Diversity of Bacilli from Disease Suppressive Soil and their Role in Plant Growth Promotion and Yield Enhancement

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Abstract: *Bacillus* is a Gram-positive aerobic endospore forming genera which has great diverse nature including antibiotic production, nitrogen fixation, degradation of cellulose, starch, pectin and protein and good plant growth promoting activities along with biological control of various fungal diseases involving various mechanisms such as antibiosis and lysis. Hence on the basis of functions of various microorganism soil may be classified as disease-inducing, disease-suppressive, zymogenic and synthetic soils. Bacilli isolated from disease-suppressive soil have many unique properties such as the production of various types of phytopathogenic compounds. Liquid, powder and granular formulations of spore-forming strains of bacilli have an advantage over the non-spore forming strains such as *Pseudomonas* (formulated as vegetative cells). Spores are more robust and resistant to the elevated temperature and high concentrations of chemicals. Moreover, the shelf-life of biological products based on bacterial spores can be up to 1-3 years. A disadvantage of the use of spores is that after application they need time to return to the metabolic active stage of a vegetative cell.
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1. Introduction

The genus *Bacillus* belongs to the family *Bacillaceae* which is distinguished by the production of highly refractile resting structures formed within the bacterial cells called endospores. This genus is Gram-positive, chemoheterotrophic rods that are usually motile and peritrichously flagellated. They are aerobic or sometimes facultative bacteria and catalase positive. Endospore formation, universally found in this group, is thought to be a strategy for survival in the soil, wherein these bacteria predominate and the endospores make them resistant to unfavorable environment condition. These features adopt the formulation and used to apply for enhanced production of valuable crops. Therefore, production of antibiotics and *Bacillus* spores suggests that these species may be attractive biological control agents and good Plant Growth Promoting Bacteria (PGPB) for growth enhancement and plant disease control (Landa et al. 1997). *Bacillus* has been one of the first successful biocontrol agents used against insects and pathogens. *Bacillus* spp. rapidly and aggressively colonize the root system, enhance the plant growth and yield by direct and indirect Plant Growth Promoting (PGP) activities and control a wide range of plant pathogens including *Erwinia corotovora, Fusarium* species, *Fusarium oxysporum*, *Macrophomina phaseolina*, *Phytophthora*, *Pythium* species, and *Rhizoctonia solani,* etc. The broad-spectrum antagonistic activities of *Bacillus* are executed by secretion of a number of metabolites including antibiotics, volatile compound HCN, siderophores, enzymes chitinase and β-1, 3-glucanase (Ongena and Jacques 2007; Singh et al. 2008; Chung et al. 2008; Chen et al. 2009; Arrebola et al. 2010).

These plant beneficial microorganisms are known to antagonize phytopathogens through competition for niches (e.g. iron through siderophores synthesis); parasitism, that may involve production of hydrolytic enzymes such as chitinase, β-1,3 glucanase, protease and cellulose, that lyse pathogen cell walls, inhibit the pathogens by secreting anti-microbial compounds and induce systemic resistance in host plants (Compant et al. 2005). Hence, suppressive soils can be considered as healthy soils. Baker and Cook (1974) described the suppressive soils as 'soils in which disease severity or incidence remains low, in spite of the presence of a pathogen and a susceptible host plant, and climatic conditions favorable for disease development'. At the dawn of biotechnology age, biological researchers turned to the study the natural disease suppressive soil where pathogens do not survive or fail to produce disease in host plant (Rovira and Wildermuth 1981). Suppressive soils have been the subject of considerable research both in past and present (Akhtar and Siddiqui 2009). There are several species of *Bacillus* known as plant growth and health supporting in nature because of beneficial characteristic features which act directly and indirectly (Tilak and Ready 2006; Singh et al. 2008). The principal mechanisms of plant growth promotion include: production of phytohormones such as indole

acetic acid (IAA), solubilization of phosphate, siderophore production, antibiosis, inhibition of plant ethylene synthesis, production of volatile compounds such as HCN and induction of plant systemic resistance to pathogens (Ongena and Jacques 2007; Idris et al., 2007; Richardson et al. 2009). One or more of these mechanisms may contribute to the increases obtained in plant growth and development that are higher than normal for plants grown under standard cultivation conditions.

2. Diversity of Bacilli

In 1872, Ferdinand Cohn, a contemporary of Robert Koch, recognized and named the bacterium as *B. subtilis,* capable of growth in the presence of oxygen and forms a unique type of resting cell called endospore. The trivial name assigned to them is aerobic spore-formers. The organism represented what was to become a large and diverse genus of bacteria named *Bacillus* in the Family *Bacillaceae.* It is very interesting to note that 95% of the Gram-positive soil bacilli belong to the genus *Bacillus*. The remaining 5 % are confirmed to be *Arthrobacter* and *Frankia* (Garbeva et al 2003). In view of the existing diversity within the genus *Bacillus* and related genera numerous valid descriptions of new genera and species as well as many classifications have emerged (Garrity 2001).The genus *Bacillus* remained intact until 2004, when it was split into several families and genera of endospore-forming bacteria. On the basis of extensive studies of the small-subunit ribosomal RNA sequence, the genus *Bacillus* comprises of 88 species and 2 subspecies (Fritze 2004).

There is a great diversity of physiology among the aerobic spore formers, not surprisingly considering their recently discovered phylogenetic diversity. Their collective features include degradation of all substrates derived from plant and animal sources including: cellulose, starch, pectin, proteins, agar, hydrocarbons and others, antibiotic production, nitrification, denitrification, nitrogen fixation, facultative lithotrophy, autotrophy, acidophily, alakliphily, psychrophily, thermophily and parasitism. Endospore formation, universally found in this group, is thought to be a strategy for survival even under adverse soil environment wherein these bacteria predominate. Aerial distribution of the dormant spores probably explains the occurrence of aerobic spore formers in most habitats. PGPR competitively colonizes plant root, stimulates plant growth and reduces plant disease (Kloepper and Scorth 1978). Some members of the *Bacillus* genus are *B. amyloliquefaciens, B. anthracis, B. cereus* and *B. subtilis. B. subtilis* established model organism for research on Gram-positive bacteria. Several *Bacillus* strains can protect plants from deleterious pathogens such as *B. subtilis*, *B. cereus* and *B. amyloliquefaciens*. *B. amyloliquefaciens* was first isolated in 1943 and named after its ability to produce amylase. It is known to produce several antibiotics and is often found in soil and associated with plants (Yu et al. 2002).

Analysis of the extracted DNA directly from soil samples, especially that use the sequencing of the 16S ribosomal RNA genes (16S rRNA), have confirmed the occurrence of easily cultivable bacteria as well as a wide variety of non-cultivable strains of species that belong to the genera *Bacillus* (Garbeva et al. 2003). Nevertheless, evidence of the relative number of cultivable and non-cultivable representatives of bacilli in different soils is surrounded by controversy. Report of some workers suggested that most 16S rRNA sequences of bacilli isolated directly from soil samples are very similar to the sequences of cultivable and named species (Garbeva et al. 2003), while other reported that the predominant sequences found in different soils are not the same as those presented by bacilli isolated and easily cultivable (Felske et al. 1999). Soil is the main reservoir of the genus *Bacillus* (Watanabe and Hayano 1993). Members of this genus are used for the synthesis of a very wide range of important medical, agricultural, pharmaceutical and other industrial products. These include a variety of antibiotics, enzymes, amino acids and sugars (Joung and Cote 2002). Sequencing of the 16S rDNA hypervariant region is a rapid and reliable way for *Bacillus* classification and basically informative at species level (Goto et al. 2000). Nevertheless, full sequencing of the16S rDNA gene is sometimes useful for more detailed classification within some *Bacillus* groups. On the other hand, closely related taxa are often extremely similar in their 16S rDNA sequences (La-Duc et al. 2004). For instance, some members of the *B. cereus* group (*B. anthracis, B. cereus* and *B. thuringiensis*) have high levels of 16S rDNA sequence similarity (>99 %) (Sacchi et al. 2002).

The 16S rRNA gene has been usually used as a trustworthy molecular marker for phylogentic identification of organisms. It contains conserved region, a unique array of sequences that are relative among species or different species (Moyer et al. 1994). It is the basis of molecular tools such as ribotyping, *in-situ* hybridization, DNA sequence analysis and restriction fragment length polymorphism (RFLP), which are now proposed to provide accurate genetic diversity information of microbes. Based on the use of the 16S rRNA, the DNA sequence analysis is used in phylogenic studies (Lagace et al. 2004). RFLP is used to identify the difference of DNA fragment length (polymorphism) by digesting with restriction enzymes. RFLP analysis on 16S rRNA gene or amplified rDNA restriction analysis (ARDRA) is a useful technique for genotype identification, to infer genetic variability and similarity of microorganisms (Yang et al. 2007).

