Plant Archives Vol. 25, No. 2, 2025 pp. 439-446 e-ISSN:2581-6063 (online), ISSN:0972-5210

Plant Archives

Journal homepage: http://www.plantarchives.org

DOI Url : https://doi.org/10.51470/PLANTARCHIVES.2025.v25.no.2.059

ROLE OF *BACILLUS SPECIES* IN SUSTAINABLE CROP PRODUCTION: A REVIEW

Huchchappa Jamakhandi[1*], Premakumar[2], Firos T. M. Basha[2], Prakash Sonnad[1], Rohit Sarkar[2], M. N. Rudra Gouda[3] and O.R. Devi[1]

[1]Division of Agronomy, ICAR-Indian Agricultural Research Institute, New Delhi, India 110012.
[2]Division of Genetics, ICAR-Indian Agricultural Research Institute, New Delhi, India 110012.
[3]Division of Entomology, ICAR-Indian Agricultural Research Institute, New Delhi, India 110012.
*Corresponding author E-mail: huchchappajamakhandi@gmail.com

(Date of Receiving-26-05-2025; Date of Acceptance-02-08-2025)

ABSTRACT

The excessive reliance on chemical fertilisers in modern agriculture has led to adverse environmental impacts, including soil degradation, groundwater contamination, and biodiversity loss. Sustainable alternatives are urgently needed, with biofertilizers offering a promising solution. In this context, *Bacillus* species, widely recognised as plant growth-promoting rhizobacteria (PGPR), has gained considerable attention for agricultural applications. *Bacillus* spp. produce a variety of compounds that enhance plant growth and act as biocontrol agents against plant pathogens, positioning them as valuable assets in both agricultural and biotechnological fields. These bacteria exhibit antagonistic properties through the secretion of extracellular metabolites, such as antibiotics, cell wall-degrading enzymes, and siderophores, which inhibit pathogen development. Additionally, *Bacillus* spp. trigger systemic resistance in plants, bolstering defence mechanisms against various pathogens. Beyond their role in biocontrol, *Bacillus* spp. support plant growth by facilitating nitrogen fixation, phosphate solubilisation, phytohormone production, and stress tolerance. They also contribute to rhizoremediation and carbon sequestration, promoting soil health and resilience. This multifaceted functionality underscores the significance of *Bacillus* spp. as biofertilizers, highlighting their potential to foster sustainable agricultural practices and ecological stability.

Key words: *Bacillus*, Biocontrol, Carbon sequestration, Induced systemic resistance, Nutrient use efficiency, Rhizoremediation.

Introduction

The genus *Bacillus*, established by Cohn in 1872, encompasses over 200 recognised species and subspecies within the phylum *Firmicutes*. Members of this genus are characterised as rod-shaped, Gram-positive, catalase-positive bacteria that can be either aerobic or facultatively anaerobic (Logan *et al.*, 2009). A defining feature of *Bacillus* species is their ability to form endospores, which confers significant resilience to extreme environmental conditions, enabling them to persist across a wide range of habitats, particularly in soil. *Bacillus* species are dominant members of soil and rhizosphere microbial communities, making up as much as 95% of the Gram-positive population in these environments (Prashar *et al.*, 2013). Additionally, they rank among the most common endophytic bacteria, establishing symbiotic relationships with plants (De Silva *et al.*, 2019). These attributes underscore the ecological versatility and adaptability of *Bacillus* species, contributing to their prominence and utility in agricultural and environmental applications.

The *Bacillus* group is highly diverse, comprising both non-pathogenic and pathogenic species, with the majority of *Bacillus* species and their derivatives considered safe for environmental applications (Bhattacharyya *et al.*, 2016). They are particularly favoured in commercial applications due to their rapid growth in diverse media, ability to secrete multiple bioactive compounds, and formation of highly resistant endospores (Wu *et al.*, 2015). These traits allow *Bacillus* spp. to maintain long-term viability, be easily formulated, and be stored effectively

(Czaja *et al.*, 2015). In soil and plant rhizosphere environments, *Bacillus* populations can persist without negatively impacting other bacterial communities, making them ideal candidates for sustainable agricultural use (Radhakrishnan *et al.*, 2017).

Commercial products containing beneficial strains such as *Bacillus subtilis*, *Bacillus amyloliquefaciens*, *Bacillus pumilus*, *Bacillus licheniformis*, *Bacillus megaterium*, *Bacillus velezensis*, *Bacillus cereus*, and *Bacillus thuringiensis* are distributed globally (Mazzola *et al*., 2017). These *Bacillus* species are among the most extensively studied biocontrol agents, commonly used as biopesticides to suppress plant pathogens through mechanisms of antagonism and competition. Pathogen inhibition by *Bacillus* spp. Involves several mechanisms, including competition for nutrients and space, production of antibiotics, hydrolytic enzymes, siderophores, and the induction of systemic resistance in plants. This array of beneficial traits underscores the value of *Bacillus* spp. as robust biocontrol agents in sustainable agriculture.

