication system accomplished by molecular dialogues. It is, therefore, essential to decode and explore this molecular language to establish a successful symbiotic relationship meant for the enhancement of crop productivity. A concerted effort is being made to search alternative practices that may provide in perpetuity.

Since, farmers use an excessive amount of chemical fertilizers and pesticides in crops, which implicated in ecological environmental and human health perspectives, require yearly treatments, toxic to beneficial microorganisms. It is, therefore, developing rhizospheric competent PGPR for a reduction in fertilizer dose and growth enhancement of some crops such as sesame, which not only equal to that of obtained after full/recommended doses of chemicals but the quality of the oil was also improved (Kumar *et al.* 2009). In other studies, growth enhancement of *B. juncea* by integrated use of two chemo-adaptive strains for commercial and agricultural benefits (Maheshwari *et al.* 2010). Such studies have been carried out with *Pseudomonas, Bacillus,* and *Azotobacter chroococcum* and chemical fertilizer for integrated disease management and growth enhancement of oil yielding crops. The study concluded that beneficial microorganisms reduce external inputs of chemical fertilizers thus, offering an eco-friendly and economical alternative (Maheshwari *et al.* 2012).

PLANT-MICROBE INTERACTIONS

Scientific reports are widening the frontiers of rhizosphere ecology by including technology-oriented manipulation in the rhizosphere. This indeed a strategy of inoculating non-cultivated plant species with beneficial microbes to build soil structure by soil-biota (ecological engineering), to serve in restoration of natural ecosystems and to conserve biodiversity

