



## *Paenibacillus polymyxa* bioactive compounds for agricultural and biotechnological applications

Nur Sazwani Daud, Abd Rahman Jabir Mohd Din, Mohamad Azzuan Rosli, Zaheda Mohamad Azam, Nor Zalina Othman\*, Mohamad Roji Sarmidi

Innovation Centre in Agritechology for Advanced Bioprocess (ICA), UTM Pagoh Research Center, Pagoh Education Hub, 84600, Pagoh, Malaysia

### ARTICLE INFO

#### Keywords:

*Paenibacillus polymyxa*  
Biofertilizer  
Antimicrobial agents  
Exopolysaccharide  
Biocontrol  
Enzymes

### ABSTRACT

*Paenibacillus polymyxa* is categorized as an endospore-forming bacterium and Gram-positive bacteria, which have innate beneficial properties in modern biotechnology application. *P. polymyxa* extensively reviewed as plant growth promoting bacteria which directly gave benefit to the plants by improving nitrogen fixation from atmosphere, increase phosphorus solubilization and iron acquisition in soil and phytohormone production. This could reduce reliance on chemical fertilizers, which is now a source of environmental conflict and appear to be harmful to human. Therefore, application of *P. polymyxa* focusing only as functional microbial species in production of biofertilizers. *P. polymyxa* have been gaining momentum over the last couple of years. The recent discovery in microbial industrial of this bacterium is the production of bioactive compounds like exopolysaccharides (EPS). EPS is not only established as biofilm for the colonization of microbes and act as a sink for the nutrients on plant roots in the rhizosphere. Hence, EPS from *P. polymyxa* is also useful for health care industries such as disease diagnosis and drug manufacturing. Synthesis of hydrolytic enzymes reported as bioconversion of agricultural wastes that helps to tackle serious environmental problems by creating wealth from waste which can also acts as productive biocontrol agents against pathogens. Hence, *P. polymyxa* having a wide range of antibacterial metabolites and antifungal compounds, inform of volatile organic compounds, peptides and hydrolytic enzymes, This compounds and biomaterials could be commercially marketed as reliable plant biocontrol agents and pharmaceutical application. Nowadays, researcher extensively reviewed and focused their attention on the potential benefits of *P. polymyxa* with multiple biological functions that cannot be ignored for human health and wellness.

### 1. Introduction

Over the past decades, *P. polymyxa* has attracted global interest as this strain holds great promise for its ecological and biotechnological significance. For now, the genus *Paenibacillus* encompassed over 150 species (Eastman et al., 2014). Previously, it was described as *P. polymyxa* (formerly *Bacillus polymyxa*) by Prazmowski in 1880, as a non-pathogenic and endospore-forming and facultative anaerobic strain. Members of *P. polymyxa* are found in diverse ecological niches from a broad range of geographical location. This species is not limited only to rhizosphere of various crops but found in marine sediments, forest trees, insect larvae and even clinical samples (Raza et al., 2011; Liang and Wang, 2015). Globally, *Paenibacillus* sp. occupied the top cited strain in the segment of plant growth promotion, nutrient cycling, exopolysaccharides (EPS) production, novel bioactive metabolites for

biological control and industrial purposes. Apart from that, *P. polymyxa* was also screened as functional microbial species in bioorganic fertilizers and has shown promising results on bioconversion of agricultural waste into valuable and high demand products. This could reduce reliance on chemical fertilizers, which is harmful to people or other animals and polluted our ecosystem. It is imperative to utilize indigenous microbes input and all their important metabolite derivatives which can maximize the ecological benefits and accelerate the emerging of their applications in biotechnological processes. This article provides a recent overview of potential biological functions of *P. polymyxa* in both medicine and agricultural applications to meet demands of green technologies which is applicable for human health and wellness.

\* Corresponding author.

E-mail addresses: [sazwanidaud94@gmail.com](mailto:sazwanidaud94@gmail.com) (N.S. Daud), [jabir@ibd.utm.my](mailto:jabir@ibd.utm.my) (A.R.J. Mohd Din), [azzuan@utm.my](mailto:azzuan@utm.my) (M.A. Rosli), [zaheda@utm.my](mailto:zaheda@utm.my) (Z.M. Azam), [norzalina@utm.my](mailto:norzalina@utm.my) (N.Z. Othman), [mroji@utm.my](mailto:mroji@utm.my) (M.R. Sarmidi).

<https://doi.org/10.1016/j.bcab.2019.101092>

Received 6 March 2019; Accepted 10 March 2019

Available online 13 March 2019

1878-8181/ © 2019 Published by Elsevier Ltd.

## 2. Biological characteristics of *Paenibacillus polymyxa*

The name *Paene* means 'almost' in Latin and therefore *Paenibacillus* means 'almost a *Bacillus*'. *P. polymyxa* is one of the well-defined soil-dwelling bacteria species and the oldest species in the genus formerly grouped with genus *Bacillus*. This bacterium be named *Bacillus polymyxa* as it has rod-shaped cells, spore forming bacteria, neutrophilic, perflagellated heterotrophic (Padma et al., 2017). In 1993, *Bacillus polymyxa* was reclassified in the new genus *Paenibacillus* as a species of the genus *Bacillus* (Jeon et al., 2010). *Paenibacillus* sp. when grown on the cooked slices of beefs and turnips when exposed to air and when grown in agar, it would form a thick creamy yellowish layer on the surface.

As studied by Ash et al. (1993), they were determining the small-subunit rRNA sequences of 51 species of *Bacillus* by reverse transcription to elucidate the phylogenetic structure of the genus. From their studied, comparative analysis of the sequence data revealed five phylogenetically distinct clusters. From the clusters, the Group 3 bacilli showing phylogenetically distinct genera when compared others genus *Bacillus*. They differentiate into ellipsoidal spores which distinctly swell from the mother cell (Ash et al., 1993). This group exhibited relatively low sequence homologies with the other *Bacillus* groups and from the branching pattern of the tree clearly constitutes a distinct lineage (Ash et al., 1993). Recently, Padma et al. (2017) have reclassified these Group 3 bacilli which comprising of *B. polymyxa* and ten other close relatives into a new genus *Paenibacillus* (meaning: almost a *Bacillus*). It was officially approved and announced by the International Committee on Systematic Bacteriology (1994) and was reclassified into a separate family name as *Paenibacillaceae* (Priest, 2009; Rawat et al., 2016; Yasin et al., 2016; Meena et al., 2016; Saha et al., 2016; Yadav and Sidhu, 2016). However, a phylogenetic analysis suggests that this bacterium is paraphyletic with the other genera (*Aneurinibacillus*, *Brevibacillus*, *Cohnella*, *Fontibacillus*, *Oxalophagus*, *Saccharibacillus* and *Thermobacillus*) forming subsidiary clades. The genus *Paenibacillus* is therefore expected to undergo significant taxonomic subdivision in the future. Conversely, the number of novel species being identified as *Paenibacillus* and established species being reclassified as such continues to grow and the genus currently comprises around 239 species (Padma et al., 2017).

