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MINI-REVIEW

Facets of rhizospheric microflora in biocontrol of phytopathogen *Macrophomina phaseolina* in oil crop soybean

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Abstract

The use of microbial bioinoculants for managing plant diseases and promoting plant growth is an effective alternative approach to integrated farming. One of the devastating phytopathogens is *Macrophomina phaseolina* (Tassi) Goid. It is an omnipresent fungus infecting more than 500 plant species. It causes charcoal rot disease in soybean leading to 30–50% yield loss. Soybean Glycine max (L.) oil seed crop produced globally is highly susceptible to *M. phaseolina*. India is the fifth largest producer of soybean in the world. Madhya Pradesh is the largest soybean-producing state in India; Around 70% yield loss of soybean is accounted to *M. phaseolina* infection in India. Control of charcoal rot is the requisite of the current situation. Chemical control is not feasible due to saprophytic nature and prolonged survival of *Macrophomina phaseolina*. Chemical fungicides are expensive, toxic, hazardous, and cause pollution. Biological control is an effective approach to control this devastating fungus. The rhizosphere of soil is rich in beneficial microflora competent to suppress plant pathogens and also promote plant growth. PGPR have well-developed mechanisms that impart antagonistic traits to them. PGPR produces various antifungal metabolites siderophores and HCN which inhibit fungal growth, and can be used as potent BCA. *Pseudomonas* and *Bacillus* species have been reported effective against *M. phaseolina*. The mechanisms and antifungal compounds produced by these bacteria to control charcoal rot can be studied extensively. BCA or the metabolites secreted by them have the potential to develop effective bioformulations for soybean at the commercial level for sustainable agriculture.

Keywords Soybean · *Macrophomina phaseolina* · Charcoal rot · BCA · Sustainable agriculture · Bioformulations

Introduction

With the increasing population, it has become indispensable to increase crop productivity using sustainable approaches in agriculture. The important constraint in crop production worldwide is plant diseases accounting for 10–30% yield loss (Strange and Scott 2005). Biological control manifests to be one of the most promising strategies for reducing disease incidence, thereby increasing agricultural productivity. Beneficial microbes present in the soil exhibiting antagonistic traits against plant pathogens are employed in biomanagement of diseases. The use of botanical extract, microorganism, or their products for control of pathogen or pest is safe and effective biocontrol for disease management (Sreevidya and Gopalkrishnan 2012). The rhizosphere of soil is rich in microflora that has fascinating properties, suppressing phytopathogens, and promoting plant growth.

These attributes have made biological control an effective and alternative measure to the use of agrochemicals which are toxic to humans and animals, pollute the environment, and are expensive. The use of biocontrol agents in agriculture reduces the problem of pollution as they decompose quickly and do not leave residues. Microbes belonging to bacteria, fungi, and actinomycetes are effective biocontrol agents (BCA) inhibiting many plant pathogens. Bacteria belonging to *Bacillus*, *Burkholderia*, *Streptomyces*, *Pseudomonas,* and *Serratia* are known to exhibit biocontrol traits (Mark et al. 2006). They are also known as plant growth-promoting rhizobacteria (PGPR) as they promote plant growth. There are various mechanisms underlying antagonism viz. competition for nutrients and space (Spadaro and Dorby

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2016); parasitism; production of antifungal compounds such as antibiotics (Kohl et al. 2019), lipopeptides, lytic enzymes; siderophores (Siddiqui 2006); volatile compounds—HCN (Raaijmakers et al. 2009)—induced systemic resistance and antibiosis (Martinez et al. 2006) (Fig. 1). Often these mechanisms operate either singly or in coordination to combat plant diseases. Rhizospheric bacteria colonize the root system and prevent pathogens to invade, thereby suppressing disease. Among the rhizobacteria, *Pseudomonas* and *Bacillus* species have proved to be efficient BCA against soil-borne pathogens.

