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Biological functions of *Paenibacillus* spp. for agriculture applications

Mariana Mohammad[1], Noor Afiza Badaluddin[1*] and Eeyad Arief Asri[2]

[1] *Universiti Sultan Zainal Abidin, Faculty of Bioresources and Food Industry, School of Agricultural Sciences and Biotechnology, Besut Campus, 22200 Besut, Terengganu, Malaysia*
[2] *Universiti Sultan Zainal Abidin, Pejabat Taman Agropreneur Inkubator UniSZA, Tembila Agrotech Resources, UniSZA Blok F2, Kampus Besut, Besut Campus, 22200 Besut, Terengganu, Malaysia*
[*] *Corresponding author:* noorafiza@unisza.edu.my

Abstract

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Due to their known mechanisms for biological control and plant growth promotion, *Paenibacillus* spp. are widely used in agriculture. However, the use of this microbial inoculant in *Paenibacillus*-based products and its potential benefits have received little attention. We describe the efficacy of *Paenibacillus* spp. in relation to crop development, biological control and bioremediation based on a study of researchers from around the world. In addition, this article addresses how *Paenibacillus* spp. produces beneficial metabolites. Agriculture will benefit from the implementation of these unexpected results if ecologically sound cultivation methods are used.

Keywords: Paenibacillus spp.; plant growth promoter; biological control agents; bioremediation; enzyme degradation

Introduction

Public health and society have been deemed to be negatively impacted by severe epidemic diseases and yield losses brought on by plant pathogens. Insects, illnesses, and weeds account for 20–40% of global agricultural productivity, making plant pests and diseases the primary causes of food loss worldwide (Savary et al., 2019). Pesticides and synthetic fertilisers are overused in order to meet consumer demand and the needs of expanding populations, which exposes living things to high levels of chemical toxicity, environmental pollution, and the emergence of pathogen resistance (Singh, 2017; Stamenković et al., 2018). To reduce chemical use and disease effects, the best alternative option is to use biological control agents like *Paenibacillus* spp. When their genes or metabolites lower plant pathogen populations, *Paenibacillus* species dramatically inhibit the growth of plant pathogenic fungi and enhance overall plant health (Heydari and Pessarakli, 2010; Soni et al., 2021). Recent studies have demonstrated that *Paenibacillus* spp. can treat a variety of common plant diseases, including Fusarium crown, root rot, Fusarium wilt, bacterial leaf blight, and others (Abdallah et al., 2018; Xu and Kim, 2014; Zhang et al., 2021). Indirectly, *Paenibacillus* sp. inhibits or lyses phytopathogen growth by secreting antimicrobial substances and hydrolytic enzymes. Direct effects include synthesis of plant hormones, phosphate dissolution, and nitrogen fixation. Consequently, *Paenibacillus* species represent potential agricultural biotechnological applications (Grady et al., 2016; Soni et al., 2021; Weselowski et al., 2016).

***Paenibacillus* spp.**

The first descriptions of *Paenibacillus* spp is they are genus *Bacillus*, based on physical similarities with the type *B. subtilis* identified in 1872, included *Paenibacillus* species. The phylogenetic tree of these sequences was later divided into at least five distinct clusters, one of which was assigned to the new genus *Paenibacillus* in 1993, according to research by Ash et al. in 1993 (Ash et al., 1993). *Paenibacillus*, meaning "almost a *Bacillus*," is derived from the Latin word paene. Genetic microdiversity is believed to vary among the different Bacillus and *Paenibacillus* species (Gardener, 2004). The general characteristics of *Paenibacillus* sp. are listed in Table 1. (Chow et al., 2012; Grady et al., 2016; Mead et al., 2012; Patowary and Deka, 2020; Yegorenkova et al., 2018). Due to their physiological properties and capacity to produce a variety of enzymes, antibiotics and other metabolites, *Paenibacillus* species are used in numerous medicinal, pharmaceutical, agricultural and industrial activities. They frequently appear in pairs or short chains.

Table 1. The general characteristics of *Paenibacillus* spp.

Properties	Terms
Current Classification	Domain: Bacteria
	Phylum: Firmicutes
	Class: Bacilli
	Order: Bacillales
	Family: Paenibacillaceae
	Genus: *Paenibacillus*
Motility	Motile
Oxygen Requirement	Facultative anaerobe

Paenibacillus spp. are Gram-positive, aerobic, endospore-forming bacteria (Figure 1). The colony morphology of *Paenibacillus* spp. is punctate with entire margins compared to Bacillus spp. which have irregular and large colonies (Badaluddin et al., 2019). Moreover, *Paenibacillus* spp. can grow well at 2.5%, 5.0%, 7.5% and 12.5% (Badaluddin et al., 2019). *Paenibacillus* spp. is more tolerant to salt stress compared to *Bacillus* spp. (Sukweenadhi et al., 2018). In addition, *Paenibacillus* spp. is able to ferment glucose and hydrolyse starch (Badaluddin et al., 2020). Moreover, the generation time for doubling *Paenibacillus* spp. is 42 minutes (Figure 2). The generation time is the time it takes for a bacterial population to double in size. When you start with a bacterium, it divides after each generation.

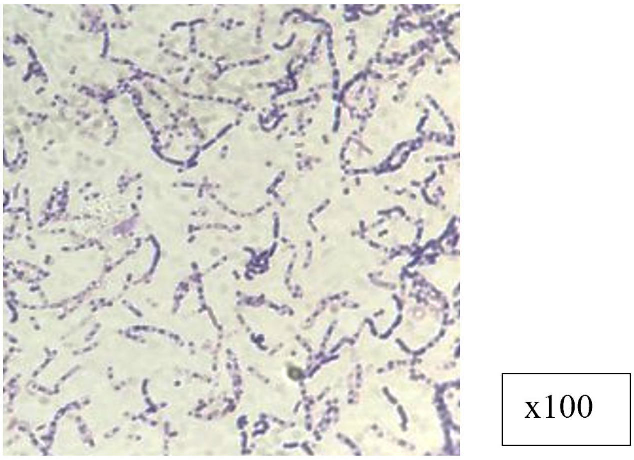

Fig. 1. Gram staining of bacteria. The result showed that the bacteria are Gram positive, rod-shaped, and endospore-forming bacteria

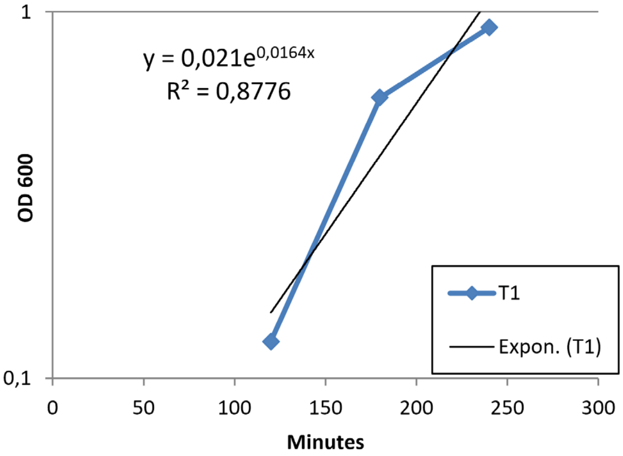

Fig. 2. Exponential growth graph of *Paenibacillus* spp.