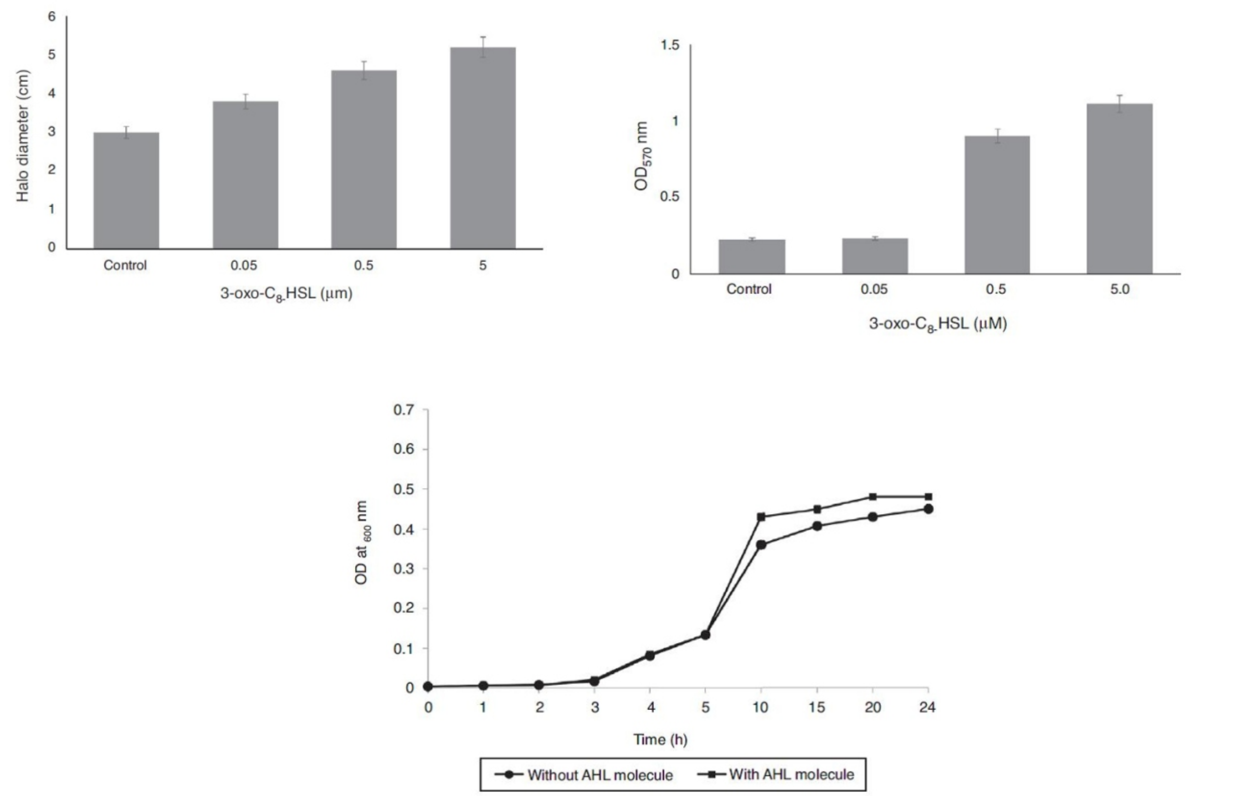


Fig. 2 Roles of quorum sensing molecules from *Rhizobium etli* RT1 in bacterial motility and biofilm formation. (a) Effect of 3-oxo-C8-HSLon swimming motility by *R. etli* RT1. Values are means of experiments performed in quadruplicate. Bars represent SEMs ($p < 0.05$). **(b)** Effect of different concentrations of 3-oxo-C8-HSL on biofilm formation by *R. etli* RT1 after 24 h of growth. Values are means of experiments performed in quadruplicate. Bars represent SEMs ($p < 0.05$). **(c)** Growth curve of *R. etli* RT1 strain in TSB broth with or without the addition of 3-oxo-C8-HSL (5 μM). Values are means ± SEMs of experiments performed in quadruplicate ($p < 0.05$). (Adopted from Dixit *et al.* 2017)

depend on interactions between plants and soil biota. Considerably quantum progresses boosted our wisdom in microbial ecology, and able us to cope with daunting challenges of abiotic and biotic adversities using microbes and their metabolites as weapons.

Intertwine network of molecular signaling in microbes–plant interactions are although onerous but, an opportunity to harness in for crop productivity enhancement and agriculture sustainability. Science reports evidenced that plants produce a giant array of signaling-metabolites that like AHLs to communicate rhizobacteria (Gao *et al.* 2003). Communication through signaling molecules, such as flavonoids (Hassan *et al.* 2012), strigolactones (Ruyter-Spira *et al.* 2013), acyl homo-lactone (AHL) and sesquiterpenes (Schnee *et al.* 2006), are important for regulation of these interactions. Quorum Sensing (QS) is a phenomenon of microbial communication at enough quantum of cell and signaling-metabolite concentration (Berendsen *et al.* 2012). PGPR is also capable of quenching signaling, plays an important role in the ecology of plant-associated consortia so far to manage the efficiency of sensing via cell density (QS), mass-transfer properties (diffusion sensing), and spatial distribution of the cells (Boyer *et al.* 2009). This integrative study of soil microbiology, and a holistic consideration of the various mechanisms serving in the management of the rhizosphere microbiota (Philippot *et al.* 2013).

A study of our laboratory on *Rhizobium etli* RT1 from root nodules of *Lens culinaris* (a lentil) detected to produce signaling molecule N-acyl homoserine lactone (3-oxo-C8-HSL and 3-OH-C14-HSL) has a biological role of 3-oxo-C8-HSL in bacterial motility and biofilm formation influenced by modified or increasing concentrations of 3-oxo-C8-HSL, thereby involved in cell-communication to develop microbial quorum for microbe development in the rhizosphere. This study concludes the importance of quorum sensing, motility and biofilm formation in the rhizosphere (*in vitro*) affected by AHL molecules (Fig. 2) and its ranging concentrations, the overall behaviour of lentil-nodulating soil-rhizobia populations as a concept of coordinated regulation of AHLs synthesis in the response to specific environmental factors (Dixit *et al.* 2017).

BELOW-GROUND ECOLOGY

The beneficial plant-microbe interactions are underlined by the effect of different plant root exudates and their organic acid component on chemotaxis, biofilm formation, and colonization by beneficial rhizosphere-associative bacteria. In our studies, we demonstrated a reduction in the dose of chemical fertilizers and growth enhancement of sesame (*Sesamum indicum* L.) with the application of rhizospheric competent *Pseudomonas aeruginosa*. Further, Rhizosphere competent *Pseudomonas aeruginosa* also showed nematicidal potential in the management of *Heterodera cajani* on sesame and more recently, bio formulations of consortia of *Pseudomonas* and *Bacillus* reported their self-life up to 360 days (Maheshwari *et al.* 2010). Covering all related studies about chemotaxis, rhizosphere-competence and root colonization proved significant concerning plant growth promotion and enhancement of yield with effective inoculant of bestowing colonizing ability in the rhizosphere.