Efficacy of *Pseudomonas* species as biocontrol agent

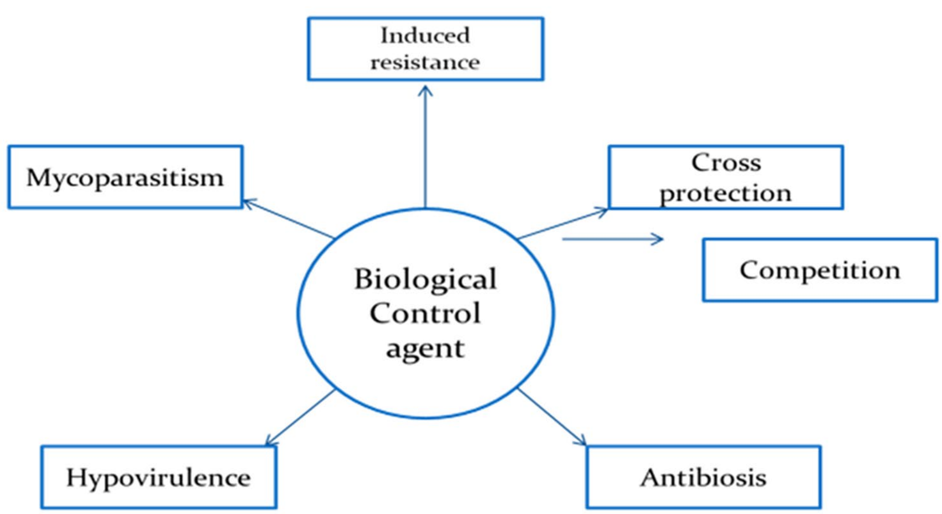
Pseudomonas is an efficient root colonizer known to produce various antifungal metabolites. Antibiotics such as pyrrolnitrin, pyoluteorin, 2,4-diacetylphloroglucinol (2,4-DAPG), volatile compounds viz. HCN and ammonia, siderophores, etc. are produced by *Pseudomonas* species which inhibit phytopathogens (Leon et al. 2009). The presence of genes involved in the synthesis of antibiotics viz. pyrrolnitrin (prnC), 2,4-DAPG (phlD), phenazine-1-carboxylic acid (phzC and phzD) and pyoluteorin (pltC) were studied by Leon et al. 2009 in *Pseudomonas* strains isolated from soybean rhizosphere. *P. fluorescence* BNM296 was found to be positive for prnC and pltC genes, exhibiting its ability to produce pyrrolnitrin and pyoluteorin. TLC analysis confirmed the production of these two antibiotics in BNM296 strain.

Induced systemic resistance is also one of the mechanisms used by *Pseudomonas* species against phytopathogens. The biocontrol activity of *P. fluorescens* isolated from soil samples of chili and sunflower against *Fusarium solani*, *Rhizoctonia solani*, *Alternaria alternata* and *Colletotrichum gloeosporioides* were studied by Anand et al. (2010). *P. fluorescens* isolates were also evaluated for inducing systemic resistance against *Fusarium solani.* The isolate Pf4 induced resistance maximally, thereby increasing germination frequency, root, and shoot length in chili.

Antagonism of *Pseudomonas putida* and *Pseudomonas fluorescens* has been studied extensively for the management of plant diseases. Priyanka et al. (2017) isolated 62 *Fluorescent Pseudomonas* isolates from soybean rhizospheric soil and evaluated their antagonistic activity against *S. rolfsii* and *C. truncatum*. 51 isolates were able to inhibit these phytopathogens. Siderophore-producing ability of the isolates was also studied in-vitro as a biocontrol mechanism. All the 51 isolates produced siderophores, which might be involved in antagonism. Siderophores chelate Fe (II) ions form siderophore–Fe complex which is recognized and taken up by membrane-bound protein receptors. As a result, iron becomes unavailable to the pathogens, thereby controlling plant pathogens.

Pseudomonas species are also known to produce plant growth hormones like IAA which improves plant growth. Kumar et al. (2005) evaluated the antifungal activity and plant growth-promoting traits of Pseudomonas *aeruginosa* PUPa3 to be used as an efficient biofertilizer. *P. aeruginosa* PUPa3 produced IAA and also exhibited antagonistic activity against various phytopathogenic fungi. The effect of IAA produced by *P. aeruginosa* in controlling charcoal rot in chickpea was studied by Khare and Arora (2010). Disease suppression by *P. aeruginosa* TO3 and its IAA defective mutants were compared *in vitro* and *in vivo*. Percent inhibition was observed to be 50% and 66.67% by IAA defective mutant and wild-type strain, respectively. The results reveal the role of IAA produced by bacteria in reducing disease incidence.