Paenibacillus spp. creates enzymes and peptides, it can control plant diseases and insect pests (Govindasamy et al., 2008; Govindasamy et al., 2010). According to Akram et al. (2016), the *Paenibacillus* spp. antagonistic activity prevents fungal infections in plants by controlling the mycelial growth of fungi. Without having lasting effects on other bacterial populations, *Paenibacillus* spp. can successfully establish populations in the soil and root rhizosphere (Chowdhury et al., 2015). *Paenibacillus* spp. deform the hyphae of the fungi by attaching to the cell walls of the mycelium, and various enzymes such as chitosanase, protease, cellulose, and glucanase of the bacteria crack, resulting in the altered cell structure of the pathogenic fungi and functioning through vacuolization and protoplast leakage (Han et al., 2015; Narendra-Babu et al., 2015; Radhakrishnan et al., 2017). By creating a biofilm in the rhizosphere around roots, *Paenibacillus* species defend plants from diseases (Rybakova et al., 2016; Timmusk et al., 2005; 2011). *Paenibacillus* species can also create antimicrobial lipopeptides such iturins, surfactins, and fengyins that interact with the cell membrane and change its permeability and structure (Fira et al., 2018; Ongena and Jaques, 2008).

According to studies, *Paenibacillus* species can create the plant hormone auxin, dissolve inorganic phosphorus, and fix atmospheric nitrogen, making them effective plant growth boosters (Berg, 2009; Jaroszuk-Ścisel et al., 2019; Lal and Tabacchioni 2009; Rybakova et al., 2016). Additionally, it fosters plant growth by dissolving inorganic substances like phosphorus or nitrogen and generating soluble and volatile metabolites (Rybakova et al., 2016). Shurigin et al. (2022) reported that *B. toyonensis* HAPH8, showed high plant growth promoter properties such as nitrogen fixation, phosphate solubilization, production of IAA, and high plant stimulatory activity. *Paenibacillus polymyxa* has been reported to stimulate growth in crested wheatgrass by producing plant growth stimulating compounds with comparable efficacy to IAA (Holl et al., 1988; Lal and Tabacchioni., 2009).

Paenibacillus spp. as a biocontrol agent of plant diseases

The use of traditional chemical fertilisers and pesticides in agriculture is currently being replaced with sustainable, ecologically friendly biofertilizers and biological insecticides. Biological control agents (BCAs) are any natural, efficient strains of any microbe or altered organism that lessen the frequency or severity of diseases brought on by plant pathogens. Chemical pesticides have historically been used to control illness, but up until recently, chemical pesticides have mostly been employed to control soil-borne diseases (Siroli et al., 2015; Wang et al., 2018a). This is a result of growing worries about the environmental issues these chemicals may bring about, including long-term chemical use, environmental pollution, outbreaks of plant pathogens that are resistant to these chemicals, rising production costs as a result of excessive spending on these chemicals, and even human toxicity (Bazioli et al., 2019).

Researchers are continually looking for effective and novel biological control agents due to the requirement to control a wide range of diseases in a variety of crops grown under various environmental circumstances (Passera et al., 2016). The BCAs must, however, also have a strong ability to control illness in their host (Bashan et al., 2013). BCAs' technical characteristics include simplicity in formulation, propensity for colonisation, endurance in agricultural settings, and non-pathogenicity to species other than their intended targets. Potential technologies to reduce vegetable losses have emerged recently, including biological control methods that are more advanced, cost-effective, and kinder than other control techniques (Oulghazi et al., 2021). *Paenibacillus* species have applications in agriculture as phytostimulants, biofertilizers, and bioagents (Zhao et al., 2022). Furthermore, the crucial function that volatile molecules play in signalling and direct biocontrol of infections has been highlighted by current studies on the mechanisms by which bacteria interact with plant hosts and illnesses (Sharifi and Ryu, 2016).

Paenibacillus spp. use a variety of mechanisms to suppress phytopathogens. Some of the activities attributed to biocontrol agents to prevent plant diseases include the synthesis of secondary metabolites, root colonisation, the formation of biofilms, and the activation of induced systemic resistance (Jiang et al., 2022; Zhao et al., 2022). These indirect and direct mechanisms can function effectively during the biocontrol process depending on the *Paenibacillus* strain, target pathogen, crop, and environmental factors like pH, temperature, salinity, and nutrient availability. There are interactions that are species- and even strain-specific, despite the fact that they have generally similar effects on crop plants. In vitro and in the field, *Paenibacillus* species have been shown to be antagonistic to a number of phytopathogenic fungi (Grady et al., 2016).

It is known that *Paenibacillus* spp. can produce a wide range of bioactive substances, including polyketides, peptides produced by ribosomes, and non-ribosomally synthesised lipopeptides (LPs) (Cochrane et al., 2015). The antibacterial properties of LPs have been described as being particularly effective against phytopathogens like pelgipeptin, iturins, surfactins, fusaricidins, fengycins, polymyxins, and polypeptins (Cochrane et al., 2015; Jiang et al., 2022). LPs are manufacture by many bacteria, particularly those from the genera *Bacillus* and *Paenibacillus* (Grady et al., 2016). Secondary metabolites known as bacterial lipopeptides are frequently created by non-ribosomal peptide synthetase. They frequently exhibit a wide range of antibacterial activities (Zhao et al., 2022). Fusaricidins exhibit remarkable antifungal action in vitro against a variety of plant pathogenic fungus, including Fusarium spp. (Tjamos et al., 2005). Fusaricidin's antifungal activity is dependent on the penetration and destruction of cell membranes (Li and Chen, 2019). Additionally, fusaricidin can increase systemic resistance to Fusarium species through salicylic acid signal transduction (SA). According to Li and Chen (2019), a biocontrol experiment has shown that fusaricidin has a significant role in controlling Fusarium wilt by developing systemic resistance to Fusarium wilt in cucumber (Figure 3). Fusaridins are generated by *Paenibacillus polymyxa* WLY78. Secondary metabolites called pelgipeptins (A-D) exert antibacterial and antifungal effects on a variety of soilborne pathogens, including *Fusarium graminearum* and *Rhizoctonia solani* (Jiang et al., 2022; Kim et al., 2019; Qian et al., 2012).

Additionally, *Paenibacillus* species produce antimicrobial proteins, the majority of which are ribosome-produced

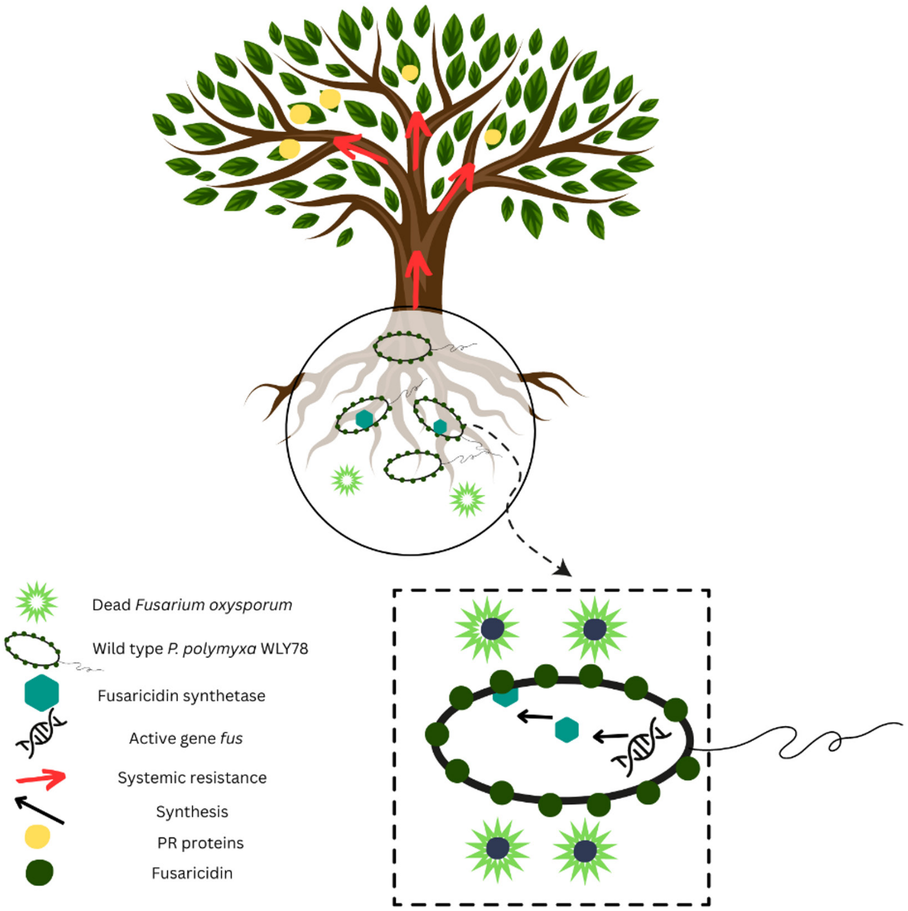

Fig. 3. The mechanism of *P. polymyxa* WLY78 suppresses Fusarium wilt of cucumber. *P. polymyxa* WLY78 produces fusaricidins that directly inhibit *F. oxysporum* f. sp. *cucumerium* and induce systemic resistance of plants to cucumber wilt (Li and Chen, 2019)