Ash et al. (1991) separated 51 *Bacillus* species into five phylogenetically distinct clusters. Further characterizations at the genotypic and phenotypic levels of selected *Bacillus* species have led to the creation of several new genera: *Amphibacillus* (Niimura et al. 1990), *Alicyclobacillus* (Wisotzkey et al. 1992), *Paenibacillus* (Ash et al. 1993), *Aneurinibacillus* and *Brevibacillus* (Shida et al. 1996a), *Virgibacillus* (Heyndrickx et al. 1998), *Gracilibacillus* and *Salibacillus* (Wainø et al. 1999), *Filobacillus* (Schlesner et al. 2001), *Geobacillus* (Nazina et al. 2001), *Ureibacillus* (Fortina et al. 2001), and *Jeotgalibacillus* and *Marinibacillus* (Yoon et al. 2001). Recently, partial 16S rDNA sequence (Goto et al. 2000) and rRNA gene restriction patterns (Joung & Cote 2002) have been used for the rapid identification or classification of *Bacillus* species and related genera, respectively.

In the second edition of Bergey's Manual of systematic Bacteriology (Bergey and Boone, 2009), phylogenetic classification schemes landed the two most prominent types of endospore-forming bacteria, clostridia and bacilli, in two different Classes of Firmicutes. Clostridia include the Order *Clostridiales* and Family *Clostridiaceae* with 11 genera including, *Clostridium.* Bacilli belong to the Order *Bacillales* and the Family *Bacillaceae.* In this family there are 37 new genera with *Bacillus.* Table 1 represent the important taxonomic relocation in the Genus *Bacillus* from Ist edition to 2nd edition.

Table 1. Important Taxonomic Relocations in The Genus *Bacillus* from 1986 to 2009

Ist Edition (1986)	2nd Edition (2009)	References
Bacillus acidocaldarius	*Alicyclobacillus acidocaldarius*	Wisotzjsey et al. (1992)
Bacillus agri	*Brevibacillus agri*	Shida et al. (1996)
Bacillus alginolyticus	*Paenibacillus alginolyticus*	Shida et al. (1997a)
Bacillus amylolyticus	*Paenibacillus amylolyticus*	Shida et al. (1997b)
Bacillus alvei	*Paenibacillus alvei*	Ash et al. (1993)
Bacillus azotofixans	*Paenibacillus azotofixans*	Logan et al. (1998)
Bacillus brevis	*Brevibacillus brevis*	Shida et al. (1996)
Bacillus globisporus	*Sporosarcina globisporus*	Yoon et al. (2001)
Bacillus larvae	*Paenibacillus larvae*	Heyndrickx et al. (1996)
Bacillus laterosporus	*Brevibacillus laterosporus*	Shida et al. (1996)
Bacillus lentimorbus	*Paenibacillus lentimorbus*	Pettersson et al. (1999)
Bacillus macerans	*Paenibacillus macerans*	Ash et al. (1993)
Bacillus pasteurii	*Sporosarcina pasteurii*	Yoon et al. (2001)
Bacillus polymyxa	*Paenibacillus polymyxa*	Ash et al. (1993)
Bacillus popilliae	*Paenibacillus popilliae*	Pettersson et al. (1999)
Bacillus psychrophilus	*Sporosarcina psychrophila*	Yoon et al. (2001)
Bacillus stearothermophilus	*Geobacillus stearothermophilus*	Nazina et al. (2001)
Bacillus thermodenitrificans	*Geobacillus thermodenitrificans*	Nazina et al. (2001)

B. polymyxa now known as *Paenibacillus polymyxa* and studied under new genera (*Paenibacillus*) on the basis of 16S rRNA (2nd edition of Bergey's manual). Members of the genus *Paenibacillus* are facultatively anaerobic organisms that produce spores in definitely swollen sporangia and have G+C contents ranging from 45 to 54 mol%. Some of these organisms excrete diverse assortments of extracellular polysaccharide-hydrolyzing enzymes to hydrolyze complex carbohydrates including alginate, chondroitin, chitin, curdlan, and other polysaccharides (Shida et al. 1997). A number of species under these genera are known to produce polysaccharides (Yoon et al. 2002), antifungal, and antimicrobial agents, such as polymyxin, octopityn, and baciphelacin (Chung et al. 2000). This review reveals the PGPR activities of *Bacillus* spp. only, and hence there is limitation about *Paenibacillus.*

3. Disease-Suppressive Soil

Healthy soils are essential for the integrity of terrestrial ecosystems to remain intact or to recover from disturbances such as drought, climate change, pest infestation, pollution, and human exploitation including agriculture (Ellert et al. 1997). Based on function of microorganisms soil can be classified in four types such as: *(i)* disease-inducing soils, *(ii)* disease-suppressive soils, *(iii)* zymogenic soils and *(iv)* synthetic soils (Higa and Parr 1994). In some soils, microorganisms are able to suppress the growth of certain phytopathogens/ parasites without the use of chemical pesticides, and these soils are referred to as disease suppressive soils (Timmusk 2003). Thus, suppressive soils are regarded as the store-house of benficial microorganisms.

Such exceptional places are known as natural suppressive soils (Hornby 1983; Weller et al. 2002). Soil quality has been defined as the capacity of a soil to

function within ecosystem boundaries to sustain biological productivity, maintain environmental quality, and promote plant and animal health (Doran and Parkin 1994), while a soil is considered suppressive when in spite of favorable conditions for disease a pathogen either cannot become established even if it establishes but produces no disease or establishes and produces disease for a short time and then declines. Suppressiveness is linked to the types and numbers of soil organisms, fertility level, and nature of the soil itself (drainage and texture). The mechanisms by which disease organisms are suppressed in these soils include: induced resistance, direct parasitism (one organism consuming another), nutrient competition, and direct inhibition by beneficial organisms (Sullivan 2004).

Soil suppressiveness to diseases caused by the most important soil-borne pathogens includes fungal and bacterial pathogens and also nematodes (Baker and Cook 1974). The response of plants growing in the soil contributes to suppressiveness. This is known as induced resistance and occurs when the rhizosphere is inoculated with a weakly virulent pathogen. After being challenged the weak pathogen, the plant develops a capacity for future effective response to a more virulent pathogen. In most of the cases, adding mature compost to a soil induces disease resistance (Sullivan 2004). The level of disease suppressiveness is typically related to the level of total microbiological activity in a soil. The larger the active microbial biomass, the greater the soil capacity to use carbon, nutrients, and energy, thus lowering their availability to pathogens. In other words, competition for mineral nutrients is high, as most soil nutrients are tied up in microbial bodies. Nutrient release is a consequence of grazing by protozoa and other microbial predators; once bacteria are digested by the predators, nutrients are released in their waste.

Timmusk (2003) depicted disease suppression due to high biodiversity of bacterial populations that crate conditions unfavorable for plant disease development. Moreover, PGPR offer a solution to the biocontrol of deleterious phytopathogens. The PGPR of the *Bacillus* group is a biological solution to the disease suppression of phytopathogenic fungi due to their ability to form heat- and desiccation-resistant spores (Emmert and Handelsman 1999). Number of traits such as production of siderophore (Wilson et al. 2006), and HCN (Fiddaman and Rossall 1993) have been reported to control the fungal pathogens and enhanced the growth and yield of plants through production of IAA (Idris et al. 2007) and solubilization of phosphate (Kumar and Chandra 2008).

In our laboratory, quantitative microbial parameters and physicochemical properties of soil sample were evaluated for detection of disease suppressive soils of different major Indian crop fields. Quantitative microbial parameters of soil sample from Haridwar and Varanasi showed higher bacterial population than fungal population which confirmed disease suppressive nature of both the samples. Higher bacterial population might be due to the production of antifungal compound that out number the fungal population (Table 2).

Table 2. Microbial Population of Disease Suppressive Soil in Different Soil Samples of Indian Towns [Values are Means of ± SD of three Replications].

	Sampling Sites (Name of Town)	Bacterial population		Fungal population	
		10^4	10^5	10^4	10^5
1.	Aligarh	6.12±0.17	5.47±0.16	5.21±0.17	5.10±0.16
2.	Bhopal	5.42±0.12	5.11±0.20	5.24±0.20	5.07±0.15
3.	Chandigarh	5.28±0.12	5.05±0.20	5.18±0.12	5.0±0.20
4.	Dehradun	6.0 ±0.17	5.68±0.16	5.14±0.17	4.75±0.16
5.	Haridwar	6.04±0.10	5.77±0.12	5.08±0.11	4.68±0.14
6.	Jhansi	5.88±0.12	5.44±0.20	5.85±0.20	5.35±0.15
7.	Kanpur	5.48±0.12	5.14±0.20	5.37±0.12	5.11±0.20
8.	Varanasi	6.24 ±0.1	6.18± 1.4	4.46±0.13	4.22±0.14

(Adopted from PhD Thesis, Khare, 2009)

3.1 Characteristic of Suppressive Soil

The ability of suppressive soils to the growth or activity of soil-borne phytopathogens has been categorized as general suppression, general or nonspecific antagonism or biological buffering (Weller et al. 2002). General suppression is defined as the total microbial biomass in soil which competes with the pathogen for resources or causes inhibition due to antagonistic activity which is enhanced by good fertility of soil by the addition of organic matter and other agronomic matter (Rovira and Wildermuth 1981). All of which can increase soil microbial activity and the suppressiveness is not transferable between soils (Rovira and Wildermuth 1981). When inoculum of a pathogen is added to raw and sterilized soil samples, greater severity of disease on a host was found in the sterilized soil over raw soil. Specific suppression is superimposed over the background of general suppression and is partly due to the effects of individual or selected groups of microorganisms during some stage in the life cycle of a pathogen. Transferability is the key characteristic of specific suppression and the term transferable suppression has been used synonymously with specific suppression (Weller et al. 2002). Suppressive soils undoubtedly owe their activity to a combination of general and specific suppression. Both function as a continuum in the soil, although they may be affected differently by edaphic, climatic, and agronomic conditions (Rovira and Wildermuth 1981). Suppressive soils also have been differentiated according to their longevity.