Fig. 1 Mechanisms of biocontrol agent



Efficacy of *Bacillus* species as biocontrol agent

Bacteria belonging to *Bacillus* are safe to be used as BCAs (El-Bendary 2006). Members of the *Bacillus* species have been reported as the first successful biocontrol agents against pathogens (Patil et al. 2015). A wide variety of plant pathogens like *Fusarium graminearum*, *Fusarium solani, Fusarium oxysporum, Macrophomina phaseolina, Rhizoctonia solani, Magnaporthe grisea, Colletotrichum gloeosporioides*, etc. can be controlled by *Bacillus* species.

Bacillus species form spores which are stress tolerant and secrete metabolites preventing pathogen infection and promoting plant growth (Radhakrishnan et al. 2017). Among the *Bacillus* species, *Bacillus licheniformis*, *Bacillus subtilis*, *B. pumilus*, and *Bacillus amyloliquefaciens* have been found effective in controlling plant diseases (Fira et al. 2018; Rabbee et al. 2019).

Five to eight percent of genomes of *B amyloliquefaciens.* and *B. subtilis* are concerned with the secondary metabolites synthesis having the antimicrobial activity (Chen et al. 2009; Stein 2005). *Bacillus subtilis* is a potent BCA owing to its ability to produce antibiotics, lipoproteins, and hydrolytic enzymes (Cavaglieri et al. 2005; Sharma and Sharma 2008). The lipopeptide antibiotics produced by *Bacillus* species are iturins, fengycins, surfactins, bacillomycin, and plipastatin. Iturins form ion-conducting pores, thereby increasing the electrical conductance of lipid membranes. They are also known to disrupt cytoplasmic membranes of pathogens (Gong et al. 2015). Zhao et al. (2016) isolated *Bacillus subtilis* Y-IVI from the rhizosphere of muskmelon and studied antifungal activity against *Fusarium oxysporum*. Antifungal compounds iturin A and fengycin were extracted, purified, and identified by LC–MS; their inhibitory activity against *F. oxysporum, R. solani,* and *V. dahliae* was evaluated. Both the antibiotics iturin A and fengycin inhibited fungal growth.

Fengycins produced by *Bacillus* species show antifungal activity by inducing defences in certain plant species. Fengycins secreted by *B. subtilis* BBG111 induced defence in rice against *R. solani* (Chandler et al. 2015). Medeot et al. (2020) isolated fengycins from *B. amyloliquefaciens* $MEP_2 18$ strain and studied their antimicrobial activity against phytopathogen *Xanthomonas axonopodis* pv. *vesicatoria* by disc diffusion method. The concentration of fengycin in discs ranged from 6.25 to 25 μg ml^{-1}. Fengycins were able to inhibit *X axonopodis* pv. *vesicatoria* at the lowest concentration of 6.25 μg ml^{-1} also. The studies reveal the potentiality of fengycins produced by *Bacillus* as an effective antimicrobial agent. Another antibiotic bacteriocin has an important role in innate host immunity (Hashem et al. 2019).

B. subtilis is known to improve the tolerance of plants to biotic stress and produce VOCs that enable plants to resist pathogen attack (Ryu et al. 2005). Exopolysaccharides and siderophores secreted by *Bacillus* sp. interfere in the movement of toxic ions released by pathogens thereby inhibiting pathogen's growth and maintaining ionic balance (Radhakrishnan et al. 2017). *B. subtilis* CTS-G24 showed antiphytopathogenic activity against *F. oxysporum* and *M. phaseolina* (Patil et al. 2014). The hydroxamate type of siderophore produced by this isolate could be the mechanism of biocontrol.