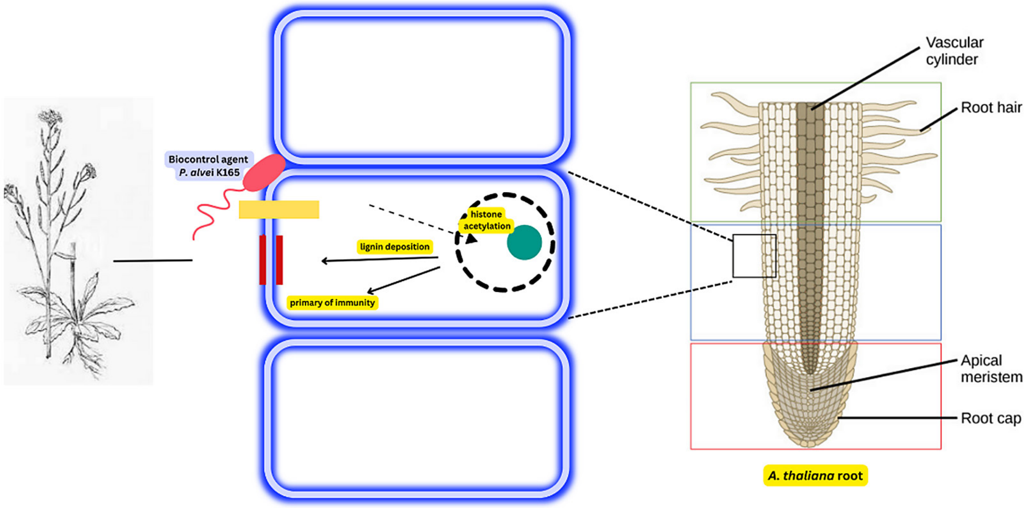

Fig. 4. Model showing the proposed function of *Paenibacillus alvei* K165-mediated plant protection (Gziki et al., 2021)

enzymes that break down cell walls, including chitinase, gelatinase, iron-chelating sidereophore, and β-1,3-glucanase (Nguyen et al., 2013; Wen et al., 2011). Most plant pathogenic fungi have cell walls that can be dissolved by β-1,3-glucanase, which stops the formation of hyphae. The three main enzymes involved in the metabolism of β-1,3-glucan are endo-β-1,3-glucanase, exo-β-1,3-glucanase, and β-1,3-glycosyltransferase (Paulus and Gray, 1964). β-1,3-glucanase caused the pathogen's cell walls to rupture and stopped Fusarium spp. from growing (Wang et al., 2018a). The precise method by which fusaricidin or β-1,3-glucanase or even both can stop the growth of pathogenic fungi's hyphae and spores is unknown. Plant health is promoted, insect pest numbers are decreased, and microbial diseases are controlled with chitin-based BCA bioformulations (Hidangmayum et al., 2019; Kamil et al., 2018). Formulations with chitin activate a plant's natural defences against pathogens such as root knotweed, damping-off infections, and nematode-caused soil illnesses (Ha et al., 2014; Rajkumar et al., 2008; Sharp, 2013). Another mechanism is transgenerational immunological resistance, where lignin and histone acetyltransferases are secreted to suppress fungal infections. In this study, the authors demonstrated that *Paenibacillus alvei* K165 produced histone acetylation, which also regulates immunological priming and lignin assembly and mediates biocontrol action and the establishment of hereditary immune resistance to *V. dahlia* (Figure 4). (Gkizi et al., 2021).

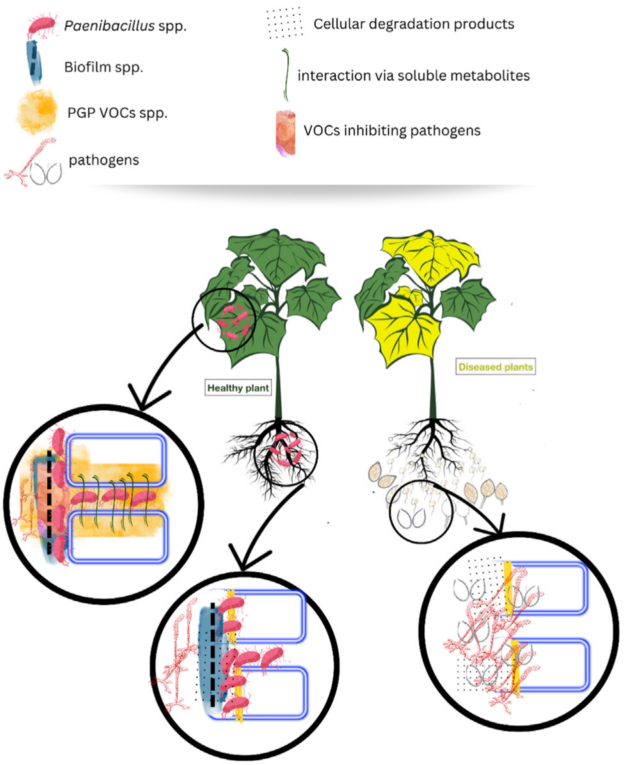

Fig. 5. The mechanism of *Paenibacillus* spp. to reduce pathogens. (A) The image in a illustrates how the interaction with *Paenibacillus* spp. improves plant health. (B) How a plant can be exposed to attacks by pathogens in the absence of *Paenibacillus* spp. and/or other beneficial endophytic bacteria (Rybakova et al., 2016)

Additionally, *Paenibacillus* species require efficient colonisation in order to carry out their biocontrol role. For instance, environmental factors and root exudates can affect *Paenibacillus* sp. colonisation. Additionally, the plant can draw in beneficial rhizobacteria by secreting metabolites, and a crucial inducible chemical released by the root specifically stimulates rhizobacteria's chemotactic motility (Jiang et al., 2022). However, one of the ways that the *Paenibacillus* species protect plants from illness is by creating a biofilm around the roots (Timmusk et al., 2005). *P. polymyxa* is one of the finest biofilm formers in the rhizosphere, and Timmusk et al. (2011) claim that it can even create root biofilms of some species when they grow naturally. By creating a biofilm around roots that shields root tissue from infection, boosting systemic resistance, and reducing pathogen development through soluble and volatile chemicals that enhance plant health, *Paenibacillus* spp. restrict pathogen growth. Therefore, a plant may be vulnerable to pathogen attack in the absence of *Paenibacillus* spp. and/or other beneficial endophytic bacteria, as you can see in Figure 5. In order to successfully colonise the rhizosphere, *Paenibacillus* spp. formed biofilms.

According to studies by Berg (2009), *Paenibacillus* spp. are potential plant growth promoting bacteria (PGPBs) and/or biological control agents (BCAs) of plant diseases. Several *Paenibacillus*-based products have received patents and have been released as commercial BCAs (Table 2). In term of products, only few of the various bacteria developed in recent years as rhizobacteria that promote plant development have been commercialised and used in practise (Regnault-Roger, 2012). In recent years, a variety of species in the genus *Paenibacillus* have been presented as the most effective BCAs and PGPR that attracted the interest of researchers (Anand et al., 2013). Several BCAs are being developed as alternatives to fungicides, although most of them are not sufficiently effective in the field. For this reason, the adoption of BCAs by farmers is limited by inconsistent performance and poor efficacy (Le Mire et al., 2016), and new reliable and stable biological control methods are urgently needed to meet farmers' demands (Parnell et al., 2016). According to recent studies, metabolites and additives should be included in next-generation formulations to increase durability and efficacy and act on a wider variety of targets (Arora and Mishra, 2016).