Role of *Bacillus* species

Bio Control of Pathogens

The formation of biofilms by *Bacillus* species around plant root surfaces enables the secretion of various bioactive compounds, including surfactin, iturin, macrolactin, bacillomycin, and fengycin. These compounds are instrumental in suppressing pathogenic bacterial populations, thereby mitigating the incidence of plant diseases (Chen *et al*., 2013; Huang *et al*., 2014; Elshakh *et al*., 2016; Hinarejos *et al*., 2016). Moreover, treatment with *Bacillus* spp. enhances the expression of key antioxidant genes and defence-related enzymes, such as peroxidase (POD), phenylalanine ammonia-lyase (PAL), superoxide dismutase (SOD), catalase (CAT), and polyphenol oxidase (PPO) (Narendra-Babu *et al*., 2015; Yang *et al*., 2015). Studies by Chowdappa *et al*., (2013) and Kang *et al*., (2015) have demonstrated that *Bacillus*-treated plants exhibit elevated levels of growth-promoting hormones, including indole-3-acetic acid (IAA) and gibberellic acid (GA), along with increased salicylic acid (SA) levels, whereas jasmonic acid (JA) and abscisic acid (ABA) levels tend to decrease in plants challenged by pathogens.

Bacillus subtilis, a Gram-positive bacterium known for forming biofilms on inert surfaces, possesses numerous transcriptional factors that regulate its adaptive functions (Stanley *et al*., 2003). Different strains of *B. subtilis* produce various hydrolytic enzymes, such as cellulases, proteases, and β-glucanases. Research by Cazorla *et al*., (2007) suggests that *B. subtilis*, through the secretion of antibiotics and hydrolytic enzymes, can modify its environment in a manner advantageous to its survival while also forming resistant endospores to endure unfavourable conditions.

Induction of Systemic Resistance (ISR)

Bacillus species are recognised for their ability to induce systemic resistance (ISR) in host plants, thereby strengthening their defence mechanisms against a wide range of pathogens. The activation of ISR by *Bacillus subtilis* stimulates the production of jasmonic acid (JA), ethylene, and the NPR1 regulatory gene in plants, crucial components in plant immunity (Garcia-Gutierrez *et al*., 2013). For instance, application of the *B. subtilis* strain AUBS1 has been shown to enhance phenylalanine ammonia-lyase (PAL) and peroxidase (POD) levels and promote new protein synthesis in rice leaves (Jayaraj *et al*., 2004).

In tomato seedlings, *B. subtilis* treatment increases the activity of defence enzymes, such as peroxidase (POD), polyphenol oxidase (PPO), and superoxide dismutase (SOD), alongside the production of various hormones, collectively contributing to ISR against early and late blight (Chowdappa *et al*., 2013). The *B. subtilis* strain Sb4-23 has been found to facilitate ISR through indirect pathways rather than direct interaction with pathogens (Wang *et al*., 2018). Additionally, another strain of *B. subtilis* has been reported to reduce root-knot nematode activity in tomato plants by activating ISR, further highlighting the broad-spectrum protective effects of ISR activation by *Bacillus* spp. (Adam *et al*., 2014).

Nutrient Solubilization

Many essential nutrients and trace elements required by plants, such as nitrogen, phosphorus, and iron, exist in forms within the soil that are not directly accessible to plants. Rhizobacteria play a critical role in transforming or mobilising these elements, making them available for plant uptake (Hayat *et al*., 2010). Phosphorus (P), alongside nitrogen, is crucial for plant growth; however, over 80% of soil phosphorus remains in an inaccessible, fixed form due to adsorption, precipitation, or transformation. *Bacillus subtilis*, part of the group known as Phosphate Solubilising Microorganisms (PSM), effectively solubilises both organic and inorganic phosphate forms, enhancing phosphorus availability to plants (Saeid *et al*., 2018). The solubilisation process involves *Bacillus* spp. producing organic and inorganic acids, siderophores, protons, hydroxyl ions, and CO, which either chelate cations or lower the pH, liberating phosphorus from its bound state. Additionally, enzymes such as phosphatases, phytases, and phospholipases are secreted by these bacteria to mineralise organic phosphates.

Furthermore, plants depend on microbial symbionts for atmospheric nitrogen fixation, as they cannot directly absorb nitrogen from the air. *Bacillus subtilis* contributes to nitrogen fixation and promotes nodulation by facilitating colonisation by native symbiotic rhizobacteria (Elkoca *et al.*, 2007). Additionally, *B. subtilis* enhances iron acquisition in plants by acidifying the rhizosphere, which mobilises iron, and by stimulating the upregulation of plant iron acquisition genes (Freitas *et al.*, 2015; Zhang *et al.*, 2009).

Enhanced Nutrient use Efficiency

The extensive use of nitrogen fertilizers poses a serious threat to the global nitrogen cycle within soil ecosystems. Between 1961 and 2007, while both nitrogen fertilizer consumption and crop production increased significantly, nitrogen use efficiency remained at only 40% (Stevens *et al.*, 2019). The intensive application of synthetic nitrogen fertilizers in agriculture has become a primary source of non-point pollution due to nitrogen losses. Biofertilizers, especially those containing *Bacillus subtilis*, have emerged as promising alternatives, though the mechanisms by which they mitigate non-point source pollution are not fully elucidated. Notably, replacing 50% of urea with a *B. subtilis*-based biofertilizer reduced nitrogen loss from soils by 54%, improved nitrogen use efficiency by 11.2%, and increased crop yield by 5.0%.

The application of *B. subtilis* biofertilizers was associated with decreased abundance of the amoA gene, an indicator of nitrification, and increased levels of denitrification genes (narG, nirS, nirK, and nosZ), reflecting reduced NO_3^{-N} accumulation and a substantial decrease in nitrogen runoff and leaching. Furthermore, the biofertilizer decreased the presence of the nitrogen-fixing gene nifH, while supporting the growth of microbial groups like *Bacteroidetes* and *Chloroflexi*, known for their roles in organic matter degradation. Overall, *B. subtilis* biofertilizers effectively modulate microbial nitrogen cycling processes, thus minimizing nitrogen losses from agricultural systems.