## 3. Importance of *Paenibacillus* sp. for agriculture and horticulture, industrial and medical applications

It inhabits diverse ecological niches from a broad range of geographical locations but not limited only to rhizosphere of various crops but also found in marine sediments, forest trees and wines. Besides this wide variety of habitats, *Paenibacillus* sp. has shown the extensive environmental adaptability. Grady et al. (2016) had extensively reviewed the plant growth promoting characteristics including nitrogen fixation, phosphorus solubilization, iron acquisition and phytohormone production. It is worth mentioning that *P. polymyxa* has remarkably diverse secondary metabolites to overcome threats and it has shown promise in the treatment of a variety of problems from food industries, agricultural and pharmaceuticals industries. It is known that *P. polymyxa* was deliberated here to secrete a variety of beneficial bioactive substances including antibiotic polymyxins, fusaricidins and antimicrobial polypeptides (Grady et al., 2016). In terms of it being a green solution for sustainable agriculture practices, *P. polymyxa* is an ideal candidate to enhance soil fertility or as pesticide to cater agricultural needs (Mohd Din et al., 2019). For example, Cheng et al. (2017) reported 11 volatile organic compounds (VOC's) from *P. polymyxa* KM2501-1 which exhibited strong nematocidal activity against *Meloidogyne incognita* juveniles. In fact, the dominant role of this wholesome strain is depicted as the phytopathogen disease control in several crops and aquatic animals that have been tested for iron acquisition and boosting their immunity shield system (Zhou et al., 2016; Gupta et al., 2016).

Shi et al. (2017) reported that *P. polymyxa* NSY50 effectively

reduced the incidence of *Fusarium* wilt (56.4%) by altering the soil physiochemical properties such as soil pH,  $C_{mic}$  (microbial biomass carbon),  $R_{mic}$  (basal respiration), total N and  $C_{org}$  (total organic carbon). Higher pH,  $C_{mic}/C_{org}$ ,  $C_{mic}$ ,  $C_{org}$ ,  $R_{mic}$ , total N and all soil enzyme activities were noted in the *P. polymyxa* NSY50 treatment condition. Through improvement plant root system via iron absorption or nitrogen fixing capabilities with the rhizosphere microbial communities for plant growth and success cannot be overstated (Zhou et al., 2016; Hao and Chen, 2017; Puri et al., 2016). To a certain extent, *P. polymyxa* is directly used as inoculant in the biofertilizer. This can give a good alternative option for maintaining the sustainable agroecosystems (Xu et al., 2014). As cultivation of bacteria are more productive than fungus that previously known as the dominant of beneficial microbes in the agriculture industry.

*P. polymyxa* also shows physiological and functional characteristics as probiotic as study by Naghmouchi et al. (2013) in the livestock feed. Its can inhibit pathogenic bacteria in the gastrointestinal tract which means *P. polymyxa* JB-0501 resistance to lysozyme, acid, bile salts, and hydrogen peroxide. Alshelmani et al. (2016) proves improvement on nutrient digestibility and gut microflora in broiler chicken when feeding trial with palm kernel cake fermented (FPKC) by *P. polymyxa* ATCC 842. Hence, the antagonistic activity of *P. polymyxa* (MF457398.1) cells including the filtered broth isolated from *Anabas testudineus* were also exhibited bactericidal activity against the tested microbial fish pathogens. The capability to be supplemented in the fish feed as probiotic supplements was supported when intraperitoneal injection of the bacterium did not induce any pathological signs, symptoms or mortalities in *Oreochromis niloticus* (Midhun et al., 2017).

## 4. Important bioactive metabolites from *P. polymyxa*

Notably, *P. polymyxa* genome have showed numerous bioactive metabolites gene cluster responsible for indole-3-acetic acid (IAA) production, cytokinin, mineral phosphate solubilization, plant cell wall degradation, antimicrobial compounds, quorum sensing, transport mechanism and biosynthesis of specific antimicrobial non-ribosomal peptides. *P. polymyxa* strains have been cited as an outstanding bacterium that responsible for producing a numerous bioactive compounds as they adapted well to unique ecological niches. This is due to it having a remarkably diverse secondary metabolism capable of catabolizing a wide variety of substrates as well as producing important bioactive metabolites to overcome threats and in response to various biotic stresses and industrial needs (Table 1).

### 4.1. Phytohormones

Phytohormones as organic substances which can regulate a variety of cellular process in plants either produced endogenously or applied exogenously. Plant hormones produced endogenously by plants control all aspects of growth and development from embryogenesis, the regulation of organ size, pathogen defense, stress tolerance and reproductive development. Generally, plant hormones are mainly divided into 5 categories: auxins, cytokinins, ethylene, gibberellins (GAs) and abscisic acid (ABA) (Yadav and Saini, 2018). Some promote growth by stimulating cell enlargement, photosynthesis or division while others inhibit growth by inducing dormancy or inhibit senescence of plants organs, especially in leaves (Davies, 2010).

Exogenous phytohormone supplementation which is secondary metabolites of microbes has been widely used to support plant growth (Premachandra et al., 2016). One of the enzymes can contribute to enhance plant growth is cytokinins. Cytokinins have key regulatory roles in plant growth and development such as to promote seed germination, denovo bud formation, release of buds from apical dominance, stimulation of leaf expansion and of reproductive development, and retardation of senescence (Mok, 1994). Timmusk et al. (1999) showing *P. polymyxa* strain B2, isolated from the rhizosphere of wheat