Due to their antagonistic behaviour toward phytopathogens, 90% of the various *Paenibacillus* strains are utilised to manage plant diseases in crops. Input costs and crop yield are compared to the outcomes of using BCAs in the field. It was discovered that the usage of BCAs, as opposed to syn-

Table 2. Commercial *Paenibacillus*-based products

Patent name (number)	Year	Strain	Target pathogen/diseases	Target plant
Paenibacillus alvei Strain TS-15 and Its Use in Controlling Pathogenic Organisms (WO2012166392A1)	2012	*Paenibacillus Alvei* TS-15	*Clavibacter michiganensis* pv. *michiganensis*, *Pseudomonas syringae* pv. tomato, *Xanthomonas capesiris* pv. *vesicatoria*, *Ralstonia solanacearum*, or *Erwinia carotovora.*	Tomato, pepper plant, pepper, cantaloupe, leafy greens, or other fruits
Paenibacillus alvei and its applications (CN 103205372 A)	2012	*Paenibacillus alvei* ZJUB2011-1	*Fusarium oxysporum*	stigma croci bulb rot
Paenibacillus terrae biological agent and application thereof in agriculture (CN 103141517 A)	2013	*Paenibacillus terrae* NK3-4	*Fusarium oxysporum*	fungal soil-borne diseases, soybean seedling root rot disease
Paenibacillus polymyxa strain and application thereof (CN111548976B)	2020	*Paenibacillus polymyxa* LQ1	preventing and treating soil-borne diseases, airborne diseases, controlling cucumber gray mold	cucumber
Paenibacillus polymyxa DYr4.4 with broad-spectrum antibacterial activity and preparation method and application thereof (CN108148793B)	2020	*Paenibacillus polymyxa* DYr4.4	*Gymnosporangium haraeanum Sydow II*	Chinese pear

thetic agents, results in lower input costs and crop production (Masso et al., 2016). However, modern farmers utilise an excessive number of chemical pesticides and synthetic fertilisers, which although less expensive, do not increase crop yields. As a result, farmers experience financial losses when input costs and crop yield are out of balance (Zin and Badaluddin, 2020). In addition to lowering crop losses, *Paenibacillus* species also boost yields, which raises profits.

Numerous researches, some of which are given in Table 3, have reported on the effectiveness of *Paenibacillus* spp. in reducing plant diseases. This is in line with the findings of Gkikas et al. (2021), who found that *P. alvei* K165 reduced the xylem discolouration caused by *Phaeomoniella chlamydospora* (Pch) infection on grapevines when compared to controls. The creation of poisonous compounds against Pch in the soil is the defence mechanism *P. alvei* K165, with elements including oxygen availability, temperature, and iron availability influencing microbial development of antibiotics. The findings of Gziki et al. (2021), which demonstrated that *P. alvei* K65 can lessen fruit reduction, necrosis, vascular colouring of stems and flowers, leaf wilt, and chlorosis in *Arabidopsis thaliana*, are likewise in line with our study. The predeposition of lignin in *P. alvei* K165 can stop *Verticillium dahlia* and its toxins or effectors from spreading in tissues. Vascular plants have a substantial quantity of lignin in their cell walls, which acts as their first line of defence against invasive pathogens (Sattler and Harris, 2013). Lignification is essential for enhancing the cell wall's resistance to enzymes that break down the cell wall (Gkikas et al., 2021). It is believed that lignin is a crucial barrier that *V. dahlia* must get through in order to infect a plant (Gziki et al., 2021). An earlier study found a favourable correlation between rising lignin content and cotton's level of *V. dahlia* resistance. The build-up of lignin in the cell walls restricts *V. dahliae* colonisation in pepper (Novo et al., 2017). According to a number of pieces of data, lignin concentrations also have a role in the biocontrol action of K165 and the development of hereditary resistance to *V. dahlia*. Their precise function is uncertain, though.

According to this study, *P. peoriae* HJ-2 may be used as a possible BCA to prevent stem rot on *P. polyphylla* (Jiang et al., 2022). According to genome study, the HJ-2 genome has around 70 genes, including 12 potential gene clusters linked to secondary metabolites that have been previously characterised as being involved in chemotaxis motility, biofilm formation, growth stimulation, antifungal activity, and inducing systemic response (ISR). Plant growth-promoting rhizobacteria (PGPR) may effectively colonise both the root and the leaf of plants, according to the ISR mechanism. Therefore, *P. peoriae* HJ-2 might activate ISR and quicken plant pathogen defences (Jiang et al., 2022).

Du et al. (2017) demonstrated that pre-treating plants with *P. polymyxa* NSY50 can produce stronger, disease-resistant plants, which lends credence to this work. In pot studies where *Fusarium oxysporum* was used to cause cucumber wilt, *P. polymyxa* NSY50 shown a potent capacity to lessen the severity of the disease. Although it is unknown how these putative BCAs work, *P. polymyxa* can generate protease, cellulose, ACC deaminase activity, and indoleacetic acid (IAA). However, the bacterium's capacity to create the enzymes

Table 3. The efficacy of *Paenibacillus* spp. in controlling plant diseases

Biological control agents (BCAs)	Name of diseases	Causal Agent	Host	References
Paenibacillus peoriae	Crown and root rot	Pythium fungi	Cereal	Araujo et al., 2019
Paenibacillus polymyxa N179	Fire blight	*Erwinia amylovora*	Pear	Fallahzadeh-Mamaghaniey al., 2021
Paenibacillus Alvei K165	leaf flaccidity, chlorosis, stunting, vascular	*Verticillium dahliae*	*Arabidopsis thaliana*	Gkizi et al., 2021
	Grapevine truck disease	*Phaeomoniella chlamydospora*	Grapevine	Gkikas et al.,2021
Paenibacillus elgii HOA73	Graymold	*Botrytis cinerea*	Tomato	Kim et al., 2019
Paenibacillus polymyxa WLY78	Fusarium wilt	*Fusarium oxysporum* f. sp. *cucumerinum*	Cucumber	Li and Chen, 2019
Paenibacillus peoriae ZF390	Bacterial soft rot	*Pectobacterium brasiliense*	Cucumber	Zhao et al., 2022
Paenibacillus peoriae HJ2	Stem rot	*Fusarium concentricum*	Herbs	Jiang et al., 2022
P. polymyxa NSY50	Cucumber wilt	*Fusarium oxysporum*	Cucumber	Du et al., 2017

cellulase and protease may allow it to suppress some harmful fungus. *Paenibacillus* spp. biocontrol strains' protease was essential for mycoparasitism and the breakdown of the pathogen's cell wall (Geremia et al., 1993). Furthermore, the protease decreased the disease's severity on bean leaf surfaces by 56 to 100%. (Elad and Kapat, 1999). The development of systemic resistance, management of the rhizosphere's microbial population, enhancement of metabolism, and activation of defense-related proteins may all have an impact on the effectiveness of biological control against the illness in this setting (Du et al., 2016; Shi et al., 2017).