In terms of managing nitrogen-polluted wastewater, *Bacillus* species have been effectively employed in various regions globally (Hlordzi *et al.*, 2020). While conventional nitrate removal methods, such as reverse osmosis, electrochemical reduction, ion exchange, and electrodialysis, are often expensive, alternative approaches using bioaugmentation with microbial agents, especially in combination with bio-electrochemical systems, offer a cost-effective and efficient solution for accelerating denitrification (Rahimi *et al.*, 2020).

Improves Drought and Stress tolerance in Plants

Plants colonised by *Bacillus* species exhibit improved water uptake, which plays a crucial role in protecting against drought-induced stress (Marulanda *et al.*, 2009). Drought conditions often limit the uptake of essential macronutrients, such as nitrogen (N), phosphorus (P), and potassium (K), but treatments with *Bacillus* spp. have been shown to increase the availability and absorption of these nutrients in drought-stressed plants (Barnawal *et al.*, 2013). This enhancement results from bacterial enzymes that facilitate the accumulation of bioavailable nutrient forms in both the soil and plants (Kang *et al.*, 2015a; Kuan *et al.*, 2016). Additionally, under drought stress, *Bacillus* spp. promote higher concentrations of sucrose and fructose in plants, aiding drought adaptation by stimulating root growth (Gagne-Bourque *et al.*, 2016). While drought conditions typically inhibit pigment synthesis and reduce photosynthesis, *Bacillus* treatments have been found to increase the levels of chlorophylls a and b and carotenoids, which in turn enhance photosynthetic activity in stressed plants (Barnawal *et al.*, 2013; Hashem *et al.*, 2015).

Bacillus spp. also produce hormones and ACC deaminase, regulating plant growth by elevating levels of stress-related hormones such as salicylic acid (SA), jasmonic acid (JA), and abscisic acid (ABA), while reducing ethylene levels via ACC deaminase activity (Barnawal *et al.*, 2013; Castillo *et al.*, 2013). The increase in ABA levels contributes to drought tolerance by activating antioxidant enzymes and reducing water loss through stomatal closure (Lu *et al.*, 2009; Zhu e*t al.*, 2011).

Improve Plant Health in Saline Soil

Climate change has disrupted the consistency of annual rainfall, leading to altered precipitation patterns. This change has exacerbated the spread of soil salinity worldwide, particularly in agricultural lands where inadequate rainfall, high water evaporation rates, and improper irrigation practices prevail (Al-Karaki, 2006). Soil salinity increases soil water potential, making it more challenging for plants to absorb water and essential nutrients through their roots (Porcel *et al.*, 2012). Introducing microbial inoculants with *Bacillus* species can mitigate salt stress effects on plants, offering an eco-friendly solution for sustainable agriculture (Radhakrishnan *et al.*, 2014; Hashem *et al.*, 2015, 2016a, b).

For instance, *Bacillus licheniformis* A2, which possesses various plant growth-promoting traits—including phosphate solubilisation and the production of ammonia, indole-3-acetic acid (IAA), and siderophores—counteracts salt stress in plants, thereby enhancing growth under stressful conditions in crops like peanuts (Goswami *et al*., 2014). *Bacillus* species help reduce the adverse effects of salinity by lowering lipid peroxidation levels (Han *et al*., 2014). Hashem *et al*., (2015) showed that *Bacillus subtilis* boosted the synthesis of essential lipids, such as oleic, linoleic, and linolenic acids, and phospholipids in salt-stressed plants, which may reduce lipid peroxidation and oxidative stress. Antioxidant enzyme regulation further aids plants in managing reactive oxygen species (ROS); in plants treated with *Bacillus*, enzymes like ascorbate peroxidase (APX) and superoxide dismutase (SOD) show decreased activity, while nitrate reductase (NR), catalase (CAT), and peroxidase (POD) activities are increased (Jha and Subramanian, 2012, 2015). This adaptive response promotes resilience against oxidative stress under saline conditions.

Rhizoremediation

Agricultural soils contaminated with trace metals from industrial effluents and agrochemicals pose significant risks to the ecological food chain, adversely affecting crop growth and altering soil microbial communities (Hu *et al*., 2009; Ashraf *et al*., 2017). Metals such as copper (Cu), manganese (Mn), and zinc (Zn) are notable pollutants in both soil and water, exhibiting resistance to degradation into harmless substances (Ma *et al*., 2009; Arthur *et al*., 2012). While chelating agents are sometimes utilised to mitigate metal toxicity, they can also pose risks to living organisms (Tandy *et al*., 2006). In contrast, microorganisms have the potential to solubilise or transform toxic metals into less harmful forms, offering a beneficial approach for heavy metal phytoremediation (Bosecker, 1997; Kang *et al*., 2015). These bacteria enhance plant growth under metal stress by improving water uptake and reducing electrolyte leakage, thereby alleviating cadmium (Cd) toxicity (Ahmad *et al*., 2014).

Bacillus species, in particular, help mitigate the effects of metal stress by decreasing lipid peroxidation and reducing the activity of superoxide dismutase (SOD), while simultaneously increasing levels of amylase and protease to promote growth in metal-contaminated soils (Pandey *et al*., 2013). They also enhance plant tolerance to zinc (Zn) and copper (Cu) stress by boosting the activity of reactive oxygen species (ROS) scavenging enzymes, including peroxidase (POD), catalase (CAT), ascorbate peroxidase (APX), and dehydroascorbate reductase (DHAR) (Gururani *et al*., 2013; Wang *et al*., 2013).