Root colonization is the ability of a microorganism, to colonize the rhizosphere of developing roots. Rhizosphere also implicit microbial diversity correlates with plant diversity due to differences in root exudation and rhizodeposition. Rhizosphere competence of rhizobacteria is strongly influenced due to their ability to use root exudates containing organic acids as carbon sources. The composition and quantity of root exudates also influence the nature of the bacterial activity which can be easily demonstrated in flagellated bacteria (Maheshwari *et al.* 2010). The biofilm architecture in plant-microbe interactions plays a significant role in plant growth promotion. The presence of biofilm in the rhizosphere is an added advantage concerning bacterial chemotaxis, colonization, and rhizospheric competence.

The study of rhizosphere and bulk soil microorganisms is of great importance for biotechnological applications. The chemotactic behavior of microorganisms allows mobility into the rhizosphere due to the root signaling molecule. Thus, exo-ecology microorganisms are considered as allochthonous and endo-ecology are autochthonous (Atlas and Bartha 1998, Cui *et al.* 2014) studied, Firmicutes and Actinobacteria are the major groups in both rhizosphere and bulk soil. Greatness in diversity indices of autochthonous microorganisms than that of allochthonous microorganisms affected by changes in rhizospheric dynamics because bulk soil is recognized to be highly stable in community structure and function, indicated that the bulk soil bacterial communities did not show a dynamic of changes. Inoculated autochthonous bacteria have a strong impact on improving plant growth mechanisms. Bacteria can help plants in the growth enhancement processes and in improving homeostatic mechanisms upon stress challenges. In our study, the best-chosen potential N-fixing autochthonous BCA *Bacillus* increased the productivity of *E. coracana* L. and provided a new dimension of research to exploit the benefits of commercial bioinoculant formulation for routine farming practices. This study signifies the importance of allochthonous and autochthonous *Bacillus* spp. for voracious invasive, root competent and biocontrol mechanisms against foot rot disease in ragi, to be utilized further in bio-inoculant commercialization for agricultural sustainability (Dheeman *et al.* 2020)

BIOFORMULATION

In India, the most common inoculant carrier under a broad group of organic carriers is lignite, charcoal, coir dust, sawdust, and composts of various origins and compositions, sugarcane filter mud bagasse, soils mixed with various organic amendments, and vermiculite. Nonetheless, some organic inoculants made of several waste materials have been tested with significant success in recent years, mainly in developing counties (Rebah *et al.* 2007). Among, non-sterile carriers, alginate beads, charcoal, sand, sawdust, and sugarcane bagasse compared to sawdust, are one of the best carriers for maintaining the desirable bacterial populations when used individually and altogether. The co-inoculant was superior in enhancing the seedling biomass and the nodule number of *Trifolium response* (Arora *et al.* 2008). Further, the enhancement of biomass of *Brassica campestris* while using an organic carrier, sawdust, vermiculite, sand from Ganga basin and cosmetic industry liquid effluent-based formulation of bioceoenotic consortia of *Bacillus* and *Pseudomonas* is interesting (Maheshwari *et al.* 2015). Based on the available information, all polymeric inoculants are used on a small scale for crop production. Among the several carriers tested, sawdust, wheat bran among solid carriers, and whey in liquid formulation proved efficient and cost-effective carrier material for microbial inoculant preparations. The long-term effect of bacteria then cost-effective nature, eco-friendly behavior, and sustainability are the added advantages of these bio formulations (Maheshwari *et al.* 2015).