P. polymyxa WLY78 has a lot of potential as a biological pest control agent for agriculture. Li and Chen (2019) showed that *P. polymyxa* WLY78 can fix nitrogen and produce fusaricidin. Fusaricidins are a class of cyclic lipopeptide antibiotics produced by *P. polymyxa*. They include both a guanidinylated-hydroxy fatty acid (GHPD) and a six-amino acid cyclic polypeptide (CP) (Kuroda et al., 2001). We suggested a mechanism of action for the fusaricidin of *P. polymyxa* WLY78 to prevent Fusarium wilt in cucumber based on recent findings and prior studies. Fusaricidins damage hyphal tips, directly impede the germination of *F. oxysporum* f. sp. *cucumerium* spores, and promote systemic resistance in the plant by activating the signal SA in the cucumber rhizosphere (Li and Chen, 2019),

P. jamilae HS-26 considerably enhanced plant biometric indices and suppressed the growth of mycelial fungus, as evidenced by the suppression of *Fusarium oxysporum* (46.30%), *Bipolaris sorokiniana* (63.86%), and *Rhizoctonia solani* (44.00%) in in vitro studies and pot tests (Wang et al., 2019). Additionally, *P. jamilae* HS-26 has the ability to produce hydrolases and antibacterial metabolites that, when in contact with the fungus, attack the cell wall directly and halt normal radial growth (Wang et al., 2018b; Watanabe et al., 2001). Additionally, advantageous bacteria have the capacity to produce volatile organic compounds (VOCs) and extracellular antifungal metabolites that aid in reducing plant pathogen proliferation and spore germination (Fernando and Linderman, 2012; Yuan et al., 2012). VOCs can travel great distances and improve the hostile population's antifungal microenvironment. Therefore, it is more probable that microbial antagonist strains that can produce volatile chemicals with substantial inhibitory effect against plant pathogens will prevent plant infection by pathogenic fungi, eliminate surviving spores in the soil, and restrict the spread of the illness (Kilic-Ekici and Yuen, 2003; Wang et al., 2019).

In addition, a prior study found that *P. elgii* HOA73 bacterial cultures cultivated on chitin-based minimum medium would be a successful formulation for the integrated control of tomato grey mould (Kim et al., 2019) (Table 3). At this early stage of growth, three foliar sprays of the entire cell-containing, 10-day-fermented culture sprayed at 10-day intervals dramatically decreased the incidence of tomato grey mould to a level comparable to that seen with fungicide treatment. Chitinase, protease, lipase, and siderophores may all be secreted by *P. elgii* HOA73 into the supernatant. According to the previous study, every enzyme found in *P. elgii* HOA73's supernatant is responsible for fighting off several pathogenic fungi (Al-Askar et al., 2015; Kim et al., 2017; Saha et al., 2016). However, tomato grey mould was suppressed when *P. elgii* HOA73 was isolated on chitin-based minimum media. Additionally, in the tomato, chitosan successfully reduced postharvest ailments such as *Alternaria alternata*- caused black rot, *B. cinerea*- caused grey mould, and *Penicillium expansum*- caused blue mould (Liu et al., 2007; Reddy et al., 2000). The activities of the cell membrane are impacted by chitosan, which thus prevents the creation of nucleic acids and proteins (Palma-Guerrero et al., 2010; Verlee et al., 2017).

Paenibacillus spp. as plant growth promoter reagent

Rhizobacteria that promote plant growth (PGPR) are the microorganisms that can do this. Generally speaking, plant growth, ultimate crop quality, and productivity are the key benefits of this PGPF (Hyakumachi and Kubota, 2003). *Paenibacillus* species can make a good PGPR, according to recent investigations. The majority of research indicate that *Paenibacillus* species enhance plant health in general by creating favourable circumstances and a considerable secondary synthesis of the metabolites listed in Table 4. *Paenibacillus* spp. are located in the rhizosphere and help to increase soil productivity, promote plant growth, and manage plant diseases, PGPRs are essential for organic agriculture (Pathania et al., 2020). PGPR are offered in the form of biofertilizers, or microbial formulations. Biofertilizers can be injected into a plant's rhizosphere or sprayed directly onto seeds, where they colonise and enhance host plant nutrition (Malusá, and Vassilev, 2014). They provide global agricultural output that is sustainable, and they are a secure alternative to conventional chemical fertilisers (Vejan et al., 2016). When biofertilizers are used, plants grow better overall, including in terms of seed germination, shoot and root development, biomass production, and disease incidence (Dal-Cortivo et al., 2020).

Additionally, the majority of PGPR strains may emit indole-3-acetic acid (IAA). Natural auxins such as IAA are created by PGPRs and plants. Up to 80% of auxin-producing rhizobacteria that colonise the seeds or roots of different plants may create IAA. IAA mediates a plant's response to light and gravity, regulates vegetative growth, initiates root development, influences pigment formation, affects photosynthesis, affects the biosynthesis of several metabolites, and affects a plant's capacity to withstand environmental stresses (Spaepen and Vanderleyden, 2011). IAA, a hormone, has the important additional benefit of strengthening the root system, which enables the plant to absorb more nutrients and hasten development (Park et al., 2005). Additionally, the cooperation of IAA and ACC deaminase can aid in the promotion of plant growth, particularly root elongation (Glick 2014; Noreen et al., 2012).

In a number of direct and indirect methods, PGPRs speed up plant development (Figure 6). (Tiwari et al., 2019). Antibiosis, competition for resources and space in the rhizosphere, and biocontrol by host defence mechanism activation (ISR) are examples of indirect stimulation (Pathania et al., 2020). By increasing the availability of nutrients by procedures like nitrogen fixation, phosphorus solubilization, and iron absorption or by changing the quantities of plant hormones like cytokinins, auxins, and ethylene, growth is stimulated directly.

Figure 6.

One possibility consists on the classification of the bacteria according to its function: biofertilizer, biostimulator or biocontrol. Biofertilizers are mixtures of living microorganisms that when applied to seeds, plants or soil, promote the increase of nutrient supply, such as NH_4, SO_4^{2-} or PO_4^{3-} (Figure 7) (Ferreira et al., 2019). A microorganism that can produce phytohormones such as auxins and cytokinins are called a biostimulant (substance that promotes cell division). A biocontrol microorganism is a microorganism that promotes plant development by reducing the number of harmful organisms, for example, by producing antibiotics, hydrocyanic acid (HCN), or enzymes that can hydrolyze fungal cell walls (Bhattacharyya and Jha, 2012).

Figure 7.

One of the direct mechanisms through which PGPR benefits plants is nitrogen fixation. Nitrogen is a necessary ingredient that is critical to plant production and growth. Even

Table 4. The efficacy of *Paenibacillus* spp. as PGPRs in various plant

Plant Growth Promoter Rhizobacteria (PGPR)	Benefits	Host	References
P. beporiae SG09-01	– Increase in fresh shoot weight – Increase stem length	Tomato	Xu & Kim, 2014
P. polymyxa SX3	– Produce IAA (42.64 µg/l^{-1} – Able to solubilize calcium phosphate, nitrogen fixation – Promoted the emergence of rice seedlings.	Rice	Abdallah et al., 2019
P. polymyxa	-Increase in shoot length, fresh weight, and germination index	Maize	Din et al., 2019
P. polymyxa BFKC01	– Enhances plant iron absorption via improved root systems – Activated iron acquisition mechanisms	*Arabidopsis thaliana*	Zhou et al., 2016
P. jamilae	– Increased seeds germination	Cucumber	Wang et al., 2019
P. jamilae	– Increase dry wheat weight and fresh weight	Wheat	Wang et al., 2019
P. polymyxa 1465	– Increase total root and shoot length – Increase total root and shoot weight	Wheat	Yegorenkova et al., 2016