Moreover, chromium (Cr) stress can reduce acid phosphatase activity in plants, but treatments with beneficial bacteria have been shown to increase this enzyme's activity, helping plants better cope with metal-induced stress (Riaz *et al*., 2010). By enhancing the resilience of plants to heavy metal contamination, *Bacillus* species play a crucial role in promoting sustainable agricultural practices and improving soil health.

Carbon Sequestration

Soil carbon sequestration currently ranges between 3.5 and 5.2 gigatons per year, but this rate needs to be increased to effectively address rising CO_2 levels that contribute to global warming (Duran *et al*., 2021). Soil microbiota, supported by root exudates, play a key role in controlling carbon influx and efflux in the rhizosphere. The introduction of microorganisms derived from biological soil crusts to drylands can enhance the soil's carbon absorption capacity, increasing it from 0.232 to 0.294 $g/m^2/day$ (Kheirfam, 2020).

Bacillus subtilis, a widely used plant growth-promoting bacterium (PGPB) in agriculture, shows significant potential for carbon sequestration under various growth conditions. Numerous studies have explored the carbon sequestration capabilities of *Bacillus*. One promising approach involves utilising carbonic anhydrase (CA)-based enzymatic technology for carbon fixation and bioremediation (Effendi & Ng, 2019). Immobilised forms of CA have proven to be efficient and suitable for industrial applications; for instance, CA derived from *B. subtilis* VSG4 can convert CO_2 into calcium carbonate ($CaCO_3$) when immobilised (Oviya *et al*., 2012).

Furthermore, *Bacillus sp. SS105*, isolated from a free-air CO_2-enriched (FACE) environment, can convert CO_2 into calcite due to the presence of beta- and gamma-carbonic anhydrase genes. The efficiency of CO_2 sequestration and calcite formation was demonstrated through assays of RUBISCO and CA enzymes (Maheshwari *et al*., 2019). This sequestration efficiency contributes to maintaining various physiological and biological functions.

In addition to carbon sequestration, *Bacillus* species produce lipopeptide-type biosurfactants, making simultaneous carbon sequestration and biosurfactant production beneficial for both commercial and agricultural applications (Maheshwari *et al*., 2017). Gaseous CO_2 and sodium bicarbonate ($NaHCO_3$) have been effectively utilised as substrates for biosurfactant production by *Bacillus sp. ISTS2* (Sundaram & Thakur, 2015). This dual functionality highlights the potential of *Bacillus* species as a sustainable strategy for enhancing soil health and addressing climate change challenges.

Future perspectives

Future research should prioritize exploring antibiotic resistance genes within *Bacillus* species, emphasizing their transfer mechanisms, interactions with other microorganisms, and potential effects on soil microbial diversity. Understanding these factors is crucial for mitigating the risks associated with antibiotic resistance in agricultural contexts. To support sustainable agriculture, developing microbial consortia that include *Bacillus* species capable of enhancing crop productivity without negatively impacting the rhizosphere's microbial ecosystem is essential. Effective applications of *Bacillus* and other Plant Growth-Promoting Bacteria (PGPB) can be pursued through several strategies, such as targeting seed endophytic microbiomes, selecting plant varieties compatible with microbial inoculants, and utilizing microbial engineering techniques to maintain beneficial microbiota across generations. Additionally, implementing soil amendments and exploring plant genetic modifications present promising strategies for preserving soil health, thereby advancing sustainable farming practices. By integrating these approaches, future research can reduce reliance on chemical inputs and enhance the overall resilience of agricultural systems.

Conclusion

Bacillus species present an eco-friendly approach to enhancing crop production through mechanisms such as biological control, biofertilization, and biostimulation. While the potential of *Bacillus* spp. to reduce disease incidence and boost crop yields is well established, their widespread application remains limited due to inconsistent performance across various conditions. The effectiveness of these bacteria in providing beneficial effects is significantly influenced by their interactions with plants or pathogens, as well as environmental factors. Given the substantial economic and ecological value of *Bacillus* spp., it is essential to broaden the range of practically important species and develop advanced methods for their rapid, comprehensive study and effective utilization. Integrating *Bacillus* spp. into agricultural systems represents a promising strategy for sustainable farming that aligns with the United Nations Sustainable Development Goals, thereby contributing to global food security.

Conflict of interest: The authors declare that they have no conflict of interest.

References

Adam, M., Heuer H. and Hallmann J. (2014). Bacterial antagonists of fungal pathogens also control root-knot nematodes by induced systemic resistance of tomato plants. *PloS one*., **9(2)**, e90402.

Ahmad, I., Akhtar M.J., Zahir Z.A., Naveed M., Mitter B. and Sessitsch A. (2014). Cadmium-tolerant bacteria induce metal stress tolerance in cereals. *Environ. Sci. Pollut. Res*., **21**, 11054–11065. doi: 10.1007/s11356-014-3010-9.

Al-Karaki, G.N. (2006). Nursery inoculation of tomato with arbuscular mycorrhizal fungi and subsequent performance under irrigation with saline water. *Sci. Hortic*., **109**, 1-7. doi: 10.1016/j.scienta.2006.02.019.

Arthur, E., Moldrup P., Holmstrup M., Schjonning P., Winding A. and Mayer P. *et al*. (2012). Soil microbial and physical properties and their relations along a steep copper gradient. *Agricult. Ecosys. Environ*., **159**, 9-18. doi: 10.1016/j.agee.2012.06.021.