Bacillus species are also known to regulate the synthesis of defense-related proteins in diseased plants. Kim et al. (2015) studied the role of *Bacillus species* JS in activation of pathogenesis-related genes, thereby inducing systematic resistance in tobacco plants infected with *Rhizoctonia solani* and *Phytophthora nicotianae*. *Bacillus* sp. JS upregulated PR genes encoding β-1,3, glucanase, chitinase, antioxidant enzyme peroxidase, and conferred resistance to tobacco plants. Treatment with *Bacillus* species stimulates the expression of antioxidants and various defense enzymes (Radhakrishnan et al. 2017).

Bacillus subtilis induce the synthesis of antioxidant enzymes peroxidase (POX), superoxide dismutase (SOD), phenylalanine ammonia-lyase (PAL), and polyphenol oxidase (PPO) (Miljakovic et al. 2020). The competitive advantage of *Bacillus* species is their characteristics which make these bacteria interesting for industrial production of biofungicides and antibiotics. The differences in the properties among *Bacillus* species can be used for integrated management of pathogens involving two or more of its species. Their combinations can be developed into effective bioformulations which needs to be focused on.

Devastating plant pathogen: *Macrophomina phaseolina*

One of the major fungal pathogens of utmost concern is *Macrophomina phaseolina* causing disease in many crops like mung bean, green gram, chickpea, sesame, soybean, sunflower, maize, sorghum, jute, and cotton. *Macrophomina phaseolina* (Tassi) Goid is a diverse omnipresent soil-borne fungal pathogen that infects more than 500 plants (Dhingra and Sinclair 1977). It has two asexual stages: sclerotial stage (*Rhizoctonia bataticola*) and pycnidial stage (*Macrophomina phaseolina*). In the sclerotial stage, fungus survives in the form of multicellular sclerotia. Mature sclerotia are pigmented with tightly packed outermost cells. Sclerotial inoculum density is directly related to disease incidence (Lodha and Mawar 2020).

The pycnidial stage is characterized by pycnidia immersed in host tissue which erumpent at maturity; 100–200 μm in diameter; dark to grayish in color and blacken with age; subcutaneous with truncate ostiole; spherical or flattened globose. Pycnidia have rod-shaped conidiophores with 10–15-μm-long conidia, single-celled, hyaline, and oval (Arora and Dhurwe 2019).

It causes different diseases viz. dry root rot, stem canker, seedling blight, damping off in a variety of crops. Crops growing in subtropical and tropical countries with semi-arid climate are prone to *Macrophomina phaseolina*. Infection is observed in roots, stem, branches, seeds, petioles, leaves of the plant. *Macrophomina phaseolina* resides in the soil as microsclerotia (black fungal structure) for a prolonged period of time (Luna et al. 2017). Being a saprophytic fungus, it can survive in the soil for 15 years (Ghosh and Biswas 2018). Germination of microsclerotia takes place between 20 and 40 °C, thereby affecting root tissue.

Mycotoxins are secreted by phytopathogenic fungi to incite disease in plants. The infection process in *Macrophomina phaseolina* is thought to be mediated by two toxins—phaseolina and botryodiplodin isolated from it (Luna et al. 2017). Phaseolina is the major toxin studied so far causing disease in crops. Management of *Macrophomina phaseolina* includes crop rotation, tillage, chemical control, and biological control. *M. phaseolina* being saprophytic and survives in soil for a longer duration; biological control is the most effective strategy to manage this devastating fungus.

Macrophomina phaseolina: infection in soybean

Soybean *Glycine max* (L.) is an important agronomic crop globally. It is known for its high quality protein and oil content. It is produced in more than 50 countries. India is Asia's second largest producer of soybean (FAOSTAT 2016). Madhya Pradesh is the largest soybean-producing state in India. Madhya Pradesh accounted for 48.30% of the total area under cultivation in India (2016–2017). The various cultivars of soybean in Madhya Pradesh are JS 95-60, JS 76-205, JS 75-46, JS 90-41, etc. Many biotic and abiotic factors affect its production; majorly, it is affected by soil-borne fungus *Macrophomina phaseolina* leading to 30–50% yield loss (Yang and Navi 2005).