**Table 1**  
Biological functions of bioactive compounds from *P. polymyxa*.

Biological functions	Compounds	Structure class	References
<b>Biofertilizer</b>			
Iron acquisition	Hydroxamate	Siderophore	Raza and Shen (2010)
<b>Phytohormones</b>			
Phytohormone	Iso-pentenyladenine riboside (iPR)	Cytokinin	Timmusk et al. (1999)
Phytohormone	Cytokinin-like substances		
Phytohormone	Indole-3-acetic acid	Auxin	Weselowski et al. (2016)
Phytohormone	Indole-3-acetic acid	Auxin	Phi et al. (2010)
<b>Antimicrobial agents</b>			
Antimicrobial	Benzothiazole, benzaldehyde, undecanal, dodecanal, hexadecanal, 2-tridecanone and phenol	Volatile organic compounds	Raza et al. (2015)
Antimicrobial	Paenilan	Lantibiotics	Park et al. (2017)
Antifungal	Fusaricidins	Polyhexapeptides	Vater et al. (2015)
Bactericidal	Polymyxin E1 & E2	Lipopeptides	Tambadou et al. (2015)
Antimicrobial	Polymyxin B	Lipopeptides	Shaheen et al. (2011)
Defense related phytohormone by induced systemic resistance	Abscisic acid and jasmonic acid	Organic acids	Hong et al. (2016)
<b>Exopolysaccharides</b>			
Biofilm	D-glucuronic acid	Polysaccharides	Timmusk et al. (2019)
Heavy metal adsorption	Polysaccharide beads	Polysaccharides	Hassiba et al. (2014)
Food products and pharmaceuticals	Curdlan	Exopolysaccharides	Rafiqh et al. (2014)
Antioxidant and antitumor	Levan	Exopolysaccharides	Liu et al. (2012)
Antioxidant and antitumor	$\beta$ -glucans	Exopolysaccharides	Hong and Jung (2014)
<b>Enzymes</b>			
Lignocellulose hydrolysis	Endoglucanase, exoglucanase and $\beta$ -glucosidase,	Hydrolytic enzyme	Bohra et al. (2018)
Heavy metal bioadsorption	Dehydrogenase, oxygenase	Hydrolytic enzymes	Kumari et al. (2014)
Lignocellulose hydrolysis	Cellulase	Cellulolytic enzymes	Górska et al. (2015)
Lignocellulose hydrolysis	Carboxymethyl cellulase	Cellulolytic enzymes	Kumar et al. (2012).
Lignocellulose hydrolysis	Cellulase	Hydrolytic enzymes	Zhao et al. (2017)
	Hemicellulase		
	Esterase		
Lignocellulose hydrolysis	Cellulase	Cellulolytic enzymes	Gastelum-Arellanez et al., 20
Thrombosis	Thrombolytic agent	Fibrinolytic enzymes	Lu et al. (2010)

produced cytokinin-like compound during its stationary phase of growth in the culture broth of shake flask study. Recent investigations have shown that phytohormones produced by root-associated microbes may prove to be important metabolic engineering targets for inducing host tolerance to improve growth and metabolism under abiotic stress. The production of hormones has been suggested to be one of the mechanisms by which plant growth-promoting rhizobacteria (PGPR) stimulate plant growth under abiotic stress. Plants are exposed to many different types of abiotic stresses includes osmotic stress caused by drought, salinity, high or low temperatures, freezing, or flooding, as well as ionic, nutrient, or metal stresses, and others caused by mechanical factors, light, or radiation (Eyidogan et al., 2012). Plants cannot escape and they need to adapt themselves to survive through physiological, biochemical, or molecular mechanisms to survive under stress conditions. As studied by Figueiredo et al. (2008), coinoculation with *P. polymyxa* and *Rhizobium tropici* was reported to alleviate drought stress on *Phaseolus vulgaris* as this strain mitigate the negative effects through phytohormonal balance including an increased leaf abscisic acid (ABA) content, a small decline in indole acetic acid (IAA) and gibberellic acid (GA<sub>3</sub>). Enhanced production of IAA by isolated *P. polymyxa* enhancing plant tolerance to abiotic stress through lowering host ethylene levels by 1-aminocyclopropane-1-carboxylate (ACC) deaminase activity (Weselowski et al., 2016). Phi et al. (2010) showed in their study that 59% of all *P. polymyxa* strains tested which were considered as IAA producing strain were found to promote growth of pepper plants; the authors noted that the IAA production ranged from 7.5 to 25.9  $\mu\text{g ml}^{-1}$  among 29 isolates. Further studies revealed that jasmonic acid and 1-aminocyclopropane-1-carboxylate (ACC) deaminase enzyme (which enhances plant growth by reducing plant ethylene) have a significant role in protecting plants from any stressors by involving a complex interplay among several pathways (Tiwari et al., 2018).

#### 4.2. Antimicrobial agents

The use of pesticides or herbicides in agriculture is harmful to human when they enter our food chain that can cause chronic diseases (Aktar et al., 2009). Recently, European Union vote for ban the world's most widely used of pesticides known as neonicotinoids. It's known as toxic pesticides from all fields due to the serious danger to biodiversity, food production and the environment. Finally affected human health through contaminated of soil and water indirectly by bees. Application of antimicrobial peptide produced by *P. polymyxa* is well known for medicine and environmental benefits for human health and wellness. Crop diseases caused by fungal phytopathogens and nematodes could be managed by using biocontrol agents from *Paenibacillus* sp. Previous publications have shown the ability of *P. polymyxa* strain as a biocontrol of plant pathogens and protection was used commercially in various important crops (Jeon et al., 2010; Phi et al., 2010; Hong et al., 2016). It was ranked as one of the applied microorganism in commerce by US Environmental Protection Agency (EPA) in 2002.

*P. polymyxa* secretes a chemically diverse range of secondary metabolites which many of them shown biocontrol ability, among which are fusaricidins, a group of cyclic depsipeptides and the peptide gava-serin (Huo et al., 2012). In another report, polymyxin, a molecule inhibiting the growth of *Erwinia amylovora* and *Erwinia carotovora* was described by Niu et al. (2013). Similarly, Vater et al. (2015) identified fusaricidins from *P. polymyxa*, displaying potent antifungal properties. Huang and Yousef (2015) investigated the biosynthesis of lantibiotic, paenibacillin and polymyxin E1 in *P. polymyxa*, OSY-DF. Mageshwaran et al. (2012) observed that antibacterial metabolite from *P. polymyxa*, HKA-15 showed the presence of amino acids and fatty acids. It was further purified and accessed for bioactivity analysis against *Xanthomonas campestris* pv. *phaseoli* M-5. They also validated the lipopeptide nature of antibacterial metabolite using <sup>1</sup>H NMR analysis where spectral peak was detected corresponding to methyl group, acyl group and

amide linkages. Recently, Vater et al. (2018) reported on the genome mining of *P. polymyxa* E681 by utilizing the MALDI-TOF MS and MALDI-LIFT-TOF/TOF MS that can elucidate the structure characterization of novel unknown family lipopeptides. They are cyclic compounds which contain a C<sub>12-13</sub>- $\beta$ -amino fatty acid integrated into the peptide ring, which encoded by gene cluster B correspond to the tridecaptin family. These techniques were used to detect and verify the presence of lipopeptide products as these compounds were most likely to be used as a promising candidate for novel antibiotics (Vater et al., 2018).

This strain can be developed into reliable biocontrol agent against various plant diseases with minimum disturbances to rhizospheric ecosystem (Raza et al., 2015; Jeon et al., 2010). Reports said that *P. polymyxa* strains were shown to stimulate antibiosis and produced polymyxin, colistin and hydrolytic enzymes which play a significant role in the biocontrol of plant pathogens (Tambadou et al., 2015; Vater et al., 2015; Niu et al., 2013). Thus, an effective and environmentally safe biocontrol using these strains become paramount alternatives to chemical pesticides. Concerning the biocontrol effectiveness, hydrolytic enzymes (glucanase and chitinase) could degrade the cell walls of various phytopathogens including *Fusarium oxysporum* and *Colletotrichum musae* (Wen et al., 2010). Li et al. (2015) also reported that *P. polymyxa* A21 had the synergistic antifungal effects of two different hydrolytic enzymes; chitinase and glucanases against *Botrytis cinerea*.