Ashraf, M.A., Hussain I., Rasheed R., Iqbal M., Riaz M. and Arif M.S. (2017). Advances in microbe-assisted reclamation of heavy metal contaminated soils over the last decade: *a review. J. Environ. Manag*., **198**, 132-143. doi: 10.1016/j.jenvman.2017.04.060.

Barnawal, D., Maji D., Bharti N., Chanotiya C.S. and Kalra A. (2013). ACC deaminase-containing Bacillus subtilis reduces stress ethylene-induced damage and improves mycorrhizal colonization and rhizobial nodulation in Trigonella foenum-graecum under drought stress. *J. Plant Growth Regul*., **32**, 809-822. doi: 10.1007/s00344-013-9347-3.

Bhattacharyya, P.N., Goswami M.P. and Bhattacharyya L.H. (2016). Perspective of beneficial microbes in agriculture under changing climatic scenario. *A review. J. Phytol*., **8**, 26-41.

Bloemberg, G.V. and Lugtenberg B.J.J. (2001). Molecular basis of plant growth promotion and biocontrol by rhizobacteria. *Curr Opin Plant Biol*., **4**, 343-350.

Bosecker, K. (1997). Bioleaching: metal solubilization by microorganisms. *FEMS Microbiol. Rev*., **20**, 591-604. doi: 10.1111/j.1574-6976.1997.tb00340.x.

Castillo, P., Escalante M., Gallardo M., Alemano S. and Abdala G. (2013). Effects of bacterial single inoculation and co-inoculation on growth and phytohormone production of sunflower seedlings under water stress. *Acta Physiol. Plant*., **35**, 2299-2309. doi: 10.1007/s11738-013-1267-0.

Cazorla, F.M., Romero D., Pérez García A., Lugtenberg B.J.J., Vicente A.D. and Bloemberg G. (2007). Isolation and characterization of antagonistic *Bacillus subtilis* strains from the avocado rhizoplane displaying biocontrol activity. *Journal of applied microbiology*., **103(5)**, 1950-1959.

Chen, Y., Yan F., Chai Y., Liu H., Kolter R., Losick R. *et al*. (2013). Biocontrol of tomato wilt disease by *Bacillus subtilis* isolates from natural environments depends on conserved genes mediating biofilm formation. *Environ. Microbiol*., **15**, 848-864. doi: 10.1111/j.1462-2920.2012.02860. x.

Chowdappa, P., Kumar S.M., Lakshmi M.J. and Upreti K.K.

(2013). Growth stimulation and induction of systemic resistance in tomato against early and late blight by *Bacillus subtilis* OTPB1 or *Trichoderma harzianum* OTPB3. *Biological control*., , **65(1)**, 109-117.

Chowdappa, P., Mohan-Kumar S.P., Jyothi-Lakshmi M. and Upreti K.K. (2013). Growth stimulation and induction of systemic resistance in tomato against early and late blight by *Bacillus subtilis* OTPB1 or *Trichoderma harzianum* OTPB3. *Biol. Control*., **65**, 109-117. doi: 10.1016/ j.biocontrol.2012.11.009.

Czaja, K., Góralczyk K., Struci nski P., Hernik A., Korcz W., Minorczyk M., Lyczewska M. and Ludwicki J.K. (2015). Biopesticides–towards increased consumer safety in the European Union. *Pest Manag. Sci*., **71**, 3-6.

De Silva, N.I., Brooks S., Lumyong S. and Hyde K.D. (2019). Use of endophytes as biocontrol agents. *Fungal Biol. Rev*., **33**, 133-148.

Duran, P., Mora M., Matus F., Barra P.J., Jofré I. and Kuzyakov Y. *et al*. (2021). Biological crusts to increase soil carbon sequestration: New challenges in a new environment. *Biology*., **10**, 1190. https://doi.org/10.3390/biolo gy101 11190.

Effendi, S.S.W. and Ng I.S. (2019). The prospective and potential of carbonic anhydrase for carbon dioxide sequestration: a critical review. *Process Biochemistry*., **87**, 55-65.

Elkoca, E., Kantar F. and Sahin F. (2007). Influence of nitrogen fixing and phosphorus solubilizing bacteria on the nodulation, plant growth, and yield of chickpea. *J. Plant Nutr*., **31**, 157-171.

Elshakh, A.S.A., Anjum S.I., Qiu W., Almoneafy A.A., Li W. and Yang Z. *et al*. (2016). Controlling and defence-related mechanisms of *Bacillu*s strains against bacterial leaf blight of rice. *J. Phytopathol*., **164**, 534-546. doi: 10.1111/ jph.12479.

Freitas, M.A., Medeiros F.H., Carvalho S.P., Guilherme L.R., Teixeira W.D., Zhang H. and Par´e P.W. (2015). Augmenting iron accumulation in cassava by the beneficial soil bacterium *Bacillus subtilis* (GBO3). *Front. Plant Sci*., **6**, 596.

Gagne-Bourque, F., Bertrand A., Claessens A., Aliferis K.A. and Jabaji S. (2016). Alleviation of drought stress and metabolic changes in timothy (*Phleum pratense* L.) colonized with *Bacillus subtilis* B26. *Front. Plant Sci*., **7**, 584. doi: 10.3389/fpls.2016.00584.

Gao, S.F., Wu H.J., Yu X.F., Qian L.M. and Gao X.W. (2016). Swarming motility plays the major role in migration during tomato root colonization by *Bacillus subtilis* SWR01. *Biol Control*., **98**, 11-17.