Macrophomina phaseolina (Tassi) Goid causes charcoal rot disease in soybean. It is of major concern causing considerable yield losses worldwide. Charcoal rot in soybean was reported in the United States in 1949 for the first time (Luna et al. 2017) It has been ranked among the five most important diseases of soybean leading to huge annual economic losses in the top ten soybean-producing countries viz. US, China, India, Brazil, Argentina Paraguay, Indonesia, Canada, Italy, and Bolivia in 1998 (Wrather et al. 2001).

Once an infection occurs, it produces enzymes and toxins degrading root tissue, stem, and root tissues get colonized within two–three weeks (Islam et al. 2012). *M. phaseolina* infects the plant's vascular system thereby interfering in nutrients and water transport across leaves, leading to wilting, premature leaf death (Gupta and Chauhan 2005). The symptoms are decreased vigor, yellowing of leaves, brown to red discoloration on stem and roots while at a later stage, wilting, premature senescence is observed; and plants die prematurely. Lower parts of the roots and stem develop gray or silver discoloration due to the formation of microsclerotia (Gupta and Chouhan 2005). Therefore, the disease is named charcoal rot.

Charcoal rot is an important disease of soybean; affecting the agricultural economy of a country, needs to be controlled at a faster pace. There is an urgent need to develop effective biofungicides with potent antagonistic activity against *Macrophomina phaseolina* for controlling charcoal rot and increasing soybean production.

Biocontrol of charcoal rot in soybean

Chemical control of charcoal rot is not feasible due to the prolonged saprobiotic survival ability of *Macrophomina phaseolina.* Management of soil-borne pathogens is difficult; biological control is the only solution for the long-term sustainability and effective management of soil-borne diseases. The yield loss caused by a pathogen can be controlled by using plant growth-promoting bacteria (PGPB) having antifungal properties, as they produce xenobiotic compounds. Rhizospheric bacteria have well-developed mechanisms able to control *M. phaseolina* (Fig. 2). *Pseudomonas* and *Bacillus* produce a wide range of antibiotic compounds, which can control *Macrophomina phaseolina* and can be isolated from the rhizosphere of soybean. *Pseudomonas* and *Bacillus* species have been found effective in controlling *Macrophomina phaseolina* infecting different agronomic crops.

Fluorescent Pseudomonas is abundantly present in the rhizosphere and has several characteristics making it an effective biocontrol of choice. *Fluorescent Pseudomonas* isolated from rhizospheric soil of variety of crops were studied for their antagonistic activity against plant pathogen *Macrophomina phaseolina* (Manjunatha et al. 2012). Members of genus Pseudomonas contain a large number of biocontrol strains; they produce a considerable and diverse amount of antifungal metabolites. Pyrrolnitrin is effective against *Fusarium, R. bataticola, and* other fungal pathogens (Ligon et al. 2000).

Belkar and Gade (2012) studied the antagonistic potential of *Pseudomonas fluorescence* against *R. bataticola* causing root rot in soybean and *Sclerotium rolfsii* by dual-culture technique. They reported alkaline isolates of *P. fluorescence* Pf3 were found to be most effective—67.04% inhibition and 74.7% inhibition against *R. bataticola* and *S. rolfsii,* respectively, after 7 DAI. Antifungal activity of *Pseudomonas*