*P. polymyxa* seem to elicit induced systemic resistance (ISR) against pathogenic microorganisms through production of volatile organic compounds (VOC). VOC can act as elicitor to trigger ISR by hypersensitizing the plant to potential threats when *P. polymyxa* present in high population densities. This can create a faster and stronger defenses against a range of pathogens or pests via primed transcription of salicylic acid, jasmonic acid, and ethylene signaling genes which are then induced upon attack (Grady et al., 2016; Pieterse et al., 2014). Cheng et al. (2017) analyzed VOC from *P. polymyxa* that acted as insecticidal agent using solid phase microextraction-gas-chromatograph-mass spectrum (SPME-GC-MS). They determined about 11 VOC's; acetone, 2-heptanone, benzaldehyde, 2-nonanone, 2-nonanol, cyclopentasiloxane decamethyl, 11-dodecen-2-one, 2-decanol, 4-acetylbenzoic acid and furfural acetone. The antimicrobial VOC's produced by *P. polymyxa* Sb3-1 has been further elucidated by Rybakova et al. (2017) to clarify the aerial warfare interaction towards the cell apoptotic of *Verticillium longisporum*. This finding was confirmed by the observed accumulation of protein breakdown and cellular stress (arabitol) indicated by *Verticillium* wilt. Zhao et al. (2011) demonstrated that 1-octen-3-ol constituents from *P. polymyxa* BMP-11 have good herbicidal effect on *Amaranthus retroflexus*, *Echinochloa crusgalli* and *Chenopodium album*. In accordance to that, *P. polymyxa* E681 produced more than 30 long chains of VOC's including tridecane to antagonize *Pseudomonas syringae* via primed transcription of those phytohormone signaling genes in order to induce defense-related genes (Lee et al., 2012). The isolated strain of *P. polymyxa* AC-1 was shown to mediate phytohormone signaling pathway by regulating salicylic acid (SA-dependent response). This response can create an enhanced structural cellulose barrier and jasmonic acid/ethylene pathway to keep crops from cell death when affected by *Pseudomonas syringae* as a leaf-inhabiting endophyte (Hong et al., 2016).

Promising new antimicrobial peptides always given attention by the medical world due to the emerging and rapid dissemination of antibiotic resistant pathogens such as Methicillin-resistant *Staphylococcus aureus* and multidrug-resistant *Mycobacterium tuberculosis* (Huang and Yousef, 2015). This is a big issues emerging as a major global threat to public health. One example of antimicrobial peptides is lantibiotics which are well studied because of commercial use as antimicrobial agents. Lantibiotics are expressed as prepropeptides that are ribosomally synthesized, with an N-terminal leader sequence and a C-terminal propeptide part, which is post-translationally modified (Dischinger et al., 2014). Additional genes, encoding proteins for leader peptide

removal, transportation, regulation and self-immunity, are usually present in lantibiotic gene clusters (Dischinger et al., 2014; Chatterjee et al., 2005). Paenibacillin is a newly discovered lantibiotic produced by *P. polymyxa* OSY-DF (He et al., 2007). An attempt has been made by Huang and Yousef (2015) to identify and characterize a new efficient antimicrobial peptide from *P. polymyxa* OSY-DF. This strain is showing potency against *Listeria monocytogenes*, methicillin-resistant *Staphylococcus aureus* and other Gram-positive bacteria. Furthermore, isolated *P. polymyxa* JSa-9 was also recorded to produce a group of cyclic lipodepsipeptides known as LI-F-type of antimicrobial peptide named as AMP-*jsa9* which have a strong antagonistic activity against Gram-positive bacteria and filamentous fungi (Han et al., 2017). In addition, mechanism was deliberated as AMP-*jsa9* disrupted the cell wall, membrane and cytoskeleton and inhibited the biosynthesis pathway of fumonisins B<sub>1</sub>. This can be used as a natural and effective antifungal agent in the agricultural, food, and animal feed industries. (Han et al., 2017). Lantibiotics which also used as food preservatives to prevent foodborne illness transmitted through food borne pathogens (He et al., 2008).

#### 4.3. Exopolysaccharides (EPS)

*P. polymyxa* was also given an attention for microbial exopolysaccharides (EPS) production with varying characteristics to suit the industrial needs. EPS produced by microbes have been widely used within bioindustries of foods, medicines and cosmetics as well as bioremediation agents for waste water treatments. The remarkable characteristics of EPS from microbial resources are environmental friendly, inexpensive and could be developed from agriculture waste materials. Its bulk production is being anticipated. As mentioned by Redmile-Gordon et al. (2015), EPS is composed of more than just polysaccharides, including a wide variety of proteins and glycoproteins and considerable quantities of extracellular DNA. Therefore, some of these EPS from *Paenibacillus* sp. TKU023 were found to have antioxidant and antitumor activities as described by Wang et al. (2011). The authors found that EPS production (4.55 g/L) showed the highest total phenolic contents with DPPH radical scavenging activity at the fifth day of incubation using squid pen powder as an inducer. The EPS produced by *P. polymyxa* SQR-21 was reported consists of mannose, glucuronic acid, glucose and fructose which is the constituents of EPS (Raza et al., 2011). The EPS showed good superoxide scavenging, flocculating and metal chelating activities while moderate inhibition of lipid peroxidation and reducing activities. These compositions showed the great potential of EPS produced by SQR-21 to be used in industry in place of synthetic compounds (Raza et al., 2011).

One of the recent potential from *P. polymyxa* ATCC 21830 is the production of curdlan. Curdlan and its derivatives widely used in manufacture of food products and pharmaceuticals industry. As curdlan, composed entirely of  $\beta$ -(1  $\rightarrow$  3)-D-glycosidic linkages with the molecular structure of purified sample was determined to be 170 kDa by gel permeation chromatography (Rafiq et al., 2014). In addition, detection of more than 869–1220 kDa of levan was observed by Liu et al. (2012) from *P. polymyxa* EJS-3. A levan-type EPS from this strain was successfully acetylated, phosphorylated and benzylated, respectively, affording its derivatives of acetylated levan, phosphorylated levan and benzylated levan which showing exhibited higher reducing power, scavenging activity against superoxide radical and scavenging activity on hydroxyl radical (Liu et al., 2012). A novel  $\beta$  -1,3/1,6-glucan produced from *P. polymyxa* JB115 which was isolated from soil (Chang et al., 2010). The physiological activities of this  $\beta$ -glucans produced by *P. polymyxa* JB115 contained anti-tumor, stimulating antioxidant by means of enhancing the production of nitric oxide (NO) in macrophages through MAPK and NF $\kappa$ B signaling pathways. Among these properties, anti-tumor and immunomodulatory activities of  $\beta$ -glucan have attracted the greatest attention in recent years (Chang et al., 2010). As further studied by Hong and Jung (2014) on  $\beta$ -glucans

produced by *P. polymyxa* JB115 of high molecular weight of  $\beta$ -glucans (> 100 kDa) showing the hydroxyl radical- and superoxide radical scavenging, maximal nitric oxide production and the antitumor activity in four tumor cell lines (HeLa, Sarcoma 180, A<sub>549</sub>, and Hep<sub>3B</sub> cells). The source and chemical characteristics such as molecular weight distribution of glucan may affect its biological activities. Therefore, application of EPS from *Paenibacillus* sp. for health care and pharmaceutical products has opened a valuable option for disease diagnosis and drug manufacturing because of the production cost is lower when compare to others cell biofactories.