Hornby (1983) again divided suppressive soils into long-standing suppression and induced suppression. Former, suppression is a biological condition naturally associated with the soil, its origin is not known and appears to survive in the absence of plants. While, induced suppressiveness is initiated and sustained by crop monoculture or by the addition of inoculum of the target pathogen. Most suppressive soils maintain their activity when brought into greenhouse or laboratory, which facilitates assessment of their properties and mechanisms of suppression under more controlled and reproducible conditions.

The first step is to determine whether suppressiveness can be destroyed by pasteurization (moist heat, 60°C for 30 min) (Shipton et al. 1973), by using selective biocides (e.g. novobiocin or chloropicrin), or by harsher treatments (e.g. steam, methyl bromide, autoclaving, or gamma radiation) (Wiseman et al. 1996; Weller et al. 2002). Both general and specific suppression are eliminated by autoclaving and gamma radiation. General suppression is reduced but not eliminated by soil fumigation, and usually survives at 70°C moist heat (Cook and Rovira 1976).

A second step which allows confirmation of the biological basis of suppression involves transfer of suppressiveness to a raw conducive, fumigated or sterilized soil by addition of 0.1-10% (w/w) or less of the suppressive soil. The impact of soil edaphic factors on disease development in soil transfer studies is minimized when suppressive and conducive soils are diluted into a common background soil allowing a direct comparison of the introduced microbiological components. Composts have been used for centuries to maintain soil fertility and plant health. Hoitink (2004) reported the control of phytopathogens with composts which indicates its disease suppressive nature. Bent et al. (2008) reported 5 to 16-fold reduction in population of root-knot nematode as compared to identical but pasteurized soil two months after infestation.

In suppressive soils the roots of crop plants are protected from diseases that would ordinarily be caused by soil-borne pathogenic microorganisms. Most of these pathogens are fungi, but some bacterial pathogens and plant-deleterious nematodes are also suppressed in certain soils. But the question is that how disease suppressive soil works and whether it is directed at specific pathogens or at pathogen in general.

3.2 Role of Disease Suppressive Soil to Protect Plants Health

The complexity of the disease-suppression phenomenon can be highlighted by four key interpretations. First, certain suppressive soils when pasteurized (by wet heat at 60ºC for 30 min) lose their suppressiveness, and other harsher antimicrobial treatments (gamma radiation or autoclaving) have the same effect (Stutz et al. 1986). Second, suppressiveness can be transferable: an inoculum of 0.1–10% of a suppressive soil introduced into a conducive soil can establish disease suppression (Weller et al. 2002). Sensitivity to antimicrobial treatments and transferability indicate that disease suppression results from the activities of soil microorganisms that act as antagonist against pathogen. The suppressiveness of some soils is not transferable (Hornby 1983; Weller et al. 2002). Third, when the pH of a *Fusarium* wilt-suppressive soil was lowered from 8 to 6 by the addition of H_2SO_4, carnations were much less protected from wilting (Scher and Baker 1980). This loss of suppressiveness caused by a simple pH change illustrates the importance of the soil environment. Clay types and the mineral-ion content of soils, humidity, temperature and fertilizer input can all affect the success of disease suppression (Lucy et al. 2004). Fourth, several years of monoculture can induce disease suppression in some soils. The best-studied example is take-all decline which has been observed in soils in the northwestern United States, the Netherlands

and Australia (Weller et al. 2002). After 2 or more years of consecutive cultivation of wheat, the symptoms of take-all disease is caused by the fungus *Gaeumannomyces graminis* var. *tritici*, usually increase, but it declined in subsequent years of wheat monoculture (Hornby 1983; Weller et al. 2002). The phenomenon of induced disease suppression shows that a host plant grown in monoculture can have a profound influence on the interaction with a pathogen. Soil-borne pathogens are notoriously difficult to control. Crop rotation, breeding for resistant plant varieties and the application of pesticides are insufficient to control root diseases of important crop plants. Since the earliest observations of antagonistic disease suppressing soil microorganisms more than 70 years ago, plant pathologists have been fascinated by the idea that such microorganisms could be used as environmental friendly biocontrol agents, both in the field and in greenhouses.

4. Plant Growth Promoting Activities of Bacilli

The mechanisms of plant growth-promotion by non-pathogenic plant-associated bacteria have not been completely elucidated but the important mechanisms are categorized into the direct and indirect plant growth-promoting mechanisms (Glick et al. 1995). PGPB stimulate plant growth either directly or indirectly or both. The essential direct plant growth-promoting (PGP) mechanisms include nitrogen fixation, solubilization of minerals such as phosphorus, production of siderophore that solubilize and sequester iron, production of plant growth regulators (hormones) that enhance plant growth at various stages of development, whereas indirect plant growth-promotion occurs when PGPR promote plant growth by improving growth-restricting conditions (Glick et al. 1999; Herridge 2008). The production of antifungal volatiles by *B. subtilis* suggests that more than one modes of action of antifungal activity is available to this bacterium and suggested that volatiles from *B. subtilis* may also contribute to the antagonistic nature of the species (Fiddaman and Rossall 1993).

In the concept of PGPR two simple terms have been adopted: intracellular PGPR (iPGPR), *i.e.* bacteria that live inside plant cells and being localized in the nodules, and extracellular PGPR (ePGPR), *i.e.* bacteria that live outside plant cells and being able to enhance plant growth through the production of signal compounds that directly stimulate plant growth to the improvement of plant disease resistance or to the mobilization of soil nutrients to the plant. The ePGPR can be subdivided into three types based on the degree of association with plant roots: bacteria living near but not in contact with the roots, bacteria colonizing the root surface, and those living in the spaces between cells of the root cortex (Gray and Smith 2005). Researches on ePGPRs were initially focused on *Bacillus* and *Anthrobacter* spp. (Brown 1974). Among the most widely studied ePGPRs bacilli are *B. cereus* (Handelsman et al. 1990; Ryder et al. 1999), and *B. thuringiensis* (Bai et al. 2002 a, b). Several workers have reported the effect of different *Bacillus* spp. on enhancement of growth of different crops (Table 3).

Table 3. Effect of Different *Bacillus* spp. on Enhancement of Growth Parameters of Different Crops

***Bacillus* spp.**	**Benefited Plants**	**Effect on growth parameters**	**References**
Bacillus strains	Conifer	Increased seedling emergency and biomass	Chanway et al. (1991)
*B. licheniformis**	Chickpea	Control *M. phaseolina*	Siddiqui and Mahmood (1992)
B. subtilis	Chickpea	Control *M. phaseolina*	Siddiqui and Mahmood (1993)
B. subtilis	Chickpea	Control *M. phaseolina*	Siddiqui and Mahmood (1995b)
B. subtilis	Pigeon pea	Control *Heterodera cajani* and *F. udum*	Siddiqui and Mahmood (1995c)
*B. pumilus**	Cucumber	Control *Colletotrichum orbiculare*	Wei et al. (1996)
Bacillus sp. L324-92	Wheat	Contorl *Gaeumannomyces graminis* var tritici, *Rhizoctonia* root rot, *R. solani* AG8, *Pythium* root rot, *Pythium irregular,P. ultimum.*	Kim et al. (1997)
B. subtilis	Pigeon pea	Control *F. udum*	Podile and Laxmi (1998)
B. pumilus *B. subtilis**	Cucumber	Control *Colletotrichum orbiculare*	Raupach and Kloepper (1998)
B. subtilis and *B. cereus*	Wheat	Control Take all (*G. graminis* var tritici), *Rhizoctonia* root rot (*R. solani* AG8)	Ryder et al. (1999)
B. subtilis, *B. cereus,* *P. putida**	Cucumber	Control *Pythium* sp.	Uthede et al. (1999)
B. polymyxa and *P. fluorescens* PRS9,	Tomato	Control *F. oxysporum* f. sp. Lycopersici	Khan and Akram (2000)
B. megaterium B 153-2-2	Soybean	Control *R. solani*	Zheng and Sinclair (2000)
B. pumilus SE34*	Loblolly pine	Control *Cronartium quercuum* f. sp. fusiforme	Enebak and Carey (2000)
B. subtilis, *P. putida*	Lettuce and Cucumber	Control *Pythium aphanidermatum*	Amer and Utkhede (2000)
B. brevis	Pigeon pea	Control Fusarial wilt	Bapat and Shah (2000)
B. subtilis AF1	Ground nut and	Control *F. udum* and	Manjula and Podile (2001)