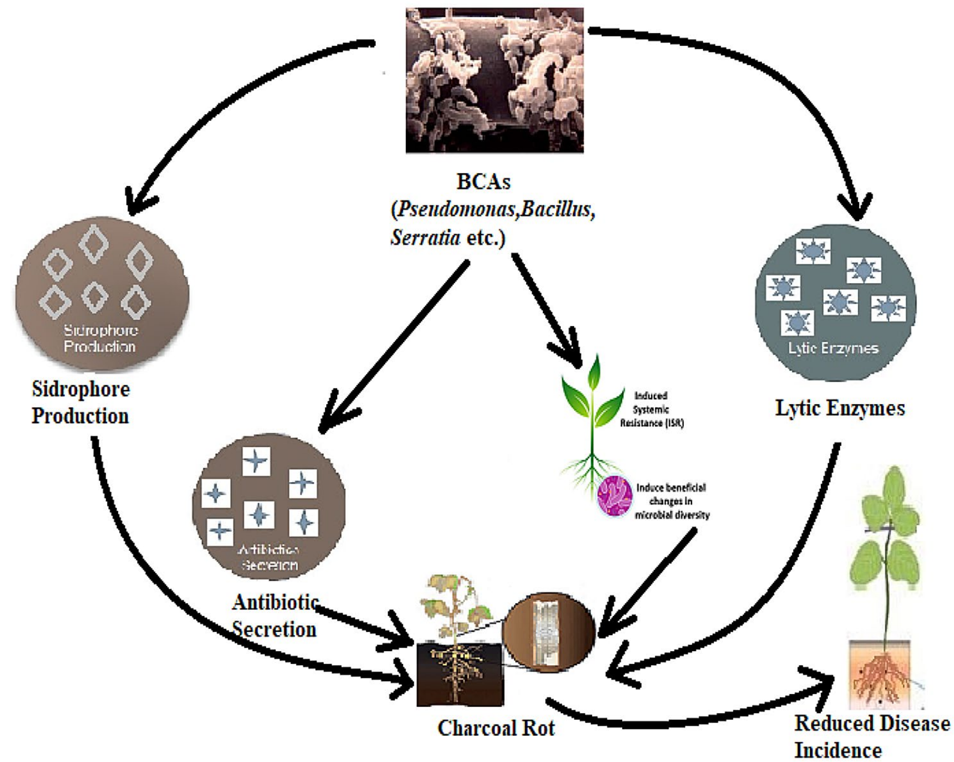


Fig. 2 Mechanism of BCAs in controlling *M. phaseolina* (Charcoal rot)

psychrotolerans against *Macrophomina phaseolina*, *Fusarium oxysporum*, and *Fusarium solani* was evaluated by Muhammad et al. (2015).

The biocontrol ability of *Bacillus* and *Pantoea agglomerans* against *Macrophomina phaseolina* infecting soybean was studied by Vasebi et al. (2013). Bacillus species BIN is the name assigned to the bacillus isolate by Vasebi et al. (2013) while P. agglomerans represents *Pantoea agglomerans*. They reduced disease incidence and also promoted the growth of plants in greenhouse conditions. Antagonistic potential of *Bacillus subtilis* and *Rhizobium meliloti* against *Macrophomina phaseolina* on sunflower was evaluated by Anis et al. (2010). *Bacillus subtilis* and *Rhizobium meliloti* are more effective in inhibiting the radial growth of *M. phaseolina* as compared to fungal antagonists. The results reveal *B. subtilis* as effective BCA against *M. phaseolina*. *B. subtilis* isolated from the rhizosphere of mung bean inhibited *Macrophomina phaseolina* (percentage inhibition 53.24%) in vitro (Kumar et al. 2015). Similar results were observed under greenhouse conditions reducing the disease incidence to 46.67%.

Bioformulations for disease control

The development of effective bioformulation for disease control in plants involves the use of potent antagonistic microorganisms along with suitable binder/carrier material. Its efficacy also depends on the method used for preparing it such as elicitation, carrier binding, immobilization, etc. Latha et al. (2017) developed bioformulations for the management of dry root rot in black gram. The microbial consortia included *Trichoderma, B. subtilis*, and *P. fluorescens* which was mixed in different combinations with farmyard manure and neem cake to prepare bioformulation. The combination of *P. fluorescens* (PfuL(A)) and *B. subtilis* (BsOP2), farmyard manure, and neem cake effectively reduced the disease incidence under field conditions. Talc-based bioformulation of *Pseudomonas* TS2 was developed using CMC as the binder against *F. oxysporum* infecting chickpea by Khare and Shrivastav (2016). A variety of enrichment materials—sucrose, molasses, skimmed milk, and trehalose were used for this purpose. Molasses-amended bioformulation showed the highest inhibition of *F. oxysporum* (89%) followed by skimmed milk (86.67%).