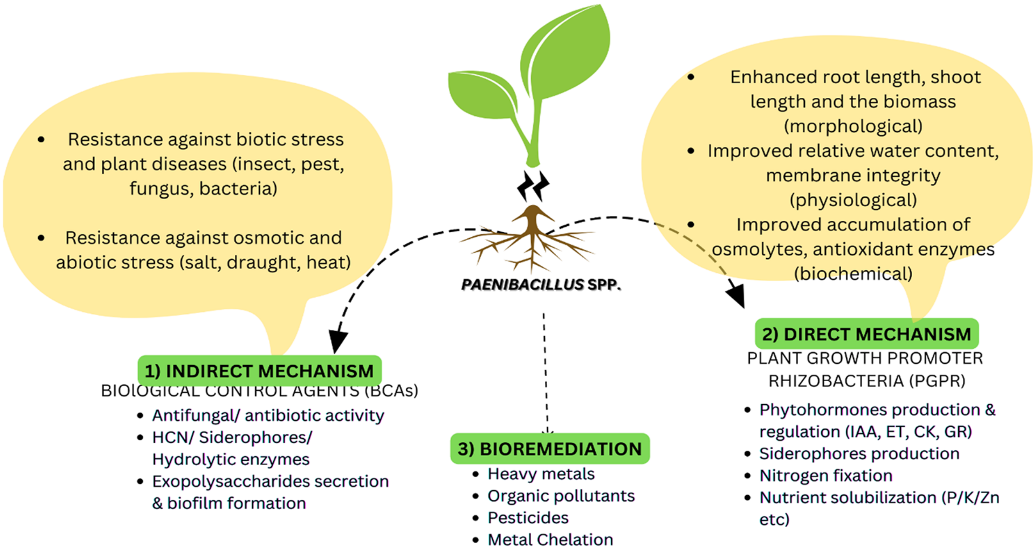

Fig. 6. A schematic representation of mechanism of plant growth promotion by *Bacillus* sp. and *Paenibacillus* sp. (Tiwari et al., 2019)

though there is 78 percent of nitrogen in the atmosphere, plants cannot use it as a nutrition. In order to make air nitrogen available to plants, soil microbes convert it. Numerous PGPR strains can fix atmospheric nitrogen and provide it to the plants through both symbiotic and nonsymbiotic relationships (Govindasamy et al., 2010; Yousuf et al., 2017). Rhizospheric inoculation of these nitrogen fixers has benefited several cereals, legume, crop, and vegetable species (Hao and Chen, 2017; Rosenblueth et al., 2018). In maize, rice, and wheat, non-symbiotic nitrogen fixation accounted for up to 24 percent of the total nitrogen, according to Ladha et al. (2016), who carried out a 50-year review.

Solubilization of phosphate is another direct process by which PGPR improve plant health. Plant development is hin-

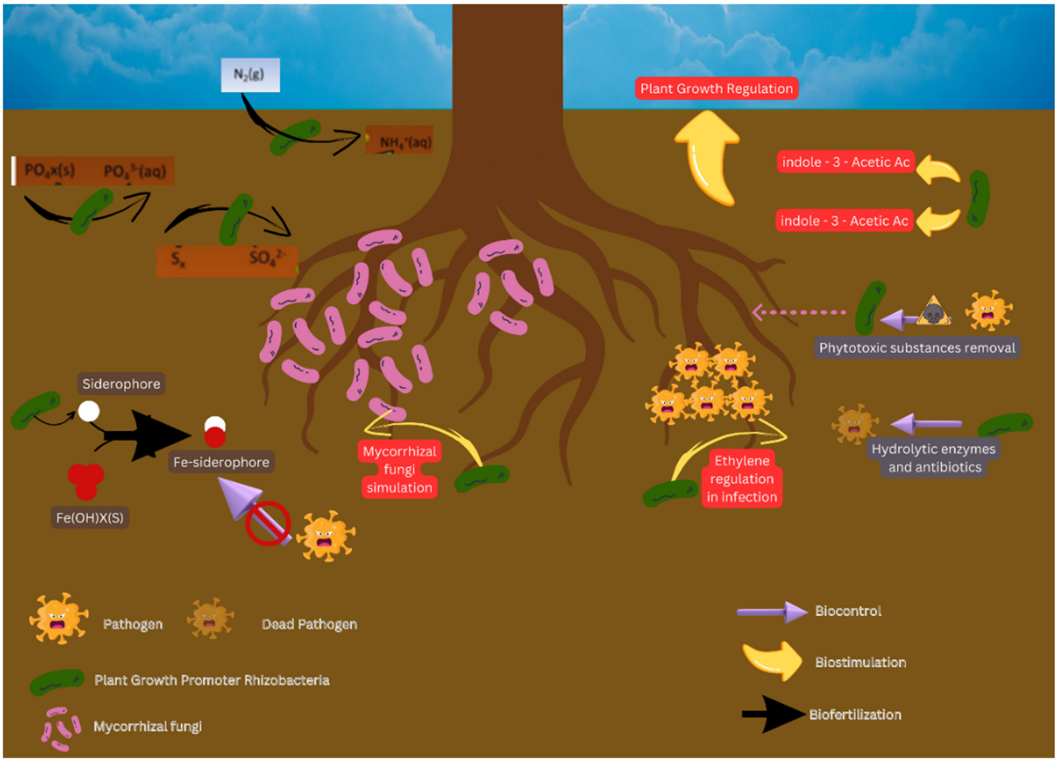

Fig. 7. Mechanisms of action of plant growth promoting bacteria in the rhizosphere (Ferreria et al., 2019)

dered because most of the phosphorus in the soil is in an insoluble form that plants cannot take up directly. Therefore, a key feature of PGPR is the solubilization and mineralization of phosphorus by phosphate-solubilizing bacteria (Tandon et al., 2020). This requires a series of chemical processes, such as the release of organic acids to dissolve the mineral complexes (a process called mineralization), followed by the production of phosphatases to break down the insoluble phosphates (a process called solubilization) (Ku et al., 2018). Quantification of phosphate solubilization by Kumari and Thakur (2018) showed that *Paenibacillus polymyxa* produced 4.78 µg/ml of soluble phosphate in the broth. Overall, the effect of phosphate solubilizing microorganisms on mobilisation and phosphorus availability in plant development was found to be successful.

A plant requires potassium for several enzymes involved in numerous plant functions, including nitrate reduction, photosynthesis, and starch production (Gallegos-Cedillo et al., 2016). Potassium, like phosphorus, is deposited in an insoluble state. PGPR are capable of releasing a variety of organic acids that convert the insoluble potassium to a soluble form. *Paenibacillus* spp. are potassium solubilizing PGPR where it can improve 35% fruit yield of pomegranate (Varsha and Singar, 2020; Xiao et al., 2017). Similarly, Chen et al. (2020) also reported improved growth of apple seedlings upon inoculations of *Paenibacillus mucilaginosus.*

Secondly, siderophores are crucial for plant development. Small molecular iron chelators called siderophores are produced by microbes, and their main job is to sequester iron (Fe2+) from the host, make iron more mobile and available, move it across plant cell membranes, and give microbes this vital metal nutrient (Behnsen and Raffatellu, 2016; Kumar et al., 2018). According to earlier research, siderophores produced by *Bacillus* sp. and *Paenibacillus* sp. contribute to improving Fe absorption. For instance, *P. polymyxa* P2b-2R has various PGP features, such as the generation of siderophores, and is known to encourage the overall development of maize plants (Padda et al., 2017). Although siderophore's main purpose is to give plants soluble iron for development, they are also known to form stable complexes with other metal atoms, including Al, Pb, Cd, Cu, Zn, and others (Torres-Cruz et al., 2018). They can also remove heavy metals like cadmium (Cd). This leads to the conclusion that the synthesis of siderophores benefits plants through direct mechanisms such as nutrient (Fe) absorption and indirect mechanisms such as metal remediation and biocontrol activities.

Auxins, ethylene, and cytokinins are phytohormones that regulate and simulate numerous aspects of plant growth, including cell division and growth, cell elongation and differentiation, and a range of physiological responses (Jiang et al., 2022). By affecting plant structure, blooming and senescence timing, and seed development, they actively control plant growth. Additionally, they affect a number of physiological and cellular functions in plants, including gene expression, cell division, cell growth, and stress response. The density and length of the root hairs are stimulated by phytohormones generated by PGPRs, increasing the plant's overall root surface area (Tsegaye et al., 2017). This improves its capacity to absorb nutrients and water. Phytohormones, which are known to be generated in very small amounts by fungi and bacteria in addition to plants (Pathania et al., 2020).