Another important biocontrol feature of *P. polymyxa* is an active participation of biopolymers of microbial origin in which biofilm microorganisms are embedded (Awasthi et al., 2017). Production of exopolysaccharide is generally important in biofilm formation, and likewise can effect the interaction of microbes with roots and root appendages (Bianciotto et al., 2004). Formation of biofilm by accumulation of EPS play an important role in the attachment and colonization of microorganisms to food-contact surfaces. Bacterial biofilms established on plant roots could protect the colonization sites and act as a sink for the nutrients in the rhizosphere. Hence reducing the availability of root exudate nutritional elements for pathogen stimulation or subsequent colonization on the root (Weller and Thomashow 1994; Yegorenkova et al., 2011). Moreover, it helps to increase the uptake of nutrients by plant, and brings subsequent increase in plant's growth through biofilm formation. The bacterial biofilms are formed during the colonization process and it serves as a multipurpose protection such as immobilization and quorum-sensing signaling. In addition, it's induced systemic resistance (ISR) as a defense mechanism and providing protection against a wide range of pathogens. Instead of that, secretion of EPS by *P. polymyxa* can protect the plants from abiotic stress (Gouzou et al., 1993; Figueiredo et al., 2008). EPS possess unique water holding and cementing properties (Gupta et al., 2016). Therefore, with these properties it plays a role in the formation and stabilization of soil aggregates and regulation of nutrients and water flow across plant roots (Awasthi et al., 2017). EPS production was also associated with lead biosorption capability as reported by Hassiba et al. (2014). They highlighted that lead removal was successfully done with 111.11 mg/g immobilized *P. polymyxa* EPS as per Langmuir model which can help bioremediation of lead in the contaminated soil to be utilized in agriculture practices.

#### 4.4. Synthesis of industrial enzymes

Commercial applications that require low-cost enzyme in bulk quantity is becoming a worthy option by using the readily abundant lignocellulosic waste material. The production of the industrial enzymes through microbial fermentation is the recent trend to cater to the demand for large scale production of lignocellulosic enzymes as it is more effective, cost-effective, robust and safer for industrial applications. Exogenous enzymes are not only known for the catalyst bioactivity process but also contributed to the decrease or elimination of the environmental pollution from the chemical reactions associated with such industrial activities. Efforts are put to convert agricultural waste using *P. polymyxa* into valuable bioproduct within a comprehensive biotechnological approach. The well-known cell wall degrading enzymes produced as cited from previous reports by *Paenibacillus* sp. which are grouped as cellulase (carboxymethyl cellulose known as endocellulase, exocellulases, and  $\beta$ -glucosidase), lignases (laccases, oxidases, and peroxidases) and hemicellulases (xylanase, xylosidase, arabinofuranosidase, feruloyl esterase, acetyl xylan esterase, galactosidase, and glucuronidase) (Grady et al., 2016; Howard et al., 2003). The major application of these hydrolytic enzymes is second generation for biofuel production, biopulping and waste management. It has been reported secretion of xylanase by *Paenibacillus* sp., optimal crude yield of approximately 60% was achieved through enzymatic extract of *Paenibacillus* sp. when grown on sugarcane residue as studied by Ghio

et al. (2017). Different types of lignocellulosic materials also can secrete xylanase by *Paenibacillus* sp. The optimal crude yield of approximately 60% was achieved through enzymatic extract of *Paenibacillus* sp. when grown on sugarcane residue as studied by Ghio et al. (2017). Utilization of lignocellulosic plant materials for productive synthesis of exogenous enzymes by *Paenibacillus* sp. is well studied under solid state fermentation (Marco et al., 2017). The effectiveness of microbial consortium including *Paenibacillaceae* group to accelerate the cellulase production from coffee husk through 4.5 L bioreactor solid state fermentation was further described by Cerda et al. (2017). Furthermore, the highest viable cell number and spore yield during cultivation is important characteristics for highly productive production of hydrolytic enzymes from the solid-state fermentation. As studied by Guoqun et al. (2016), the viable cell number and spore yield of *P. polymyxa* D1 obviously increased when supplementation with wheat bran, urea, sodium nitrate and soybean meal in a solid-state fermentation from pear residues as compared with submerged fermentation. However, addition of minerals such as NH<sub>4</sub>NO<sub>3</sub>, NH<sub>4</sub>Cl and degossypolized cottonseed protein inhibited the cell growth and spore formation (Guoqun et al., 2016).

According to Bohra et al. (2018), *P. polymyxa* ND25 was mentioned as a pivotal candidate in hydrolysis of lignocellulosic plant material. Lignocellulosic enzymes normally worked as a consortium to be more efficient by formation of cellulosome (Bayer et al., 2004). The process started with the binding of carbohydrate-binding module (CBM) as a high affinity domain for polysaccharides such as cellulose used by carrier proteins as scaffolds to form a multi-enzyme complex before continuous hydrolysis of the cellulose (Orencio-Trejo et al., 2016). It's reported the existence of three cellulolytic enzymes with molecular mass of 130, 200, 220 kDa respectively which noted as cellulosome production by *P. polymyxa* EG2 and EG14 strains (Górska et al., 2015). For high yield of composting as reported by Zhao et al. (2017) through utilization of a microbial consortium agent containing *P. polymyxa* in composting putrescible kitchen waste. They indicated that the strain comprised of wide lignocellulolytic coding gene especially 12 cellulase along with 23 hemicellulase and 11 esterases. A wide variety of extracellular endoglucanases with molecular weight of 38 and 220 kDa with catalytic properties towards full cellulase yield optimization was reported in *P. polymyxa* BEB-40 (Gastelum-Arellanes et al., 2014). There is also a study on other types of lignocellulolytic enzyme through fermentation of mango peel waste as a substrate for production of carboxymethyl cellulase (CMCase) production by *P. polymyxa* (Kumar et al., 2012).