García-Gutiérrez, M.S., Ortega-Álvaro A., Busquets-García A., Pérez-Ortiz J.M., Caltana L., Ricatti M.J. and Manzanares J. (2013). Synaptic plasticity alterations associated with memory impairment induced by deletion of CB2 cannabinoid receptors. *Neuropharmacology*., **73**, 388-396.

Gardener MS., Fravel DR., Gardener MS. and Fravel DR. (2002). Biological control of plant pathogens: research, commercialization, and application in the USA. *Plant Health Prog*., https://doi. org/10.1094/PHP-2002-0510-01-RV.

Goswami, D., Dhandhukia P., Patel P. and Thakker J.N. (2014). Screening of PGPR from saline desert of Kutch: growth promotion in *Arachis hypogea* by *Bacillus licheniformis* A2. *Microbiol. Res*., **169**, 66-75. doi: 10.1016/ j.micres.2013.07.004.

Gururani, M.A., Upadhyaya C.P., Baskar V., Venkatesh J., Nookaraju A. and Park S.W. (2013). Plant growth-promoting rhizobacteria enhance abiotic stress tolerance in *Solanum tuberosum* through inducing changes in the expression of ROS-scavenging enzymes and improved photosynthetic performance. *J. Plant Growth Regul*. **32**, 245-258. doi: 10.1007/s00344-012-9292-6.

Han, Q.Q., Lu X.P., Bai J.P., Qiao Y., Pare P.W., Wang S.M. and Zhang J.L. *et al*. (2014). Beneficial soil bacterium *Bacillus subtilis* (GB03) augments salt tolerance of white clover. *Front. Plant Sci*., **5**, 525. doi: 10.3389/fpls.2014.00525.

Hashem, A., Abd-Allah E.F., Alqarawi A.A., AL-Huqail A.A., Alshalawi S.R.M. and Wirth S. *et al*. (2015). Impact of plant growth promoting *Bacillus subtilis* on growth and physiological parameters of *Bassia indica* (Indian bassia) grown udder salt stress. *Pak. J. Bot*., **47**, 1735-1741.

Hashem, A., Abd-Allah E.F., Alqarawi A.A., Al-Huqail A.A. and Shah M.A. (2016). Induction of osmoregulation and modulation of salt stress in *Acacia gerrardii benth*. by arbuscular mycorrhizal fungi and *Bacillus subtilis* (BERA 71). *Bio. Med. Res. Int*., 6294098. doi: 10.1155/2016/ 6294098.

Hashem, A., Abd-Allah E.F., Alqarawi A.A., Al-Huqail A.A., Wirth S. and Egamberdieva D. (2016a). The Interaction between arbuscular mycorrhizal fungi and endophytic bacteria enhances plant growth of *Acacia gerrardii* under salt stress. *Front. Microbiol*., **7**, 1089. doi: 10.3389/ fmicb.2016.01089.

Hayat, R., Ali S., Amara U., Khalid R. and Ahmed I. (2010). Soil beneficial bacteria and their role in plant growth promotion: A review. *Ann. Microbiol*., **60**, 579-598.

Hinarejos, E., Castellano M., Rodrigo I., Belles J.M., Conejero V. and Lopez-Gresa M.P. *et al*. (2016). *Bacillus subtilis* IAB/BS03 as a potential biological control agent. *Eur. J. Plant Pathol*., **146**, 597-608. doi: 10.1007/s10658-016-0945-3.

Hlordzi, V., Kuebutornye F., Gyamfua A., Abarike E., Lu Y. and Chi S. *et al*. (2020). The use of *Bacillus* species in maintenance of water quality in aquaculture: A review. *Aquaculture Reports*., **18**, 100503.

Hu, N., Zheng J.F., Ding D.X., Liu J., Yang L.Q. and Yin J. *et al*. (2009). Metal pollution in Huayuan river in hunan province in China by manganese sulphate waste residue. *Bull. Environ. Contamin. Toxicol*., **83**, 583-590. doi: 10.1007/s00128-009-9802-9.

Huang, J., Wei Z., Tan S., Mei X., Shen Q. and Xu Y. (2014). Suppression of bacterial wilt of tomato by bioorganic fertilizer made from the antibacterial compound producing strain *Bacillus amyloliquefaciens* HR62. *J. Agric. Food Chem.*, **62**, 10708–10716.doi: 10.1021/jf503136a.

Jayaraj, J., Yi H., Liang G.H., Muthukrishnan S. and Velazhahan R. (2004). Foliar application of *Bacillus subtilis* AUBS1 reduces sheath blight and triggers defense mechanisms in rice/Blattapplikation von *Bacillus subtilis* AUBS1 reduziert die Blattscheidendürre und induziert Abwehrmechanismen in Reis. *Zeitschrift für Pflanzenkrankheiten und Pflanzenschutz/Journal of Plant Diseases and Protection*., 115-125.

Jha, Y. and Subramanian R.B. (2012). Paddy physiology and enzymes level is regulated by rhizobacteria under saline stress. *J. Appl. Bot. Food Qual.*, **173**, 168-173.

Jha, Y. and Subramanian R.B. (2015). Reduced cell death and improved cell membrane integrity in rice under salinity by root associated bacteria. *Theor. Exp. Plant Physiol.*, **27**, 227-235. doi: 10.1007/s40626-015-0047-1.