Monoculture vs. Mixed Culture

The bacterial consortium is a mixed culture containing a group of different species of single bacteria or sometimes even diverse genera, which act together as a community. These include bacterial species that are not only imparting resistance to abiotic stress conditions but contain natural biomolecule which has different PGP traits where single-strain inoculum is unable to perform better, the development of multi-strain inoculum proved quite effective and significant (Roy *et al.* 2015). The combined application of *Sinorhizobium fredii* KCC5 and *Pseudomonas fluorescens* reduced the wilt disease in one of our field trials (Kumar *et al.* 2010). Similarly, multi-strain bacterial consortia bearing ability to produce phytohormone, HCN, siderophore, and having biocontrol activity prove useful for enhancing plant growth and development particularly in conditions where single inoculation was not so effective (Maheshwari *et al.* 2015). Broadly, two-species and multi-species microbial consortia in bio formulations have been found wide applicability in the growth promotion of several crops (Pandey and Maheshwari 2007a, b). These are applied through different modes such as via soil drench, seed bacterization, seedling drip treatment, or in the form of foliar spray. The nature of the formulation and display on the level of their mode of application to the crop plants is a prerequisite. In the present scenario, individual microbe at one time approach has been replaced with that of mixture/consortia of bearing multifarious characteristics. But the prior studies to determine balancing or synergistic behaviors during microbe-microbe interaction provide a better and consistent effect. Although PGPR inoculation of single inoculant (strain) proved useful for enhancing plant growth and development even in salt-stress conditions, inconsistency in their outcome lies due to the involvement of various factors. This drawback might be due to the adverse effect of biotic and abiotic factors and low-quality inoculum (Moënne-Loccoz *et al.* 1999). Under the circumstances, more effort is to be made on multi-strain inoculum to gain agricultural sustainability (Maheshwari 2012).

Shelf Life

The main difficulty with the formulation is survival of the organisms during the period of storage that sometimes-reaching mortality >90% of the initial incorporated population and an acute difficulty for the survival of non-spore-forming bacteria, comprises most genera in PGPR. Additional stress is the condition of reviving the bacteria at the time of inoculation, which faces hydration stress. Besides, survival is affected by several other variables: such as the culture medium used for raising the bacteria, the physiological state of the bacteria when harvested from the medium, the process of cell encapsulation, the use of protective materials, the type of drying technology, and the rate of dehydration. If properly dehydrated, the shelf life of the dried formulation is much longer in comparison to any moist product. The highest death rate occurs either soon after manufacturing, while in storage, or immediately after coating over the seed surface or during supplementing in soil.

In summary, a practical formulation must maintain, over acceptable periods, enough viable bacteria to ensure successful inoculation. Longer shelf life is obtained by increasing the number of microbes in the inoculant, so despite in decline in population over time, enough cells remain alive at seeding time. Alternatively, the use of an additive in the formulation is beneficial to increase growth during storage. Such conditions reduce the rate of mortality of the bacteria. Among several carriers tested, a saw-dust soil combination carrier-based PGPR inoculant efficiently controlled different disease-causing fungi by the involvement of multifarious approaches that indirectly support the growth promotion and yield of various crops. Formulation and field application of inoculants are a pure technological platform with knowledge that is mainly based on fundamental principles of Microbiology and Material sciences. Yet, the unification of these fields creates useful products that are and will be, an important input in sustainable agriculture and environmental solutions.

INDIGENOUS VS. NON-INDIGENOUS PGPRs

Knowledge of the native bacterial population, their characterization, and identification is required for understanding the distribution and diversity of indigenous bacteria (Chahboune *et al.* 2011). The use of indigenous PGPR is an added advantage since it can easily acclimatize and adapted to the natural ecosystems and enhance the plant-microbe interactions.

The influence of indigenous and non-indigenous rhizosphere competent PGPR indicated that a crop is influenced by the use of single inoculants and there is marked variation in growth and yield of the crop when local rhizosphere is the source of the beneficial strain over a non-local strain. Effective root colonization prerequisite attribute for the success of PGPR in plant growth and yield promotion. Thus, the successful colonization by PGPR in both oil yielding crops as well as the pulse crop rhizosphere promotes growth and establishes the performance of indigenous microflora over non-indigenous microflora. A carrier-based formulation as bio inoculants are viable and showed a long term effect on the crops cultivated in the farmer's field (Deshwal *et al.* 2006, Aeron *et al.* 2010).

In our study, the root colonization by indigenous and non-indigenous strains, in two subsequent years of field trials of *Brassica campestris* where the average population of *P. aeruginosa* PSI5$^{azio+ \ kan+}$ was higher compared to the treatment by other isolates. Further, a population of homeostasis was recorded in all treatments. Pseudomonads did not have any inhibitory effect. Recently, we reported that a mixture of microbes or consortia recommended for the engineering rhizosphere for increased plant growth and disease control. A crop is influenced by the use of single inoculants and there can be marked variation in growth and yield of a crop when local rhizosphere is the source of the beneficial strain over a non-local strain. Effective root colonization is proved prerequisite attribute needed for the successful establishment of PGPR in the plant rhizosphere. Thus, the colonization by fluorescent pseudomonads in sesame rhizosphere promotes growth and proves the efficacy of indigenous microflora over non-indigenous microflora on the plant growth promotion and development (Aeron *et al.* 2010).