Fibrinolytic enzymes are important enzymes in the therapeutic treatment of thrombosis because of their use as effective thrombolytic agents. The fibrinolytic enzymes have been isolated from *Paenibacillus* sp. as a promising thrombolytic agent which is cheaper and safer than using plasminogen activators which is known to give negative impacts to the cardiovascular patients (Vijayaraghavan et al., 2016). At present, the plasminogen activators such as tissue plasminogen activator, urokinase, and streptokinase have undesirable side effects when used in a large therapeutic dosage, limited fibrin specificity, re-occlusion, and a bleeding tendency (Lv et al., 2015). A novel fibrinolytic enzyme from *P. polymyxa* EJS-3 (PPFE-I) was purified and characterized by Lu et al. (2010). The characterization of these PPFE-1 fibrinolytic enzyme with a molecular mass of 63.3 kDa can rapidly hydrolyzed the  $\alpha$ -chain of fibrinogen, followed by the  $\beta$ -chains. It also hydrolyzed the  $\gamma$ -chains (Lu et al., 2010). Additionally, metal ions showed different effects on the activity which are more slowly through activation of metal ions such as Zn(2+), Mg(2+), and Fe(2+), but inhibited by Ca(2+) and Cu(2+). In conclusion this isolated fibrinolytic enzyme exhibits a profound fibrinolytic activity. An attempt has also been made to clone and expressed gene encoding the fibrinolytic enzyme (PPFE-I) from *P. polymyxa* EJS-3 in *Escherichia coli* BL21 (Lv et al., 2015). This soluble recombinant enzyme (rPPFE-I) was purified to homogeneity and enzymatic properties were well characterized and exhibited both

fibrinolytic and platelet aggregation-inhibition activities. It's have a great potential with potential applications in thrombolytic therapy to overcome high morbidity and mortality of a variety of cardiovascular diseases.

## 5. Conclusion

The reputation of *P. polymyxa* in the scientific community and industry depends on its biological characteristics potential. But these properties are fully expressed in the field only when they meet the requirements and fulfil all the laboratory parameters to justify their commercial feasibility. Constant quality control and consistency result driven need to be well synchronized for the widespread commercialization of *P. polymyxa* obtained from different geographical locations to be applied in certain areas. The most recent biotechnological importance of *P. polymyxa* has been mentioned in this review to cater to the tremendous increase in the demand of these strain derivatives as exopolysaccharides, antimicrobial agents, industrial and medical enzymes. Recent advancements in biotechnology particularly in recombinant genetic engineering, proteomic analysis and development of suitable bioreactors have made the optimization of large-scale volume production of particular bioactive compounds will help more discoveries and optimizations that will allow *P. polymyxa* to contribute positively to human health and wellness.

## Conflict of interest

The authors state that there are no conflicts of interest.

## Acknowledgement

The authors are thankful to Universiti Teknologi Malaysia for work was supported by Research University Grant Scheme (Tier 1:18H83 and 4J270) and thanks are due to the Ministry Education Malaysia (Higher Education Department) for the financial assistance.

## References

Aktar, M.W., Sengupta, D., Chowdhury, A., 2009. Impact of pesticides use in agriculture: their benefits and hazards. *Interdiscip. Toxicol.* 2 (1), 1–12. 2009 Mar.

Alshelmani, M.I., Loh, T.C., Foo, H.L., Sazili, A.Q., Lau, W.H., 2016. Effects of feeding different levels of palm kernel cake fermented by *Paenibacillus polymyxa* ATCC 842 on nutrient digestibility, intestinal morphology and gut microflora in broiler chicken. *Anim. Feed Sci. Technol.* 216, 216–224.

Ash, C., Priest, F.G., Collins, M.D., 1993. Molecular identification of rRNA group 3 *bacilli* (Ash, Farrow, Wallbanks and Collins) using a PCR probe test. *A Van Leeuw J Microb* 64, 253–260.

Awasthi, S., Srivastava, P., Mishra, P.K., 2017. Application of EPS in agriculture: an important natural resource for crop improvement. *Agric. Res. Technol.* 8 (2).

Bayer, E.A., Belaich, J.P., Shoham, Y., Lamed, R., 2004. The cellulosomes: multienzyme machine for degradation of plant cell wall polysaccharides. *Annu. Rev. Microbiol.* 58, 521–554.

Bianciotto, V., Andreotti, S., Balestrini, R., Bonfante, P., Perotto, S., 2004. Mucoïd mutants of the biocontrol strain *Pseudomonas fluorescens* CHA0 show increased ability in biofilm formation. *Curr. Opin. Microbiol.* 7, 602–609.

Bohra, V., Dafale, N.A., Purohit, H.J., 2018. *Paenibacillus polymyxa* ND25: candidate genome for lignocellulosic biomass utilization. *3 Biotech* 8, 248.

Cerda, A., Gea, T., Vargas-García, M.C., Sánchez, A., 2017. Towards a competitive solid state fermentation: cellulases production from coffee husk by sequential batch operation and role of microbial diversity. *Sci. Total Environ.* 589, 56–65.

Chang, Z., Lee, J., Gebru, E., Hong, J., Jung, H., Jo, W., Park, S., 2010. Mechanism of macrophage activation induced by B-glucan produced from *Paenibacillus polymyxa* JB115. *Biochem. Biophys. Res. Commun.* 391, 1358–1362.

Chatterjee, C., Paul, M., Xie, L., Van Der Donk, W.A., 2005. Biosynthesis and mode of action of lantibiotics. *Chem. Rev.* 105 (2), 633–684.

Cheng, Yang, J., Nie, Q., Huang, D., Yu, C., Zheng, L., Cai, M., Thormashov, L.S., Weller, D.M., Yu, Z., Zhang, J., 2017. Volatile organic compounds from *Paenibacillus polymyxa* KM2501-1 control *Meloidogyne incognita* by multiple strategies. *Sci. Rep.* 7, 16213.

Davies, P.J., 2010. The Plant Hormones: Their Nature, Occurrence, and Functions from Book *Plant Hormones: Biosynthesis, Signal Transduction, Action*. Springer, pp. 1–15.

Dischinger, J., Basi Chipalu, S., Bierbaum, G., 2014. Lantibiotics: promising candidates for future applications in health care. *Int. J. Med. Microbiol.* 304 (1), 51–62.

Eastman, A.W., Heinrichs, D.E., Yuan, Z., 2014. Comparative and genetic analysis of the

four sequenced *Paenibacillus polymyxa* genomes reveals a diverse metabolism and conservation of genes relevant to plant-growth promotion and competitiveness. *BMC Genomics* 15, 851.

Eyidoğan, F., Oz, M.T., Yucel, M., Oktem, H.A., 2012. In: Khan, N.A., Nazar, R., Iqbal, N., Anjum, N.A. (Eds.), *Signal Transduction of Phytohormones under Abiotic Stresses in Phytohormones and Abiotic Stress Tolerance in Plants*. Springer-Verlag Berlin Heidelberg.

Figueiredo, M.V., Burity, H.A., Martinez, C.R., Chanway, C., 2008. Alleviation of drought stress in the common bean *Phaseolus Vulgaris* L. By Co-inoculation with *Paenibacillus polymyxa* and *Rhizobium tropici*. *Appl. Soil Ecol.* 4, 182–188. 2008.