Kang, S.M., Radhakrishnan R., Lee K.E., You Y.H., Ko J.H. and Kim J.H. *et al.* (2015a) Mechanism of plant growth promotion elicited by *Bacillus* sp. LKE15 in oriental melon. *Acta Agric. Scand. Sect. B Soil Plant Sci*. **65**, 637-647. doi: 10.1080/09064710.2015.1040830.

Kheirfam, H. (2020). Increasing soil potential for carbon sequestration using microbes from biological soil crusts. *Journal of Arid Environments*., **172**, 104022.

Kilian, M., Steiner U., Krebs B., Junge H., Schmiedeknecht G. and Hain R. (2000). FZB24® *Bacillus subtilis*–mode of action of a microbial agent enhancing plant vitality. *Pflanzenschutz-Nachrichten Bayer*., **1(00)**, 1.

Kuan, K.B., Othman R., Rahim K.A. and Shamsuddin Z.H. (2016). Plant growth-promoting rhizobacteria inoculation to enhance vegetative growth, nitrogen fixation and nitrogen remobilisation of maize under greenhouse conditions. *PLoS ONE*., **11**, e0152478. doi: 10.1371/journal.pone.0152478.

Lee, S.W.., Lee S.H., Balaraju K., Park K.S., Nam K.W., Park J.W. and Park K. (2014). Growth promotion and induced disease suppression of four vegetable crops by a selected plant growth-promoting rhizobacteria (PGPR) strain *Bacillus subtilis* 21-1 under two different soil conditions. *Acta Physiol Plant*., **36**, 1353-1362.

Liu B., Qiao H., Huang L., Buchenauer H., Han Q., Kang Z. and Gong Y. (2009). Biological control of take-all in wheat by endophytic *Bacillus subtilis* E1R-j and potential mode of action. Biol Control., **49**, 277-285.

Logan, N.A., De Vos P. and Genus Bacillus (2009). In Bergey's Manual of Systematic Bacteriology, 2nd ed.; De Vos, P., Garrity, G.M., Jones, D., Krieg, N.R., Ludwig, W., Rainey, F.A., Schleifer, K.H., Whitman, W.B., Eds.; Springer: Dordrecht, The Netherlands; Berlin/Heidelberg, Germany; London, UK; New York, NY, USA, **3**, 21-128.

Lu, S., Su W., Li H. and Guo Z. (2009). Abscisic acid improves osmotic tolerance of triploid Bermuda grass and involves H_2O_2 and NO induced antioxidant enzyme activities. *Plant Physiol. Biochem*., **47**, 132-138. doi: 10.1016/j.plaphy.2008.10.006.

Ma, Y., Rajkumar M. and Freitas H. (2009). Inoculation of plant growth promoting bacterium *Achromobacter xylosoxidans* strain Ax10 for the improvement of copper phytoextraction by *Brassica juncea*. *J. Environ. Manag*., **90**, 831-837. doi: 10.1016/j.jenvman.2008.01.014.

Maheshwari, N., Kumar M., Thakur I.S. and Srivastava S. (2017). Recycling of carbon dioxide by free air CO_2 enriched (FACE) *Bacillus sp*. SS105 for enhanced production and optimization of biosurfactant. *Bioresource Technology*., **242**, 2-6.

Maheshwari, N., Kumar M., Thakur I.S. and Srivastava S. (2019). Cloning, expression and characterization of β- and γ-carbonic anhydrase from *Bacillus sp*. SS105 for biomimetic sequestration of CO_2. *International Journal of Biological Macromolecules*., **131**, 445-452.

Marulanda, A., Barea J.M. and Azcon R. (2009). Stimulation of plant growth and drought tolerance by native microorganisms (AM fungi and bacteria) from dry environments. Mechanisms related to bacterial effectiveness. *J. Plant Growth Regul*., **28**, 115-124. doi: 10.1007/s00344-009-9079-6.

Mazzola, M. and Freilich S. (2017). Prospects for biological soilborne disease control: Application of indigenous versus synthetic microbiomes. *Phytopathology*., **107**, 256-263.

Miljakoviae, D., Marinkoviae J. and Baleševiae-Tubiae S. (2020). The significance of *Bacillus spp*. in disease suppression and growth promotion of field and vegetable crops. *Microorganisms*., **8(7)**, 1037.

Narendra-Babu, A., Jogaiah S., Ito S.I., Kestur-Nagaraj A. and Tran L.S.P. (2015). Improvement of growth, fruit weight and early blight disease protection of tomato plants by rhizosphere bacteria is correlated with their beneficial traits and induced biosynthesis of antioxidant peroxidase and polyphenol oxidase. *Plant Sci*., **231**, 62-73. doi: 10.1016/j.plantsci.2014.11.006.

Oviya, M., Giri S.S., Sukumaran V. and Natarajan P., Immobilization of carbonic anhydrase enzyme purified from *Bacillus subtilis* VSG-4 and its application as CO_2 sequesterer. *Preparative Biochemistry and Biotechnology*, **42(5)**, 462-475.

Pandey, S., Ghosh P.K., Ghosh S., De T.K. and Maiti T.K., Role of heavy metal resistant *Ochrobactrum sp*. and *Bacillus spp*. strains in bioremediation of a rice cultivar and their PGPR like activities. *J. Microbiol*., **51**, 11-17. doi: 10.1007/s12275-013-2330-7.

Porcel, R., Aroca R. and Ruiz-Lozano J.M. (2012). Salinity stress alleviation using arbuscular mycorrhizal fungi. A review. *Agron. Sustain. Dev*., **32**, 181-200. doi: 10.1007/s13593-011-0029-x.