	Pigeon pea	*A. niger*	
Bacillus spp*	Wheat	Control *G. graminis, R. solani, R. oryzae, P. ultimum,*	Cook et al. (2002)
Bacilus sp. BC121	Not specified	Control *Curvularia lunata*	Basha and Ulaganathan (2002)
B. pumilus SE34*	Tomato	Control *Phytophthora infestans*	Yan et al. (2002)
B. pumilus	Pearl millet	Control *S. graminicola*	Niranjan Raj et al.(2003)
*B. subtilis**	Tomato	Control *R. solani*	Szczech and Shoda (2004)
B. subtilis GB03 *B. amyloliquefaciens* IN937a *B. pumilus* SE-34 *B. pumilus* T4, *B. pasteurii* C9 *Paenibacillus polymyxa* E681 *	*Arabidopsis*	Increased foliar fresh weight	Ryu et al. (2005)
B. pumilus *	Indian mustard and Rape	Increased root elongation in cadmium supplemented soil	Belimov et al. (2005)
B. and fluorescent pseudomonads	Not specified	Control *F. udum*	Siddiqui et al. (2005)
B. subtilis CE1	Maize	*F. verticilloides*	Cavaglieri et al. (2005)
B. cereus and *B.circulans*	Maize	Increased grain yield	Tilak & Reddy (2006)
Bacillus spp CIMAP-B1	Pyrethrum	Control Root rot and wilt *R.solani* (PyRh1)	Abdul et al. (2007)
Bacillus spp CIMAP-B1	Geranium	Control Wilt *R. solani* (GRh1)	Abdul et al. (2007)
Bacillus spp CIMAP-B1	Geranium	Control Anthracnose *Colletotrichum acutatum*	Abdul et al. (2007)
Bacillus spp CIMAP-B1	Indian basil	Control Leaf blight *Colletotrichum capsici*	Abdul et al. (2007)
Bacillus spp CIMAPF-B1	Aloe	Control Leaf spot *Colletotrichum gloeosporiodes*	Abdul et al. (2007)
Bacillus spp CIMAP-B1	Opium poppy	Control Collar rot *R. solani* (OPRh1)	Abdul et al. (2007)
Bacillus spp CIMAP-B1	Java citronella	Control Yellowing *Pythium aphanidermatum*	Abdul et al. (2007)
Bacillus spp CIMAP-B1	Java citronella	Control Leaf blight *Curvularia andropogonis*	Abdul et al. (2007)
Bacillus spp CIMAP-B1	Menthol mint	Control Leaf spot *Alternaria alternata*	Abdul et al. (2007)
Bacillus spp CIMAP-B1	Menthol mint	Control Leaf blight *Corynespora cassiicola*	Abdul et al. (2007)
Bacillus spp CIMAP-B1	Menthol mint	Control Wilt *F. oxysporum*	Abdul et al. (2007)
Bacillus spp CIMAP-B1	Menthol mint	Control Wilt *Fusarium semitectum*	Abdul et al. (2007)
Bacillus spp CIMAP-B1	Menthol mint	Control Leaf blight *Helminthosporium carbonum*	Abdul et al. (2007)
Bacillus spp CIMAP-B1	Menthol mint	Control Stolon & root rot *Thielavia basicola*	Abdul et al. (2007)
Bacillus sp.*	Wheat	Control *A. triticina*	Siddiqui (2007)
Bacillus sp. *	Tea	Control *Exobasidium vexans*	Saravanakumar et al. (2007)
B. subtilis BN1	Pinus	Control root rot *M. phaseolina* and growth enhancement	Singh et al. (2008)
B. cereus *	Wheat	Improved plant growth and nutrition under salt stress	Egamberdieva et al. (2008)
Bacillus OSU-142, *Bacillus* M-3 *	Strawberry	Increased total soluble solids, total sugar and reduced Sugar	Pirlak and Kose (2009)
B. cepacia strain OSU-7	Stored potatoes	Control Fusarium dry rot	Recep et al. (2009)
B. subtilis strain BA 142, *B. megaterium strain* M 3 *	Radish	Improved the percentage of seed germination under saline conditions	Kaymak et al. (2009)
B. subtilis EU07	Tomato	Control *F. oxysporum* f. sp. radicislycopersici	Baysal et al. (2009)
B. subtilis, *B. lecheniformis*, *B. cereus**	Sorghum	Control *F. oxysporum*	Jedabi (2009)

* Other group of PGPR also included.

4.1 IAA Production

Auxins (Greek *auxein,* to increase) are plant hormones originated from the amino acid tryptophan. The natural auxin is called indol acetic-acid (IAA). Tryptophan is the precursor of IAA. Although there are four different pathways for IAA biosynthesis, all of them are originated from tryptophan (Raven et al. 1996). Production of IAA (auxin) is widespread among plant associated bacteria. The first studies were conducted in the 1970's. Beneficial bacteria synthesize IAA predominantly by an alternate tryptophan dependant pathway, while IAA production in plant growth promotion remains undetermined. Promotion of root growth is one of the major markers by which the beneficial effect of PGPB is measured (Glick et al. 1995).

Idris et al. (2007) reported that the Gram-positive *B. amyloliquefaciens* and *B. subtilis* secreted significant amounts of IAA. Increased IAA production after addition of tryptophan and drastic reduction of IAA production in engineered *trp* mutants suggested that the main route of IAA biosynthesis in this bacterium is dependent on tryptophan.

Several routes of tryptophan-dependent IAA biosynthesis in microorganisms have been reported. IAA biosynthesis generally occurs either by

involvement of the indole acetamide (IA) pathway which is constitutive in nature or by inducible indole pyruvic acid (IPA) pathway (Patten and Glick 1996). Srinivasan et al. (1996) reported 45% *Bacillus* isolates are IAA producers such as *B. megaterium*, *B. brevis*, *B. pumilus*, *B. polymyxa* and *B. mycoides*. Enhancement of plant growth by root-colonizing *Bacillus* and *Paenibacillus* strains is well documented (Kloepper et al. 2004). PGP *B. pumilus* SE34 secreted the high levels of indole-3-acetic acid (IAA) in tryptophan-amended medium in stationary phase as determined by chromogenic analysis and high-performance liquid chromatography (Kang et al. 2006).

It has been suggested that 80% of bacteria isolated from the rhizosphere can produce IAA (Antoun et al. 1998). Spaepen et al. (2007) reviewed different pathways involved in the biosynthesis of IAA based on the chemical nature of intermediate molecules produced using tryptophan as precursor. The plant beneficial Gram-negative bacteria synthesize IAA following different pathways that involves indole-3-pyruvic acid (IPA), indole-3-acetamide (IAM), or indole-3-acetonitrile (IAN) as important intermediates (Patten and Glick 1996). However, in Gram-positive bacteria the main route for biosynthesis of IAA involves IPA (Vandeputte et al. 2005) IAA production by PGPR can vary among different species and strains and influenced by culture growth stage and substrate availability (Idris et al. 2007).

Idris et al. (2004) demonstrated that growth elongation of maize seedlings was significantly enhanced in the presence of diluted culture filtrate of *B. amyloliquefaciens* FZB42. Moreover, strong curvature obtained after application of bacterial culture filtrates on maize coleoptiles indicated the presence of an auxin (IAA)-like compound in the supernatant of FZB42. The presence of IAA-like compounds in the culture filtrates of several members of this group, including FZB42 was detected by enzyme-linked immunosorbent assay (ELISA) tests with IAA-specific antibodies, when those strains were grown at low temperature and low aeration. Singh et al. (2008) reported that *B. subtilis* BN1stimulated chir-pine seedling growth possibly due to PGP attributes. Significant growth enhancement of lodgepole pine seedlings has been reported due to IAA production by *Bacillus* isolates (Chanway et al. 1991).

Bacillus group offers a biological solution to the formulation problem due to their ability to form heat and desiccation resistant spores (Emmert and Handelsman 1999). It is also likely that PGP effects exerted by some plant-beneficial bacteria are due to the production of plant hormones such as indole-3-acetic acid (IAA), cytokinins, and gibberellins.

Besides IAA, GC-MS analysis verified gibberellin production in *B. pumilus* and *B. licheniformis* (Gutierrez-Mareño et al. 2001), while Ortíz-Castro et al. (2008) reported plant growth promotion by *B. megaterium* due to cytokinin signaling.