Gastelum-Arellanez, A., Parades-Lopez, O., Oralde-Portugal, V., 2014. Extracellular endoglucanase activity from *Paenibacillus polymyxa* Beb-50: production, optimization, enzymatic characterization. *World J. Microbiol. Biotechnol.* 30, 2953–2965.

Ghio, S., Ontañón, O., Piccinni, F.E., De Villegas, R.M.D., Talia, P., Grasso, D.H., Campos, E., 2017. *Paenibacillus* sp. A59 GH10 and GH11 extracellular endoxylanases: application in biomass bioconversion. *Bioenergy Res.* 11, 174–190.

Górska, E.B., Jackiewicz, U., Dobryznski, J., Russel, S., Pietkiewicz, H., Kalaji, H., 2015. Degradation and colonization of cellulose by diazotrophic strain of *Paenibacillus polymyxa* isolated from soil. *J. Biorem. Biodegrad.* 6, 271.

Gouzou, L., Burtin, G., Philippon, R., Bartoli, F., 1993. Effect of inoculation with *Bacillus polymyxa* on soil aggregation in the wheat rhizosphere: preliminary examination. *Geoderma* 56, 479–490.

Grady, E.N., MacDonald, J., Liu, L., Richman, A., Yuan, Z.C., 2016. Current knowledge and perspectives of *Paenibacillus*: a review. *Microbial Cell Factory* 1 (1), 203 15.

Guoqun, Z., Mentian, N., Shikang, L., Junfeng, G., 2016. Cultivation of *Paenibacillus polymyxa* by solid-state fermentation of pear residues. *Trans. Chin. Soc. Agric. Eng.* 32 (7), 303–308.

Gupta, A., Gupta, P., Dhawan, A., 2016. *Paenibacillus polymyxa* as a water additive improved immune response of *Cyprinus carpio* and disease resistance against *Aeromonas hydrophila*. *Aquaculture Reports* 4, 86–92.

Han, J., Wang, F., Gao, P., Ma, Z., Zhao, S., Lu, Z., Lv, F., Bie, X., 2017. Mechanism of action of AMP-Jsa9, a LI-F-type Antimicrobial peptide produced by *Paenibacillus polymyxa* Jsa-9, against *Fusarium moniliforme*. *Fungal Genet. Biol.* 104, 45–55.

Hao, T., Chen, S., 2017. Colonization of wheat, maize and cucumber by *Paenibacillus polymyxa* WLY78. *PLoS One* 12, 1.

Hassiba, M., Naima, A., Yahia, K., Zahra, S., 2014. Study of lead adsorption from aqueous solutions on agar beads with EPS produced from *Paenibacillus polymyxa*. *Chem. Eng. Trans.* 38, 31–36.

He, Z., Kislá, D., Zhang, L., Yuan, C., Green-Church, K.B., Yousef, A.E., 2007. Isolation and identification of a *Paenibacillus polymyxa* strain that coproduces a novel lantibiotic and polymyxin. *Appl. Environ. Microbiol.* 7, 168–178.

He, Z., Yuan, C., Zhang, L., Yousef, A.E., 2008. N-terminal acetylation in *paenibacillin*, a novel lantibiotic. *FEBS Lett.* 582, 2787–2792.

Hong, J., Jung, H.K., 2014. Antioxidant and antitumor activities of β-glucan-rich exopolysaccharides with different molecular weight from *Paenibacillus polymyxa* JB115. *J. Korean Soc. Appl. Biol. Chem.* 57, 105–112.

Hong, C.E., Kwon, S.Y., Park, J.M., 2016. Biocontrol activity of *Paenibacillus polymyxa* AC-1 against *Pseudomonas syringae* and its interaction with *Arabidopsis Thaliana*. *Microbiol. Res.* 185, 13–21.

Howard, R.L., Abotsi, E., Jansen van Rensburg, E.L., Howard, S., 2003. Lignocellulose biotechnology: issues of bioconversion and enzyme production. *Afr. J. Biotechnol.* 2 (12), 602–619.

Huang, E., Yousef, A.E., 2015. Biosynthesis of *paenibacillin*, a lantibiotic with N-terminal acetylation by *Paenibacillus polymyxa*. *Microbiol. Res.* 181, 15–21.

Huo, Z., Zhang, N., Raza, W., Huang, X., Yong, X., Liu, Y., Wang, D., Li, S., Shen, Q., Zhang, R., 2012. Comparison of the spores of *Paenibacillus polymyxa* Prepared at different temperatures. *Biotechnol. Lett.* 34, 925–933.

Jeon, Y.H., Kim, S.G., Hwang, I., Kim, Y.H., 2010. Effects of initial inoculation density of *Paenibacillus polymyxa* on colony formation and starch-hydrolytic activity in relation to root rot in Ginseng. *J. Appl. Microbiol.* 109, 461–470.

Kumar, D., Ashfaq, M., Muthukumar, M., Singh, M., Garg, N., 2012. Production and characterization of carboxymethyl cellulose from *Paenibacillus polymyxa* using mango peel as substrate. *J. Environ. Biol.* 33, 81–84.

Kumari, M., Ghosh, P., Swati Thakur, I.S., 2014. Microcosmic study of endosulfan degradation by *Paenibacillus* sp. ISTP10 and its toxicological evaluation using mammalian cell line. *Int. Biodeterior. Biodegrad.* 96, 33–40.

Lee, B., Farag, M.A., Park, H.B., Kloepper, J.W., Lee, S.H., Ryu, C., 2012. Induced resistance by A long-chain bacterial volatile: elicitation of plant systemic defense by a C13 volatile produced by *Paenibacillus polymyxa*. *PLoS One* 7, E48744.

Li, J., Liu, W., Luo, L., Dong, D., Liu, T., Zhang, T., Lu, C., Liu, D., Zhang, D., Wu, H., 2015. Expression of *Paenibacillus polymyxa* B-1,3-1,4-glucanase in *Streptomyces lydicus* A01 improves its biocontrol effect against *Botrytis cinerea*. *Biol. Control* 90, 141–147.

Liang, T., Wang, S., 2015. Recent advances in exopolysaccharides from *Paenibacillus* spp.: production, isolation, structure and bioactivities. *Mar. Drugs* 13, 1847–1863.

Liu, J., Luo, J., Ye, H., Zeng, X., 2012. Preparation, antioxidant and antitumor activities *in vitro* of different derivatives of levan from endophytic bacterium *Paenibacillus polymyxa* EJS-3. *Food Chem. Toxicol.* 50, 767–772.

Lu, F., Lu, Z., Bie, X., Yao, Z., Wang, Y., Lu, Y., Guo, Y., 2010. Purification and characterization of a novel anticoagulant and fibrinolytic enzyme produced by endophytic bacterium *Paenibacillus polymyxa* EJS-3. *Thromb. Res.* 126 (5), e349–e355.