According to Han et al. (2018), phytohormones may be divided into five classes: auxins, gibberellins, cytokinins, ethylene, and abscisic acid. But according to earlier research, only auxins, cytokinins, and ethylene are produced by PGPR strains. The most prevalent auxin is indole-3-acetic acid (IAA), which influences pigment formation, photosynthesis, the biosynthesis of various metabolites, and plant tolerance to various environmental stresses. IAA also stimulates seed and tuber germination, regulates vegetative growth, starts root development, mediates reaction to light and gravity, and influences root development (Spaepen and Vanderleyden, 2011).

Ethylene is a further crucial plant growth regulator that regulates the development of roots, leaves, flowers, and fruits in addition to the interaction of roots with microbes (Dubois et al., 2018; Gamalero and Glick, 2011). Ethylene may influence a plant's general growth in a variety of ways, including by promoting fruit ripening, root initiation, and inhibiting root elongation. It can also stimulate the synthesis of other plant hormones. In response to different biotic or abiotic stressors such as pathogenicity, heavy metals, waterlogging, and soil salinity, ethylene is produced.

Paenibacillus species, which are shown in Table 4, have been used successfully in several investigations as PGPR. According to reports, *P. polymyxa* produces chemicals that are as effective as IAA at promoting plant development in crested wheatgrass (Holl et al., 1988; Lal and Tabacchioni., 2009). This is in line with the findings of Xu and Kim (2014), who used several *Paenibacillus* strains to enhance the weight of tomato shoots and the length of roots and stems. These findings demonstrated the ability of *Paenibacillus* species to synthesise phytohormones like IAA. Then, *Paenibacillus* spp. may also convert insoluble organic phosphate to soluble phosphate. *Paenibacillus* spp. have diverse metabolites that can indirectly encourage plant development and enhance plant health and wellbeing.

Next, *P. polymyxa* Sx3 can promote rice growth in China (Abdallah et al., 2019). In this study, the *P. polymyxa* Sx3 significantly promotes rice seedlings' emergence and growth, producing a siderophore and amylase. Moreover, *P. polymyxa* Sx3 can produce 42.654 μg^{-1} of IAA after 24 hours of incubation and increase in shoot height, root length, fresh weight, and dry weight compared to control plants without inoculation (Abdallah et al., 2019). Consistent with these results, the production of IAA and the capability of phosphate solubilization and nitrogen fixation is a vital mechanism of *Paenibacillus* spp.

In addition, the study by Din et al. (2018) showed that *P. polymyxa* can increase significantly in all growth promoter properties from control in maize seedlings. This is might be due to the utilization of released phosphate by phosphate-solubilizing bacteria (PSB). The mechanism of PSB, such as *P. polymyxa*, modulating plant hormones such as IAA, indirectly produces inhibitory effects through a siderophore in the form of biocontrol agents.

This is also supported by Breedt et al. (2017), where the *P. Alvei* can produce IAA. This phytohormone is involved in root initiation, cell division, and cell enlargement. Moreover, *P. Alvei* also tested positive in N-fixation, and phosphate solubilization, which enhances the availability of phosphate by secretion of organic acids. In this study, *P. Alvei* increased maize yield by 3.71 and 3.15 t ha compared to the control. The current study demonstrates the ability of effective microbes' strains to enhance the field's maize yield. Thus, making the development and commercialization of these strains a viable option.

IAA has a significant benefit in that it strengthens the root system, which helps the plant get more nutrients to promote development (Park et al., 2005). Additionally, IAA and ACC deaminase may cooperate to enhance plant development, particularly root elongation (Noreen et al., 2012; Glick, 2014). Rhizobacteria that promote plant growth (PGPRs) are crucial to organic farming. They are present in the rhizosphere and are crucial for boosting soil production, promoting plant development, and controlling plant diseases (Pathania et al., 2020).

***Paenibacillus spp*. as bioremediation of agricultural soil**

Global industrialisation and the widespread use of chemicals including petroleum products, solvents, insecticides, and heavy metals are to blame for soil, water, and air pollution. As a result, public concern about the dangers these contaminated sites represent to both human and environmental health is rising. Due to the accelerated population increase in urban regions and the need for rehabilitation and productive usage, contaminated sites must be cleaned up. Additionally, fast industrialisation, intensive farming, and other unsustainable development practises raise the danger of explosions and degrade ecosystems (soil, water, and air), which can impair soil fertility and structure (Pawelczak et al., 2015). Crop yields decrease as a result, and irrigation systems, economics, public health, and biodiversity all experience further impacts (Mauricio-Gutiérrez et al., 2020; Rawat and Rai, 2019; Ujowundu et al. 2011). However, soil aeration, water permeability, heat transfer and root development are examples of agricultural practises that increase soil organic matter and promote soil structure (Mehmet Tuğrul, 2020).

Bioremediation comes from two words, bios, meaning life, and remediate, meaning to decipher a problem (Gomathi et al., 2020). The scientific world can boast that science is behind many of the most important events in human history. Bioremediation is one of the remediation techniques. A subfield of biotechnology called "bioremediation" employs microbial and bacterial communities to clean up contaminated environments. It is applied to clean up contaminated areas including water, soil, and other habitats. Bioremediation, which employs living organisms, typically microorganisms (bacteria, fungus, and microalgae), or their processes to breakdown or detoxify environmental toxins, is a less expensive and more ecologically responsible way of decontaminating contaminated soil and water. More and more often, this technology is used in place of more expensive physical-chemical clean-up techniques. Some microorganisms may utilize toxic organic pollutants as sources of carbon, energy, or other nutrients. These microbes include bacteria, microalgae, and cyanobacteria.

The ability of bacteria to survive in contaminated soil or water, the effects of abiotic factors on bacterial growth, the mechanism of metal detoxification, the rate at which metal detoxification genes are expressed, and the effects of contaminants on bacterial activity all have a significant impact on bacterial bioremediation, (Govarthanan et al., 2016). However, bacterial bioremediation is less expensive and less harmful to the environment (Govarthanan et al., 2015; Praburaman et al., 2015; Suja et al., 2014). Nitrogen supply has a considerable influence on bioremediation. It is well known that pH is an important factor in the effectiveness of bioremediation of heavy metals (Singh et al., 2008). The pH value affects the microorganisms, as the ideal pH value varies depending on the species. In addition, pH affects the redox and solubility of heavy metals (Brito et al., 2015; Gomathi et al., 2020). Spontaneous decontamination indicates that organisms have developed the ability to break down organic contaminants (Brito et al., 2015).

These bacteria can be utilised in a bioremediation procedure that is both affordable and adaptable (Gomathi et al., 2020). The biodegradability, solubility, and bioavailability of hydrocarbons to bacteria are therefore connected to the effectiveness of bioremediation, which also offers the optimum testing setting (Ghafari et al., 2019). Numerous Gram-positive microorganisms, including *Bacillus cereus*, *Bacillus subtilis*, *Bacillus* sp., Cellulosimicrobium cellulans, *Corynebacterium* sp., *Gordonia* sp., *Paenibacillus ehimensis*, *Paenibacillus naphthalenovora*, and *Rhodococcus* sp. among others, exhibit basic metabolic capabilities to utilise various chemical constituents of the organic contaminant.

It has been demonstrated that some contaminated pesticides, hydrocarbons, diesel used in agricultural soils, and heavy metals can all be broken down by *Paenibacillus* species (Table 5). Pesticides like mancozeb and carbendazim are used to stop the spread of fungal diseases to crops like rice, fruits, vegetables, and oilseeds (Didwania et al., 2019; Singh and Sharma, 2018). However, the excessive and regular use of these two fungicides is a concern since they kill environmental living things (Tiwari et al., 2016).