Prashar, P., Kapoor N. and Sachdeva S. (2013). Rhizosphere: Its structure, bacterial diversity and significance. Rev. *Environ. Sci. Biotechnol*., **13**, 63-77.

Radhakrishnan, R., Kang S.M., Baek I.Y. and Lee I.J. (2014). Characterization of plant growth-promoting traits of

Penicillium species against the effects of high soil salinity and root disease. *J. Plant Interact.*, **9**, 754-762. doi: 10.1080/17429145.2014.930524.

Radhakrishnan, R., Hashem A. and Abd Allah E.F. (2017). *Bacillus*: A biological tool for crop improvement through bio-molecular changes in adverse environments. *Front. Physiol.*, **8**, 667.

Rahimi, S., Modin O., Roshanzamir F., Neissi A., Alam S.S. and Seelbinder B. *et al.* (2020). Coculturing *Bacillus subtilis* and wastewater microbial community in a bio-electrochemical system enhances denitrification and butyrate formation. *Chemical Engineering Journal.*, **397**, 125437.

Riaz, S., Faisal M. and Hasnain S. (2010). *Cicer arietinum* growth promotion by *Ochrobactrum intermedium* and *Bacillus cereus* in the presence of CrCl3and K2CrO4. *Ann. Microbiol.*, **60**, 729-733. doi: 10.1007/s13213-010-0123-3.

Ryu, C.M., Murphy J.F., Reddy M.S. and Kloepper J.W. (2007). A two-strain mixture of rhizobacteria elicits induction of systemic resistance against *Pseudomonas syringae* and cucumber mosaic virus coupled to promotion of plant growth on *Arabidopsis thaliana*. *J. Microbiol Biotechnol.*, **17**, 280-286.

Saeid, A., Prochownik E. and Dobrowolska-Iwanek J. (2018). Phosphorus solubilization by *Bacillus* species. *Molecules.*, **23**, 2897.

Stanley, N.R., Britton R.A., Grossman A.D. and Lazazzera B.A. (2003). Identification of catabolite repression as a physiological regulator of biofilm formation by *Bacillus subtilis* by use of DNA microarrays. *Journal of Bacteriology.*, **185(6)**, 1951-1957.

Stevens, C.J. (2019). Nitrogen in the environment. *Science.*, **363(6427)**, 578-580.

Sun, B.O., Gu L., Bao L., Zhang S., Wei Y., Bai Z. and Zhuang X. (2020). Application of biofertilizer containing *Bacillus subtilis* reduced the nitrogen loss in agricultural soil. *Soil Biology and Biochemistry.*, **148**, 107911.

Sundaram, S. and Thakur I.S. (2015). Biosurfactant production by a CO_2 sequestering *Bacillus* sp. strain ISTS2. *Bioresource Technology.*, **188**, 247-250.

Tandy, S., Schulin R. and Nowack B. (2006). The influence of EDDS on the uptake of heavy metals in hydroponically grown sunflowers. *Chemosphere.*, **62**, 1454-1463. doi: 10.1016/j.chemosphere.2005.06.005.

Van Dijl, J.M. and Hecker M. (2013). *Bacillus subtilis*: from soil bacterium to super-secreting cell factory. *Microb Cell Factories.*, **12**, 3.

Wang, H., Xu R., You L. and Zhong G. (2013). Characterization of Cu-tolerant bacteria and definition of their role in promotion of growth, Cu accumulation and reduction of Cu toxicity in *Triticum aestivum* L. *Ecotoxicol. Environ. Saf.*, **94**, 1-7. doi: 10.1016/j.ecoenv.2013.04.005.

Wang, X. Q., Zhao D.L., Shen L.L., Jing C.L. and Zhang C.S. (2018). Application and mechanisms of *Bacillus subtilis* in biological control of plant disease. *Role of rhizospheric microbes in soil: Volume 1: Stress management and agricultural sustainability.*, 225-250.

Weller, D.M., Raaijmakers J.M., Gardener B.B.M. and Thomashow L.S. (2002). Microbial populations responsible for specific soil suppressiveness to plant pathogens. *Annu Rev Phytopathol.*, **40**, 309.

Wu, L.,Wu H.-J., Qiao J., Gao X. and Borriss R. (2015). Novel routes for improving biocontrol activity of *Bacillus* based bioinoculants. *Front. Microbiol.*, **6**, 1395.

Yang, R., Fan X., Cai X. and Hu F. (2015). The inhibitory mechanisms by mixtures of two endophytic bacterial strains isolated from Ginkgo biloba against pepper phytophthora blight. *Biol. Control.*, **85**, 59-67. doi: 10.1016/j.biocontrol.2014.09.013.

Zhang N., Wu K., He X., Li S., Zhang Z., Shen B., Yang X., Zhang R., Huang Q. and Shen Q. (2011). A new bioorganic fertilizer can effectively control banana wilt by strong colonization with *Bacillus subtilis* N11. *Plant Soil.*, **344**, 87-97.

Zhang, H., Sun Y., Xie X., Kim M.S., Dowd S.E. and Par´e P.W. (2009). A soil bacterium regulates plant acquisition of iron via deficiency inducible mechanisms. *Plant J.*, **58**, 568-577.

Zhu, S.Q., Chen M.W., Ji B.H., Jiao D.M. and Liang J.S. (2011). Roles of xanthophylls and exogenous ABA in protection against NaCl induced photo damage in rice (*Oryza sativa* L) and cabbage (*Brassica campestris*). *J. Exp. Bot.*, **62**, 4617-4625. doi: 10.1093/jxb/err170.