4.2 Phosphate Solubilization

Phosphorus plays a key role in many essential processes including cell division, photosynthesis, break down of sugar, energy and nutrient transfer in crop plant. Phosphorus is second only to nitrogen in mineral nutrients most commonly limiting the growth of crops. It is an essential element for plant development and growth making up about 0.2 % of plant dry weight. Plants acquire P from soil solution as phosphate anions. However, phosphate anions are extremely reactive and may be immobilized through precipitation with cations such as Ca^{2+}, Mg^{2+}, Fe^{3+} and Al^{3+}, depending on the particular properties of a soil. In these forms, P is highly insoluble and unavailable to plants. As a results of which amount available P to plants is usually a small proportion. The phosphorus content in soil is about 0.05% (w/w) on an average; in fact phosphorus is one of the least soluble elements in the natural environment with less than 5% of the total soil phosphate content being available to the plants (Dobbelaere et al. 2003). Availability of phosphorus depends largely on microbial activity (IFA 1992). Maintenance of available phosphorus remains a major challenge. Organic compounds containing phosphorus are decomposed and mineralized by bacteria. The biogeochemical cycle of phosphorus is influenced by various microorganisms which affect phosphorus metabolization in soil. The precipitated inorganic phosphate is solubilized by the action of minerals and organic acids produced by soil bacteria (Deshwal et al. 2003). Several reports have examined the ability of different bacterial species to solubilize insoluble inorganic phosphate compounds such as tricalcium phosphate, dicalcium phosphate, hydroxyapatite, zink phosphate and rock phosphate. There are so many bacterial genera including *Bacillus* that are able to solubilize these phosphorus sources in soil. There are considerable populations of phosphate-solubilizing bacteria in soil and in plant rhizospheres. These include both aerobic and anaerobic strains, with a prevalence of aerobic strains in submerged soils. A considerably higher concentration of phosphate solubilizing bacteria is commonly found in the rhizosphere in comparison with non-rhizosphere soil (Rodríguez and Fraga 1999).

Many bacteria isolated from the rhizosphere (rhizobacteria) are capable of increasing the availability of phosphorus to plants either by mineralization of organic phosphate (solubilization by action of phosphatase) or by solubilization of insoluble inorganic phosphates by production of acids. Such bacteria, often termed as phosphobacteria, have attracted considerable attention for their potential use as inoculants. Microorganisms frequently stimulate plant growth by

increasing phosphorus uptake (Nautiyal 1999; Deshwal et al. 2003). The sink of fixed phosphorus can be harnessed biologically using the mineral phosphate solubilizing microorganism that convert the fixed phosphorus into HPO_4^{2-} and H_2PO_4 (Gaur et al. 1980). A number of factors are responsible for the enhancement of phosphate solubilizing process. Phosphate solubilization is highly dependent on pH. Phosphate dissolving bacteria are known to reduce the pH by secretion of a number of organic acids such as formic acid, acetic acid, succinic acid, etc. Some of these acids may form chelators with the cations such as Ca and Fe, and such chelation results in effective solubilization of phosphates (Taalab and Badr 2007).

The principal mechanism for phosphate solubilization is the production of organic acids, and phosphatases. Soil microorganisms are able to solubilize insoluble mineral phosphate by producing various organic acids. This results in acidification of the surrounding soil releasing soluble orthophosphate ions that can be readily taken up by plants. Furthermore, they are able to solubilize organic P compounds through the action of phosphatase, phytases, phosphonatases and C-P lyases enzymes (Lugtenberg and Kamilova 2009). Gluconic acid seems to be the most frequent agent of mineral phosphate solubilization. 2-ketogluconic acid is another organic acid identified in strains with phosphate solubilizing ability. Strains of *Bacillus* were found to produce mixtures of lactic, isovaleric, isobutyric and acetic acids. Other organic acids such as glycolic, oxalic, malonic, and succinic acid have also been identified among phosphate solubilizers. Strains from the genera *Pseudomonas, Bacillus* and *Rhizobium* are among the most powerful phosphate solubilizers (Rodriguez and Fraga 1999).

Chelating substances and inorganic acids such as sulphideric, nitric, and carbonic acid are considered as the other mechanisms for phosphate solubilization. However, the effectiveness and their contribution to P release in soils seems to be less than organic acid production. Production of halo zones on solid agar and efficient release of phosphate in solution have been attributed due to release of different type of organic acids viz. citric, glyoxalic, malic, succinic, and fumaric acid (Khan et al. 2007). Patel and Dave (2000) reported an increase in effectiveness of organic acid production in increased phosphate solubilization. Trivedi et al. (2007) reported that *B. subtilis* exhibited strong phosphate solubilizing activity *in vitro* resulting in an increase in grain yield of rice in pot and field trials. They suggested that *B. subtilis* cultures can be developed as an efficient bioinoculant for rice fields due to its nature for phosphate solubilization.

Rdresh et al. (2004) demonstrated the variability in phosphate solubilization value due to the production of different organic acids in varying amounts resulting in the acidification of the microbial cell and its surroundings. Production of organic acids by phosphate solubilizing bacteria has been well documented (Sheng et al. 2002; Deshwal et al. 2003; Bhatia et al. 2005). Nautiyal (1999) and Trivedi et al. (2007) suggested *Bacillus* as the most powerful phosphate-solubilizer available in majority of the soils. A number of workers have reported phosphate solubilization by *Bacillus* as dominant inorganic phosphorus compound solubilizing microbes (Gupta et al. 2002; Jana 2007). Hariprasad and Niranjana (2009) reported that solubilization of P in the rhizosphere is the most common mode of action implicated in PGPR that increase nutrient availability to host plants.

4.3 Siderophore Production

Iron is an essential nutrient for all living organisms. In the soil it is unavailable for direct assimilation by microorganisms because ferric iron (Fe III) which predominate in nature is only sparingly soluble and too low in concentration to support microbial growth. Some bacteria have developed iron uptake systems (Neilands and Nakamura 1997). These systems involved siderophore- an iron-binding legend and an uptake protein needed to transport iron into the cell. Siderophores (*sid* = iron, *phores* = bearer) are low molecular weight (400-10,000 D) virtually ferric-specific ligands produced by microorganisms as scavenging agents in order to combat low iron stress.

Siderophores are common products of aerobic and facultative anaerobic bacteria and of fungi. Greater attention has been paid to bacterial siderophores especially those produced by rhizobacteria and some human pathogens than fungal siderophores due to high chelating affinity for Fe^{3+} and a low affinity for Fe^{2+} ions produced under iron limiting conditions. The chelated form of iron (III) is transported into bacterial cells (Neiland 1995). Kloepper et al. (1980) were the first to demonstrate the importance of siderophores in plants. Inside the cell, the siderophore becomes free from the transporter protein and again released outside as free ligand (desferriform) to repeat the cycle. Iron is a component of cell and its deficiency can cause growth inhibition, decrease in RNA and DNA synthesis and inhibits sporulation, it can also change cell morphology. Siderophores solubilise iron which is then transported into the bacterial cells using specific receptors. This gives possibility to bacteria to deplete the available iron source from other potentially harmful bacterial strains (Wilson et al. 2006).

Pathogens are thought to be sensitive to suppression by siderophores for several reasons: *(i)* they produce no siderophores of their own, *(ii)* they are unable to use siderophores produced by the antagonists or by other microorganisms in their immediate

environment, *(iii)* they produce too few siderophores or biocontrol PGPR produce siderophores that have a higher affinity for iron than those produced by fungal pathogens, allowing the former microbes to scavenge most of the available iron, and thereby prevent proliferation of fungal pathogens, or *(iv)* they produce siderophores that can be used by the antagonist, but they are unable to use the antagonist's siderophores (Bashan and de-Bashan 2005).

The extent of disease suppression as a consequence of bacterial siderophore production is affected by several factors (Bashan and de-Bashan 2005) including the specific pathogen, the species of biocontrol PGPR, the soil type, the crop and the affinity of the siderophore for iron. Bashan and de-Bashan (2005) reported that depletion of iron from the rhizosphere normally does not affect plant growth as plants can thrive on less iron than can microorganisms. However, some plants can bind and release iron from bacterial iron-siderophore complexes and use the iron for growth. Thus, these plants benefit in two ways: from the suppression of pathogens and from enhanced iron nutrition resulting in increased plant growth.

Park et al. (2005) reported that the growth of *B. cereus* was stimulated in proportion to the iron-saturation level of the transferrin, and catechol-siderophores were produced in inverse proportion to this level. *B. megaterium* ATCC 19213 provides an excellent system to study the effects of such siderophore formation and transport on heavy metal toxicity. This bacterium produces two hydroxamate siderophores under iron-deficient conditions (Hu and Boyer 1996).

The amount and type of siderophore produced by bacteria depend on organic and inorganic nutrients (Berraho et al. 1997). Hu and Boyer (1996) achieved hydroxamate siderophore in *B. megaterium*. A direct mechanism of action of bacterial siderophores is that they may be available to the plant as a source of iron which directly helps in the growth of the plant. Siderophore production by *Bacillus* strains has been well documented (Park et al. 2005; Wilson et al. 2006). However, other type of siderophore like mono catecholate siderophore has been reported in *B. cereus* by Park et al. (2005). Temirovet et al. (2003) also reported catecholic siderophore in *B. licheniformis*.