The success of any bioformulation depends on the long shelf life of the organism used and its stability at different temperatures. Incorporating suitable additives in the bioformulations can increase their efficiency. Also, the co-inoculation of two or more compatible microbes to prepare biofungicide/biopesticide will definitely result in an elite formulation having broad-spectrum activity. Some of the commercial bioformulations using different microbes are given in Table 1.

The studies show the potential of rhizobacteria to inhibit *Macrophomina phaseolina* and other phytopathogens.

Table 1 List of commercial bioformulations in India and other countries (Mishra and Arora 2016; Miljakovic et al. 2020)

Brand name	Organism	Name of company	Country
Symbion-N	*Azospirillum, Rhizobium, Acetobacter* and *Azotobacter*	T.Stanes & Company Limited	India
Symbion-P®	B.*megaterium* var. *Phosphaticum*		
Symbion-K	*Frateuria aurantia*		
Symbion-S	*Thiobacillus thiooxidans*		
Symbion-VAM	*Glomus fasciculatum*		
CALOBIUM	*Rhizobium* sp.	Camson Bio Technologies Limited	
CALMONAS	*Pseudomonas* sp.		
CALSPIRAL	*Azospirillum* sp.		
CALZOTO	*Azotobacter* sp.		
CALTASH	K solubilizer		
CALPHOROUS	PSB		
BIOPHOS	PSB	Ajay Biotech	
Sardar Biofertilizers	*Azotobacter, Azospirillum* and PSB	Gujarat State Fertilizers and chemicals	
Biosubtillin®	*Bacillus subtilis*	Biotech International Ltd	
EcoGuard®	*Bacillus licheniformis*	Novozymes LLc	USA
Nitragin Gold	*Rhizobium meliloti*		
Tag Team	Combines the best in rhizobia strain with *Penicillium bilaii*		
Jump Start	*P. bilaiae*		
Jump Start®	*P. bilaiae* and LCO Promoter Technology		
Rizoliq LLI	*Rizobacter* sp.	Rizobacter S.A	Argentina
Signum	*Bradyrhizobium* sp.		
Rizo Liq Top	B. japonicum		
Pro-Mix®	*Bacillus subtilis*	Premier Horticulture Inc.,	Canada
Sublic®	Bacillus sp.	Several Crops	Italy
Phylazonit-M	*B.megaterium* and *Azotobacter chroococcum*	Phylazonit Kft	Hungary
Mamezo	*Rhizobium* sp.	TFAC, Tokachi Nokyoren	Japan

Researches reveal the efficacy of *Pseudomonas* and *Bacillus* species in inhibiting *M. phaseolina.* Microbial interactions in the soil involve various mechanisms; understanding these mechanisms is a prerequisite in the present scenario of changing environment. The use of any BCA or its bioformulation cannot be considered an effective control measure unless these mechanisms are not studied. Efficient bio formulations can be prepared from them that can prevent yield loss due to phytopathogens and also enhance plant growth.

Conclusion

Management of soil-borne plant pathogens is one of the major requisites for agricultural sustainability owing to the high yield losses. Biocontrol strategy is the best alternative to combat pathogens compared to the use of chemicals that are not ecofriendly, show toxicity, and make soil infertile. The rhizosphere is a factory of beneficial microbes having immense potential to promote plant growth as well as suppress disease. Biocontrol agents isolated from the rhizosphere have well-developed mechanisms to inhibit phytopathogens and reduce disease incidence. Antifungal metabolites produced by BCAs are efficient tools for managing plant diseases. Soil-borne plant pathogen *Macrophomoina phaseolina,* causing charcoal rot in soybean, is of utmost concern due to its severity and economic losses. BCAs belonging to *Pseudomonas* and *Bacillus* species have found to be effective in controlling charcoal rot. Both of these species are efficient biofungicide/ biopesticides for production at an industrial scale. The strategy for preparing competent bioformulation of *Pseudomonas* and *Bacillus* for inhibiting *M. phaseolina* is to be focused on thereby reducing disease severity in soybean. Also, bioformulation using a single organism is not effective in all cases; environmental changes in soil may affect the activity. A combination of microorganisms/antifungal metabolites can be used for integrated management of charcoal rot and other diseases.

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