Oil is mainly used in agriculture, for example as diesel. Diesel is the main fuel for many farms. It powers tractors and other vehicles, pumps, machinery, and remote-controlled electricity generators (Bakri et al., 2016). In oil palm plantations, diesel consumption for maintenance and servicing is 9.46 litres ha-1. Furthermore, diesel is one of the pollutants commonly found in these agricultural soils because too much diesel is consumed in agricultural operations, resulting in oil leaking into the soil and sewage system. Petroleum spills increase the risk of explosion and pollute ecosystems (soil, water, and air), which can affect soil fertility and structure (Paweczak et al., 2015). As a result, crop yields decline and further changes occur to biodiversity, irrigation systems, the economy, and public health (Ujowundu et al., 2011).

However, according to Mauricio-Gutiérrez et al. (2020), the *Paenibacillus lautus* M1HC27 can degrade 4087 mg L^{-1} (17.03 %) of 24000 mg L^{-1} diesel in 10 days of in-vitro experiment. According to research by Al-Saleh & Obuekwa (2014), *Paenibacillus* spp. is an effective hydrocarbon mineralizing bacteria that can use PAHs such as anthrone, biphenyl, naphthalene, or phenanthrene as its only carbon source to decompose different polychlorinated biphenyls, diesel, and crude oil. Due to the fact that diesel is a hydrocarbon mixture, two processes—the activation of metabolic enzymes and the transfer of alkanes into the bacterial cell—generally favour the biodegradation of n-alkanes (Ghafari et al., 2019). Numerous metabolites, including lipase, hydrolase, and organophosphorus, are produced by *Paenibacillus* species.

A major problem on a global scale is the pollution of soils and rivers by heavy metals. Heavy metals need to be removed from polluted soils and rivers due to their bioconcentration, subsequent biomagnification, and high toxicity to living organisms (Govarthanan et al., 2014). In the study by Govarthanan et al. (2016), it was shown that *Paenibacillus* brasilensis RM was used for resistance to excessive heavy metals such as Zn, Cu, As, and Pb. This is because indole acetic acid (IAA) and other substances that promote plant development are produced by endophytic bacteria that can improve the growth and remediation of habitats polluted with heavy metals (Zhang et al., 2011). *P. brasilensis* was able to produce 17.2 mg/l IAA in this study, while Tiwari et al. (2016) found that endophytic bacteria from the root of Pteris vitata were able to produce 18.5 mg/l IAA, confirming their results. *P. brasilensis* also showed positive results in

Table 5. *Paenibacillus* spp. degraded various polluted pesticides, hydrocarbons, diesel used in agricultural soils, and heavy metals

No	Species	Degradation value	Contaminated	References
1	*Paenibacillus lautus* M1HC27	17.03 %	24000mg L^{-1} Diesel	Mauricio-Gutiérrez et al., 2020
2	*Paenibacillus brasilensis* RM	Cu – 65 %, Pb (40%), Zn (60 %) and As (45 %)	Copper (Cu), Lead (Pb), Zinc (Zn) and Arsenic (As)	Govarthanan et al., 2016
3	*Paenibacillus dendritiformis* SJPS-4	80.72 %	Lindane insecticide	Jaiswal et al., 2022
4	*Paenibacillus polymyxa* + *Azosprilium lipoferum*	85.9 %	Chlorpyrifos and Cyanophos pesticides	Romeh and Hendawi, 2014
5	*Paenibacillus lentimorbus* B-30488^{r}	200 ug/mL	136 mg/kg of Chromium	Khan et al., 2012
6	*Paenibacillus sp. OL15*	45 %	Lubricating oil	Pongsilp and Nimnoi, 2022
7	*Paenibacillus glucanolyticus* T7-AHV	22.13 %	Seven types of hydrocarbons	Ghafari et al., 2019
8	*Paenibacilus lautus*	89.89 %	n-Hexadecane	Samaei at al., 2020
9	*Paenibacillus validus* strain MP5	Chalcopyrite – 64 % and Covellite – 54 %	Chalcopyrite and Covellite	Rawat and Rai, 2012

the ability to produce biosurfactants. Endophyte bacteria are considered promising for environmental applications due to their ability to produce biosurfactants that detoxify pollutants in polluted soils and rivers (De Franca et al., 2015).

Soil and water ecosystems are contaminated by excessive and persistent use of organophosphorus chemicals. Organophosphorus pesticides are widely used worldwide to control pests in homes and agriculture. Overall, 38% of all pesticides used worldwide consist of organophosphorus chemicals (Singh and Walker, 2006). Luckily, these problems are solved by *Paenibacillus polymyxa* to degrade organophosphorus pesticides. As a source of carbon and phosphorus in a mineral salt medium, *Paenibacillus polymyxa* was able to degrade the organophosphorus insecticides malathion, cyanophos, chlorpyrifos, and chlorpyrifos-methyl (Romeh and Hendawi, 2014). According to Romeh and Hendawi (2014), the dual inoculation of *Azospirillum lipoferum* and *Paenibacillus polymyxa* were improve in degradation of Chlorpyrifos (85.9%) and cyanophos (100%) after 14 days in improved loam soil than in the uninoculated control soil. Numerous pesticides have been successfully removed by bacterial involvement (bioagumentation), including coumaphos, ethoprophos, dicofol and malathion (Kanade et al., 2012; Romeh and Hendawi, 2014).

Bioremediation is an environmentally friendly, non-invasive and less costly treatment that can lead to the degradation or transformation of environmental toxins into harmless or less toxic forms (Gomathi et al., 2020; Xu and Lu, 2010). The main advantage of bioremediation is that on-site treatment often reduces site disturbance and eliminates the need for transportation. Detoxification or mineralization of the contamination into CO_2, H_2O and biomass is a key component of bioremediation, as it results in complete and permanent removal of the contaminant. This also eliminates the hazard and long-term liability of the contaminant. Then, bioremediation generates less secondary waste, fewer air and water emissions and soils remain in place. However, temperature, pH, moisture content, the presence of electron acceptors, the local microbial flora, the type of pollutant and other environmental conditions all have a significant impact on the bioremediation process. Therefore, the limitation of bioremediation is shallow soil, contaminants may be mobilized into the ground water and the toxicity and bioavailability of degradation product is not known. Then, the high concentrations of hazardous materials can be toxic to plant (Gomathi et al., 2020)

Bioremediation is a financially viable and environmentally sound choice because it breaks down organic pollutants into CO_2 and H_2O and high public acceptance. Hence the researchers should research genetically different type of microbes which can also work on any conditions. Therefore, bioremediation is still considered as a developing technology to regulate the day-today environmental problems faced by humans residing in an area.

Conclusion

In agriculture, new and tested technologies boost crop yields, however, some of these traditional methods have a negative impact on the environment. The difficulty facing contemporary agriculture is producing a lot of harvests while protecting the environment. Therefore, it is imperative to look for ecologically friendly alternatives right away. It is widely recognised that *Paenibacillus* strains are effective biocontrol agents against a variety of harmful bacteria. Recent research has also revealed that these bacteria function as plant growth promoters (PGPRs) that boost crop output. Typical mechanisms include activation of plants' systemic immunity, creation of secondary metabolites such as proteins and enzymes, activation of the immune system throughout generations, and development of biofilms around roots. *Paenibacillus* species have recently been employed in a sustainable disease management strategy to combat plant diseases. *Paenibacillus* spp. can be utilised to decompose garbage and organic materials, detoxify contaminated environments, and prevent illnesses in addition to promoting plant development. Numerous studies have reported the increase in nutritional content of compost that has been broken down by *Paenibacillus* spp. Therefore, *Paenibacillus* spp. advantages include the prevention of various plant diseases, promotion of plant growth and development, enhancement of the composting process, and the promise of a cleaner environment in terms of sustainable agriculture when integrated in a product.

Declaration of competing interest

None

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