4.4 HCN Production

Hydrocyanic acid production plays a major role in suppressing the growth of phytopathogen. HCN is a volatile compound which on interaction with fungi can easily degrade its cell wall (Fiddaman and Rossall 1993). Defago et al. (1990) presented the evidence that HCN is beneficial to biological control of diseases; hence indirectly it plays a role in plant growth promotion.

PGPR produce HCN which depend on soil and plant characteristics. A number of environmental factors influence the rate of HCN production by *B. subtilis* (Fiddaman and Rossall 1993). Its production depends highly on the amino acid composition of the substrate. Glycine was shown to be the direct precursor of microbial cyanide production and exerts the strongest effect of the amino acids (Bakker and Schipper 1987). Proline stimulates microbial cyanide production but to a lesser extent.

On the other hand, production of volatile compounds in liquid culture proved inhibitory to spore germination and mycelial growth and were reported by numerous workers (Defago and Hass 1990). Cyanide also seems to play a role in the suppression of take all disease of wheat, charcoal rot disease of sunflower and peanut disease caused by *M. phaseolina* (Gupta et al. 2001; Bhatia et al. 2005). Production of HCN by certain *Bacillus* is believed to be involved in suppression of root pathogens.

The production of antifungal volatiles by *B. subtilis* suggests that more than one modes of action of antifungal activity is available to this bacterium and this new study suggested that volatiles from *B. subtilis* may also contribute to the antagonistic nature of the species (Fiddaman and Rossall 1993).

In general, cyanide is formed during the early stationary growth phase (Knowles and Bunch 1986). Cyanide occurs in solution as free cyanide which includes the cyanide anion (CN-) and the non-dissociated HCN. It does not take part in growth, energy storage or primary metabolism, but is generally considered to be a secondary metabolite that has an ecological role and confers a selective advantage on the producer strains (Vining 1990). Nevertheless, at present its applications in areas of biocontrol methods are increasing (Voisard et al. 1989; Devi et al. 2007). Cyanogenesis in bacteria accounts in part for the biocontrol capacity of the strains that suppress fungal diseases of some economically important plants (Voisard et al. 1989). Hydrogen cyanide effectively blocks the cytochrome oxidase pathway and is highly toxic to all aerobic microorganisms at picomolar concentrations. However, producer microbes, mainly pseudomonads, are reported to be resistant (Bashan and de-Bashan 2005).

4.5 N_2 Fixation by *Bacillus* spp.

Nitrogen fixing bacteria have been used for centuries to improve the fertility of soils. In recent years, the interest in soil microorganisms has increased as they play an important role in the maintenance of soil fertility. The potential and pitfalls of exploiting nitrogen fixing bacteria in agricultural soils as substitute for inorganic fertilizer have been reviewed by Cummings et al. (2008). The ability to fix nitrogen is

widely distributed among phylogenetically diverse bacteria. Evolutionarily conserved amino acid sequences within the *nif*H gene have been exploited to design PCR primers to detect the genetic potential for nitrogen fixation in any environment (Auman et al. 2001; Rosch et al. 2002; Mehta et al. 2003). Table 4 represents the nitrogen fixing *Bacillus* spp. A major challenge for the development of sustainable agriculture lies in the use of nitrogen-fixing bacteria which are able to assimilate gaseous N_2 from the atmosphere (Seldin et al. 1998).

Table 4. *Bacillus* Species and Nitrogen Fixation.

Bacillus spp.	Nitrogenase activity	*nifH* gene	References
B. megaterium	+		Xie et al. (1998)
B. cereus	+		Xie et al. (1998)
B. pumilus	+		Xie et al. (1998)
B. circulans	+		Xie et al. (1998)
B.licheniformis	+		Xie et al. (1998)
B. subtilis	+		Xie et al. (1998)
B. brevis	+		Xie et al. (1998)
B. firmus	+		Xie et al. (1998)
B. sphaericus UPMB10	+		Amir (2001)
B. fusiformis (strain PM-5 and PM-24)	+		Park et al. (2005)
B. marisflavi	+		Ding et al. (2005)
B. megaterium		+	Ding et al. (2005)
B. cereus		+	Sorokin et al. (2008)
B. alkalidiazotrophicus (*Anaerobacillus alkalidiazotrophicus*)		+	Sorokin et al. (2008)
Bacillus sp.	+		Ahmad et al. (2008)
Bacillus sp. RFNB6	+		Islam et al. (2009)

+ = Present

Note: Now *Bacillus sphaericus* is named as *Lysinibacillus sphaericus* comb. nov. and *B. fusiformis* is *Lysinibacillus fusiformis* comb. nov (Ahmed et al. 2007).

4.6 Biocontrol Potential

Species of *Bacillus* and related forms are common inhabitants of soil, and they have been identified as potential biological control agents against various pathogenic microbes (McSpadden Gardener and Fravel 2002; Romeis et al. 2006; Choudhary and Johri 2009). Furthermore, their spore forming ability makes them an ideal candidate for developing efficient biopesticide products from technological point of view; spores possess a high level of resistance to dryness necessary for formulation into stable products.

Bacilli have great potential uses in agriculture. Its members are able to produce antimicrobial metabolites to control plant pathogens, to fix nitrogen and to form endospores to resist desiccation, heat, and UV irradiation, and to survive in adverse conditions. Root colonization by *Bacillus* shows various colonization patterns on plants like tomato roots, stems, and leaves at 6 weeks after inoculation. Root colonization studies of *Bacillus* strains were proved by re-isolating it via marking with rifampicin (Rif) resistance gene (Liu et al. 2006). *B. subtilis* as the model component of Gram-positive organisms is able to produce over two dozens of antibiotics with amazing variety of structures (Stein 2005). Hundreds of wild type strains of *B. subtilis* have been studied globally for the production of a variety of molecules with antibiotic properties. However, until today the genetic basis of biocontrol ability of *B. subtilis* strains is not clearly understood and much has been emphasized on the antibiotic production (Joshi and McSpadden Gardener 2006).

Fiddaman and Rossall (1993) reported a strain of *B. subtilis* which produced an antibiotic metabolite. It was also found to produce a volatile compound(s) which is antifungal to *Rhizoctonia solani* and *Pythium ultimum.*

Although biological control is subject of academic research for more than 50 years, the next successful attempt to apply endospore-forming bacilli in large scale was performed nearly hundred years after Alinit was commercialized. In the 1990s, several PGPR-based products became commercially available in the US. Earlier attempts to commercialize products containing fluorescent pseudomonades failed due to the lack of long term viability (Kloepper et al. 2004). Intensive screening and field testing led to commercial development of diverse *Bacillus* strains as biological control agents (McSpadden Gardener and Fravel 2002).

Bacillus spp. are reported to inhibit several soil-borne phytopathogenic fungi including *Macrophomina phaseolina*, *Fusarium* species, *Rhizoctonia solani*, *Pythium* species, *Phytophthora* species and *Erwinia corotovora* (Siddiqui et al. 2005). *Bacillus* strains were studied for their antifungal activity, effect on seedling emergence and plant growth promotion in *Cicer arietinum* (Sivaramaiah et al., 2007). The antagonistic activities of *Bacillus* are mainly due to the production of antibiotics, antimicrobial and antifungal metabolites, lytic enzymes and secondary metabolites (Chan et al. 2003).

Chitin is one of the most abundant natural renewable polysaccharides and is present in fungi, algae, insects and marine invertebrates. Chitin is hydrolysed by two main enzymes chitinase (E.C.3.2.1.14) and β-N-acetyl hexosaminidase (E.C.3.2.1.52) (Patil et al. 2000). Numerous cell wall-degrading enzymes especially chitinase have been isolated from *Bacillus* species. Many strains of *Bacillus* can produce a high level of chitinolytic enzymes (Xiao et al. 2009; Huang et al. 2005). Moreover, many researches have shown that chitinase is involved in antifungal activity and can enhance the insecticidal activity of *Bacillius* sp. Diverse nature of hydrolytic

enzymes plays a role in disease controlling practices. The enzymatic digestion or deformation of cell wall components of phytopathogenic fungi occurred by the enzymes chitinase and β-1, 3-glucanase, protease and lipase that can degrade fungal cell wall and lyse the fungal cells (Lim and Kim 1995).

Production of hydrolytic enzymes by PGPB in general and bacilli in particular is an important phenomenon for plant growth. Chitinases have a broad range of biotechnological applications such as production of fungal protoplasts, crustacean chitin waste management, production of single cell protein and chitooligosaccharides for various applications and biocontrol of fungal plant pathogens (Vyas and Deshpande, 1991). Many PR-proteins induced in plants treated with inducing agents have been shown to be chitinases and β-1, 3-glucanases. Production of induced chitinases in plants has been suggested to be a part of their defense mechanism against fungal pathogens (Gupta et al. 2006). Huang et al. (2005) isolated *B. cereus* 28-9, a chitinolytic bacterium, from lily plant in Taiwan. This bacterium exhibited biocontrol potential on Botrytis leaf blight of lily as demonstrated by a detached leaf assay and dual culture assay.