SUMMARY OF SUCCESS AND BOTTLENECKS: The most commonly occurring phytohormone is auxin (indole-acetic acid) i.e. IAA evaluated in a wide array of soil and rhizospheric bacteria subdued a positive pathway to make mark-ups on the ways to success. We have investigated siderophores in rhizobia, pseudomonads, and in the variety of microorganisms including Bacilli. Novel siderophore was characterized by a few microbial strains. Another bacterial mechanism that beneficially influences plant growth both directly and indirectly in the production of the enzyme 1 aminocyclopropane-1-carboxylate (ACC) deaminase was experimenting pioneer in North India. We were the first group from India to report a beta class of Proteobacteria as rhizobia, identified as *Burkholderia* sp. Later a similar enzyme was noted in *Bacillus* sp. *Sinorhizobium meliloti* bearing *acdS* gene. Working on bio-control myriad of microbial strains was found working on a wide spectrum of fungal pathogens. More intense studies like SEM have revealed the major factors of biocontrol in microbial strains that produce differential to combinatorial effect on fungal physiology and structural integrity.

We developed fertilizer adaptive variants of microbes able to thrive on half to full/recommended doses of chemicals. The chemo-adaptive strains were obtained for commercial and agricultural benefits. Worked on the importance of quorum sensing, motility, and biofilm formation in the rhizosphere (in vitro) affected by AHL molecules and its ranging concentrations, the overall behavior of lentil-nodulating soil-rhizobial populations as a concept of coordinated regulation of AHLs. Covered all the related studies concerning chemotaxis, rhizosphere-competence, and root colonization. Identified the significance of allochthonous and autochthonous *Bacillus* spp. for voracious invasive, root competent, and biocontrol mechanisms against foot rot disease in ragi, to be utilized further in bio-inoculant commercialization for agricultural sustainability. Many inorganic and organic carrier materials were investigated to produce a strategy of bacteria delivery from laboratory to land. Success was achieved in bacterial consortium broadly, two-species, and multispecies microbial consortia in bio formulations. This hurdle might be due to the adverse effect of biotic and abiotic factors and low-quality inoculum under a few circumstances affecting multi-strain inoculum to gain agricultural sustainability. Maintaining the self-life of carrier is always daunting because of the survival of the organisms during the period of storage that sometimes-reaching mortality. Additional stress is the condition of reviving the bacteria at the time of inoculation, which faces hydration stress. Besides, survival is affected by several other variables: such as the culture medium used for raising the bacteria, the physiological state of the bacteria when harvested from the medium, the process of cell encapsulation, the use of protective materials, the type of drying technology, and the rate of dehydration. If properly dehydrated, the shelf life of the dried formulation is much longer in comparison to any moist product. Beside all bottlenecks, longer shelf life is obtained by increasing the number of microbes in the inoculant, so despite in decline in population over time, enough cells remain alive at seeding time. Among several carriers tested, a saw-dust soil combination carrier-based PGPR inoculant efficiently controlled different disease-causing fungi by the involvement of multifarious approaches that indirectly support the growth promotion and yield of various crops. Formulation and field application of inoculants are a pure technological platform with knowledge that is mainly based on fundamental principles of microbiology. Yet, the unification of these fields creates useful products that are and will be, an important input in sustainable agriculture and environmental solutions. The use of indigenous PGPR is an added advantage since it can easily acclimatize and adapted to the natural ecosystems and enhance the plant-microbe interactions. The influence of indigenous and non-indigenous rhizosphere competent PGPR indicated that a crop is influenced by the use of single inoculants and there is marked variation in growth and yield of the crop when local rhizosphere is the source of the beneficial strain over a non-local strain.

CONCLUSIONS

Based on the above, the current and future progress of agriculture depends, indeed on our knowledge of microbial ecology is facing various challenges. But, understanding the molecular signaling network involved in microbe–plant interaction is a promising opportunity to improve our knowledge as well as crop productivity for agriculture sustainability. Besides, thrust for integrative studies in soil microbiology, and a holistic consideration of the various mechanisms play an important role in the rhizospheric establishment of beneficial microorganisms which would undoubtedly improve prediction and management of the rhizosphere microbiome.

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