In recent years the biocontrol agent *Bacillus* belonging to plant growth promoting rhizobacteria (PGPR) has been shown to induce systemic resistance against several pathogens in plants (M' Piga et al. 1997). The role of chitinases in the competitive interactions of well-known chitinolytic bacteria *Bacillus* has been well documented (Patil et al. 2000; Rangel-Castro et al. 2002; Gupta et al. 2006; Singh et al. 2008). Enhanced accumulation of chitinase was observed in chickpea leaves in response to *Bacillus* sp. (Joseph et al. 2007). The chitinases of *Bacillus* play a crucial role in hydrolyzing fungal cell walls. *B. circulans* and *B. licheniformis* produce the enzyme chitinase that degrade chitin. This is why chitinolytic enzymes are considered important in the biological control of soil-borne pathogens (Singh et al. 1999). Extensive research on biocontrol potential of *Bacillus* and its effect on agriculture crop productivity have been carried out by several workers (Idris et al. 2006, 2007; Singh et al. 2008).

Boer et al. (1998) have reported 47% chitin and 14% laminarin composition in cell wall of *F. oxysporum.* Hence, chitinase has been found as an enzyme involved in fungal antagonism (Rangel-Castro et al. 2002). Therefore, it is supposed that cell wall lysis occurred by action of chitinase and β-1, 3-glucanase. Shanmugaiah et al. (2008) reported the role of chitinase isolated from *B. laterosporous*, while its importance in biological control as well as in plant defense mechanisms has been demonstrated by the other workers (Huang et al. 2005; Singh et al. 2008).

The enzyme β-1, 3-glucanase has bean less attention in biocontrol of plant pathogenic fungi, even though in some cases both chitinase and β-1, 3-glucanase produced by bacterial strains have biocontrol activity (Lim and Kim 1995). Yuli et al. (2004) reported thermostable chitinase enzyme purified from the Indonesian *Bacillus* sp. that control the growth of various pathogenic fungi. *In vitro* assay showed that the purified chitinases ChiCW from *B. cereus* had inhibitory activity on conidia germination of *Botrytis elliptica*, a major fungal pathogen of lily leaf blight (Huang et al. 2005). Furthermore, the presence of rhizobacteria near root tips and at sites of secondary root emergence places them in a good position to prevent nematode penetration, to produce their own antagonistic metabolites. The rhizosphere is considered the first line of defense for the plant against nematode attack and, therefore, rhizosphere bacteria are well located to become effective biocontrol agents (Compant et al. 2005).

For any disease suppressive mechanism to be effective, it is important that the antagonist first becomes able to efficiently establish itself in the rhizosphere of that crop (Kloepper et al. 1980). Many workers documented that inadequate colonization leads to decreased PGP activities (Schippers et al. 1987). Root colonization is an initial step in the interaction of antagonistic bacteria with host plant. The inhibition of soil-borne pathogens by biocontrol agents depends on growth, competence, and ability of these agents to colonize the pathogens in soil. It is also essential to understand the recognition of pathogens by potential antagonists in order to formulate effective biocontrol disease management strategies (Barak and Chet 1990).

Srivastava et al. (1996) revealed that diversity of potential microbial parasites colonizing sclerotia of *Macrophomina phaseolina* in soil was inhibited by introducing *Bacillus* sp. Barriuso et al. (2008) revealed that bacterization of chick pea seeds with a siderophore-producing fluorescent *Pseudomonas* strain RBT13 and an antibiotic-producing *B. subtilis* strain AF1, isolated from tomato rhizoplane and pigeon pea rhizosphere, respectively increased the shoot height, root length, fresh weight, dry weight and grain yield in soils infested with *Fusarium oxysporum* f. sp. *ciceris*. Seed bacterization also resulted in a significant reduction in chick pea wilt caused by the same pathogen.

5. Antimicrobial Compound Secreted by *Bacillus* spp.

Antibiotics encompass a heterogeneous group of organic, low-molecular-weight compounds deleterious to the growth or metabolic activities of other microorganisms. Numerous antibiotics have been isolated from bacterial and fungal biocontrol strains.

Biocontrol agents not only exhibit diversity in the type but also in the number of antibiotics produced by an individual strain. It means several antibiotics may be responsible for the suppression of specific or multiple plant diseases. Furthermore, many of the antibiotics produced by biocontrol agents have a broad-spectrum activity.

The antifungal activity of *B. coagulans* against three pathogenic species of *Fusariurn* was examined by Czaczyk et al. (2002). Singh et al. (2008) have reported that *B. subtilis* BN1 strongly colonized the root of *Pinus roxburghii* and exhibited strong antagonistic activity against *M. phaseolina*. Vacuolation, hyphal squeezing, swelling, abnormal branching and lysis of mycelia was visualized and confirmed by root colonization study through antibiotic resistant marker. About 167 biological compounds produced by *Bacillus* species are reported to be active against bacteria, fungi, protozoa, and viruses (Bottone and Peluso 2003).

There are numerous studies on antibiotics produced by antagonistic microorganisms and their role in biocontrol of plant pathogenic fungi and bacteria (Whipps 2001; Raaijmakers et al. 2002). The activity and chemical structure of many of these antibiotics have been determined but the mode of action of relatively a few is known. Several studies have addressed the variation in sensitivity of pathogenic fungi and bacteria to antibiotics produced by antagonists *Bacillus* species are appealing candidates as biocontrol agents. They have the capability to produce effective and broad-spectrum antibiotics like peptides, lipopeptides, aminoglycosides, and aminopolyols (Silo-Suh et al. 1994). *B. cereus* strain UW85 synthesizes both zwittermicin A (He et al. 1994) and kanosamine (Milner et al. 1996a). Bacteria were insensitive to kanosamine but the growth of 26 fungal species was inhibited by kanosamine, ranging from less than 30% for most species to more than 50% for *Ustilago maydis* (Milner et al. 1996a). For the four oomycete species tested, significant variation in sensitivity was observed with *Pythium aphanidermatum* and *Pythium torulosum* being less sensitive to kanosamine than *Aphanomyces euteiches* and *Phytophthora medicaginis*. The *zmaR* gene in *B. cereus* encoding ZmaR protein inactivates zwittermycin A by acetylation (Milner et al. 1996b; Stohl et al. 1999). Understanding the self-resistance in antibiotic-producing biocontrol strains may provide valuable insight into potential self-defense mechanisms that could develop in pathogen populations. Leifert et al. (1995) characterized the antibiotics produced by *B. subtilis* strain CL27 and *B. pumilus* strain CL45. The strain CL27 produced three compounds of which two were identified as peptides. One had activity against *Alternaria brassicicola* and the other against both *A. brassicicola* and *B. cinerea*. The third antibiotic was not peptide-based and also showed the activity against *B. cinerea*. Based on TLC analysis, a similar compound was present in CL45. Although CL27 produces different compounds with antibiotic activity against *B. cinerea*, results obtained by Li and Leifert (1994) suggested that the pathogen could develop resistance against the biocontrol agent after repetitive treatment of *Astilbe hybrida* plants. In glasshouse experiments, *B. cinerea* was effectively controlled in the first seven growth cycles of *Astilbe* plants, but in cycles eight and nine the biocontrol efficacy dropped dramatically. In the tenth cycle, strain CL27 was completely ineffective in controlling *B. cinerea* infection, and *in vitro* assays showed that culture filtrates of strain CL27 were no longer able to inhibit mycelial growth of the recovered *B. cinerea*.

Antibiotics produced by *Bacillus* have been found to play an important role in disease control. Some populations suppress plant pathogens and pests by producing antibiotic metabolites prior to infection (Gardener 2004). Peptide antibiotics and other compounds toxic to plant pathogens have been isolated from several *Bacillus* strains (Pinchuk et al. 2002). Antibiotic resistance markers have also been used to monitor and re-isolate the introduced beneficial rhizobacteria from soil and rhizosphere; hence, this is the first choice of scientists due to simplicity, non-expensive and time saving measures. A number of workers have successfully used such markers (Obaton et al. 2002). Kishore et al. (2005) reported that the rifampicin-resistant mutants of *B. firmis* GRS 123 and *Pseudomonas aeruginosa* GPS 21 colonized the ecto- and endorhizospheres of groundnut, respectively up to 100 days after sowing (DAS). The strain-specific genomic marker for monitoring a *B. subtilis* biocontrol strain in the rhizosphere of tomato was developed by Felici et al. (2008). *B. subtilis* strains strongly inhibited the growth of *F. oxysporum in vitro* in liquid medium as well as in solid medium in comparison to the corresponding growth of fungi without bacterial inoculation mediated by chitinase production that was grown in the presence of colloidal chitin as the sole carbon source in a liquid medium (Swain et al. 2008). Various antimicrobial compounds produced by *Bacillus* spp. and their effect on different crops have been given in Table 5.

Table 5. Various Antimicrobial Compounds Produced by *Bacillus* spp. and their effect on Different Crops.

Antimicrobial compounds	*Bacillus* spp.	Against Phytopathogens	Benefitted Crops	References
Zwittermicin-A	*B. cereus*	*Phytophthora megasperma* f. sp. *medicaginis*	Alfalfa	Handelsman et al. (1990)
Iturin D	*B. subtilis*	*Colletotrichum trifolii,*	Alfalfa	Douville and Boland (1992)
Zwittermicin A, and Antibiotic B	*B. cereus* UW85	*Phytophthora medicaginis*	Alfalfa	Silo-Suh et al. (1994)
Zwittermicyne A,	*B. cereus*	*Phytophthora medicaginis*	Alfalfa	Stabb et al. (1994)
Peptide	*B. subtilis* CL27 and CL45	*Alternaria brassicicola*	NS	Leifert et al. (1995)
Iturin A and Surfactin	*B. sublitis*	*Rhizoctonia solani*	Tomato	Asaka and Shoda (1996)
Zwittermicine and Kanosamine	*B. cereus* UW85	Oomycetes	NS	Milner et al. (1996a,b)
Antibiotic	*B. subtilis* BS 107	*Erwinia carotovora* subsp. *atroseptica* and *Erwinia carotovora* subsp. *carotovora*	Potato	Sharga & Lyon (1998)
TasA-(protein with broad spectrum antibacterial activity)	*B. subtilis* PY 79	*Agrobacterium tumefaciens* GV3101, *Pseudomonas* sp., *Klebsiella* sp., *Erwinia* sp.;		Stover & Driks (1999)
Broad spectrum of antimicrobial agents/several compounds with different activities	*B. subtilis* IFS -01	*Aspergillus wentii*, *Penicillium chrysogenum)* yeasts *(Yarrowia lipolytica, Rhodotorula mucilaginosa*) and Gram-positive bacteria (*Listeria monocytogenes*, *Staphylococcus aureus)*		Foldes et al. (2000)
NS	*B. subtilis* B2g	*Pythium ultimum, R. Solani*		Marten et al. (2000)
Reduction of mycotoxin accumulation	*B. subtilis* RRC101	*Fusarium moniliforme*	Maize	Bacon et al. (2001)
X16sI fraction (Partially purified)	*B. cereus* X16	*Fusarium roseum* var. *sambucinum*	Potato	Sadfi et al., (2002)
Antibiotic	L-forms *B. subtilis*	*Botrytis cinerea*	Chinese cabbage	Walker et al. (2002)
Iturins A-2–A-8	*B. amyloliquefaciens* RC-2	*Colletotrichum dematium*	Mulberry	Hiradate et al. (2002)
Iturin A	*B. amyloliquefaciens* B94	*R. solani*	Soybean	Yu et al. (2002)
Inhibition of fumonisin B1	*B. subtilis* RC 8; RC 9; RC 11	*Fusarium verticillioides*	NS	Cavaglieri et al. (2004)
Induction of host defense response	*B. subtilis* AF 1	*A. niger* (crown rot of groundnut, soft rot in lemons);	Groundnut, Lemons	Manjula et al. (2004)
Reduction of pathogen inoculums and displacement of pathogen	*B. subtilis* BS 21; BS 22; BS 23	*Colletotrichum lindemuthianum*	Cowpea	Adebanjo & Bankole (2004)
Antimicrobial biofilms, lipopeptide (surfactin)	*B. subtilis* 6051	*P.syringae* pv. *tomato* DC3000	Arabidopsis	Bais et al. (2004)
Iturins, engycins type A; B, Surfactin families	*B. subtilis* GA1	*Botrytis cinerea*	Apples	Toure et al. (2004)
Surfactin and Iturin	*B. amyloliquefaciens* BNM 122	*F.oxysporum* f. sp *lycopersici, F.solani, R.solani, S.sclerotiorum*	NS	Souto et al. (2004)
Biosurfactant – lipopeptide N1	*B. subtilis* C1	*Mycobacterium smegmatis*, *Staphylococcus aureus*	NS	Singh & Cameotra, (2004)
Subtilosin A	*B. subtilis* Natural isolate	diverse range of Gram-positive and Gram-negative bacteria	NS	Thennarasu et al. (2005)
Lipopetide	*Bacillus* spp	*Xanthomonas campestris* pv. *Campestris* Leila	Crucifers	Monteiro et al. (2005)
Mycosubtilin and Surfactin	*B. subtilis* BBG100	*Botrytis cinerea, F.oxysporum Pythium aphanidermatum*, *Pichia pastoris* and *S. cerevisiae*	NS	Leclere et al. (2005)
Mycotoxin	*B. subtilis* CE1	*Fusarium verticillioides*	Maize	Cavaglieri et al. (2005)
	B. subtilis B1	*Penicillium oxalicum, A. niger, F. solani*	Storage barns	Okigbo (2005)
Secondary metabolites	*B. subtilis* ZJY-116	*Fusarium graminearum (Fusarium* head blight)	wheat and Barley	Zhang et al. (2005)

Iturin group	*B. subtilis* PRBS-1	*R.solani, Colletotrichum truncatum, S.sclerotiorum, M. phaseolina and Phomopsis* sp.	Soybean	Araujo et al. (2005)
Fengycins	*B.subtilis* S499	*Botrytis cinerea*	Apple	Ongena et al. (2005)
Fengycin	*B. subtilis* JA; JA026	*Gibberella zeae* (anamorph of *Fusarium graminearum*)	Wheat, Barle and Corn	Liu et al. (2005)
Production of active factors (heat stability, resistance to extreme pH values — putative antibiotic character)	*B. subtilis* B2; B5; B7; B8	*R.solani* SX-6, *Pythium aphanidermatum* ZJP-1, *F. oxysporum* f.sp. *cucumerinum* ZJE-2 (root-knot nematode and soil-borne fungi); larvae *Meloidogyne javanica*		Li et al. (2005)
Fengycins A and B	*B. subtilis* LEV -006	*R. solani, S. sclerotiorum, Alternaria brassicae, Leptosphaeria maculans*		Hou et al. (2006)
Iturin A	*B. subtilis* PY-1	*F. oxysporum*	Cotton	Gong et al (2006)
Iturin A	*B. subtilis* RB 14–CS	*R. solani*	Tomato	Mizumoto et al. (2007)
Surfactin, Fengycin, IturinA, Bacillomycin	*B. subtilis* UM AF6614; UM AF6619; UM AF6639; UM AF8561	*Podosphaera fusca*	Cucurbit	Romero et al. (2007)
Bacillomycin D	*B. subtilis* ME488	NS	NS	Chung et al. (2008)
Bacilysin bacD	*B. subtilis* ME488	*F. oxysporum* f.sp. cucumerinum	Cucumber	Chung et al. (2008)
Ericin	*B. subtilis* ME488	NS	NS	Chung et al. (2008)
Fengycin	*B. subtilis* ME488	NS	NS	Chung et al. (2008)
Iturin	*B. subtilis* ME488	*Phytophthora capsici*	Pepper	Chung et al. (2008)
Mersacidin	*B. subtilis* ME488	NS	NS	Chung et al. (2008)
Mycosubtilin	*B. subtilis* ME488	NS	NS	Chung et al. (2008)
Sublancin	*B. subtilis* ME488	NS	NS	Chung et al. (2008)
Subtilin	*B. subtilis* ME488	NS	NS	Chung et al. (2008)
Subtilosin	*B. subtilis* ME488	NS	NS	Chung et al. (2008)
Surfactin	*B. subtilis* ME488	NS	NS	Chung et al. (2008)
Polypeptide	*B. subtilis*	*Microsporum fulvum* and *Trycophyton* spp.	NS	Kumar et al. (2009)
Jiean-peptide (JAA)	*B. subtilis* ZK8	*Fusarium* wilt	Cotton	Zhang et al. (2010)
Jiean-peptide (JAA)	*B. subtilis* ZK8	*Rhizoctonia* rot	Tomato	Zhang et al. (2010)
Jiean-peptide (JAA)	*B. subtilis* ZK8	Powdery mildew	Wheat	Zhang et al. (2010)

*NS – Not Specified.

6. Future Prospect and Conclusion

The natural disease-suppressive characteristic of soils is consistent over years and seems to be pathogen-specific. The application of *Bacillus* species as PGPR from disease suppressive soil offers an environment friendly sustainable approach to enhance crop productivity and plant health. At present, there are many scientific challenges for research in the field of *Bacillus*. If other approach like molecular techniques is used for *in situ* study of genome expression of plant-beneficial and pathogenic microorganisms, it will be very important aspect to obtain a full picture of rhizosphere biodiversity. From the above study it is concluded that the endospore forming bacilli from disease suppressive soil is very useful and have many PGP attributes in general and in particular enhance the growth, protect plants by producing various types of antifungal compound, besides it an interesting fact about nitrogen fixation by these bacilli has also been mentioned.

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