Lv, F., Zhang, C., Guo, F., Lu, Y., Bie, X., Qian, H., Lu, Z., 2015. Expression, purification, and characterization of a recombinant fibrinolytic enzyme from endophytic *Paenibacillus polymyxa* EJS-3 in *Escherichia coli*. *Food Sci. Biotechnol.* 24, 125–131.

Mageshwaran, V., Wallia, S., Annapurna, K., 2012. Isolation and partial characterization of antibacterial lipopeptide produced by *Paenibacillus polymyxa* HKA-15 against phytopathogen *Xanthomonas campestris* pv. Phaseoli M-5. *World J. Microbiol.*

- Biotechnol. 28, 909–917.
- Marco, E.D., Soraire, P.M., Romero, C.M., Villegas, L.B., Martínez, M.A., 2017. Raw sugarcane bagasse as carbon source for Xylanase production by *Paenibacillus* species: a potential degrader of agricultural wastes. *Environ. Sci. Pollut. Control Ser.* 24, 19057–19067.
- Meena, S.K., Rakshit, A., Meena, V.S., 2016. Effect of seed bio-priming and N doses under varied soil type on nitrogen use efficiency (NUE) of wheat (*Triticum aestivum* L.) under greenhouse conditions. *Biocatal Agric Biotechnol* 6, 68–75.
- Midhun, S.J., Neethu, S., Vysakh, S., Arun, D., Radhakrishnan, E.K., Jyothis, M., 2017. Antibacterial activity and probiotic characterization of Autochthonous *Paenibacillus polymyxa* isolated from *Anabas testudineus* (Bloch: 1792). *Microb. Pathog.* 113, 403–411.
- Mohd Din, A.R.J., Rosli, M.A., Mohamad Azam, Z., Othman, N., Sarmidi, M.J., 2019. *Paenibacillus polymyxa* role involved in phosphate solubilization and growth promotion of Zea mays under abiotic stress condition. *Proc. Natl. Acad. Sci. India B Biol. Sci.* 1–9.
- Mok, M.C., 1994. Cytokinins and plant development - an overview. In: Mok, D.W.S., Mok, M.C. (Eds.), *Cytokinins: Chemistry, Activity and Function*. CRC Press, New York, pp. 115–166.
- Naghmouchi, K., Baah, J., Cudennec, B., Drider, D., 2013. Required characteristics of *Paenibacillus polymyxa* JB-0501 as potential probiotic. *Arch. Microbiol.* 195, 537–543.
- Niu, B., Vater, J., Rueckert, C., Blom, J., Lehmann, M., Ru, J.J., Chen, X.H., Wang, Q., Borriss, R., 2013. Polymyxin P is the active principle in suppressing phytopathogenic *Erwinia* spp. by the biocontrol rhizobacterium *Paenibacillus polymyxa* M-1. *BMC Microbiol.* 13, 137–150.
- Orencio-Trejo, M., Torre-Zavala, S.D., Rodriguez-Garcia, A., Aviles-Arnaut, H., Gastelum-Arellanez, A., 2016. Assessing the performance of bacterial cellulases: the use of *Bacillus* and *Paenibacillus* strains as enzyme sources for Lignocellulose saccharification. *Bioenergy Res.* 9, 1023–1033.
- Padda, K.P., Puri, A., Chanway, C.P., 2017. *Paenibacillus polymyxa*: a prominent bio-fertilizer and biocontrol agent for sustainable agriculture. In: Meena, V.S., Mishra, P.K., Bisht, J.K., Pattanayak, A. (Eds.), *Agriculturally Important Microbes for Sustainable Agriculture. Applications in Crop Production and Protection*. Springer, Singapore, pp. 165–191.
- Park, J.E., Kim, H.R., Park, S.K., Choi, S.K., Park, S.H., 2017. Identification of the biosynthesis gene cluster for the novel lantibiotic panilam from *Paenibacillus polymyxa* E681 and characterization of its product. *J. Appl. Microbiol.* 123 (5), 1133–1147.
- Phi, Q., Park, Y., Seul, K., Ryu, C., Park, S., Kim, J., Ghim, S., 2010. Assessment of root-associated *Paenibacillus polymyxa* groups on growth promotion and induced systemic resistance in pepper. *J. Microbiol. Biotechnol.* 20, 1605–1613.
- Pieterse, C.M.J., Zamioudis, C., Berendsen, R.L., Weller, D.M., Van Wees, S.C.M., Bakker, P.A.H.M., 2014. Induced systemic resistance by beneficial microbes. *Annu. Rev. Phytopathol.* 52, 347–375.
- Premachandra, D., Hudek, L., Brau, L., 2016. Bacterial modes of action for enhancing of plant growth. *J. Biotechnol. Biomater.* 6, 3.
- Priest, F.G., 2009. Genus I: *Paenibacillus* Ash, priest and Collins 1994, 852VP. In: second ed. In: De Vos, P., Garrity, G.M., Jones, D., Krieg, N.R., Ludwig, W., Rainey, F.A., Schleifer, K.H., Whitman, W.B. (Eds.), *Bergey's Manual of Systematic Bacteriology, the Firmicutes*, vol. 3. Springer, New York, pp. 269–295.
- Puri, A., Padda, K.P., Chanway, C.P., 2016. Seedling growth promotion and nitrogen fixation by a bacterial endophyte *Paenibacillus polymyxa* P2b-2r and its GFP derivative in corn in a long-term trial. *Symbiosis* 69, 123–129.
- Rafiq, S.M., Yazdi, A.V., Vossoughi, M., Safekordi, A.A., Ardjmand, M., 2014. Optimization of culture medium and modeling of curdlan production from *Paenibacillus polymyxa* by RSM and ANN. *Int. J. Biol. Macromol.* 70, 463–473.
- Rawat, J., Sanwal, P., Saxena, J., 2016. Potassium and its role in sustainable agriculture. In: Meena, V.S., Maurya, B.R., Verma, J.P., Meena, R.S. (Eds.), *Potassium Solubilizing Microorganisms for Sustainable Agriculture*. Springer, New Delhi, pp. 235–253.
- Raza, W., Shen, Q., 2010. Growth, Fe<sup>3+</sup> reductase activity and siderophore production by *Paenibacillus polymyxa* SQR-21 under differential iron conditions. *Curr. Microbiol.* 61, 390–395.
- Raza, W., Makeen, K., Wang, Y., Xu, Y., Qirong, S., 2011. Optimization, purification, characterization and antioxidant activity of an extracellular polysaccharides produced by *Paenibacillus polymyxa* SQR-21. *Bioresour. Technol.* 102, 6095–6103.
- Raza, W., Yuan, J., Ling, N., Huang, Q., Shen, Q., 2015. Production of volatile organic compounds by an antagonistic strain *Paenibacillus polymyxa* WR-2 in the presence of root exudates and organic fertilizer and their antifungal activity against *Fusarium oxysporum* f. sp. *Niveum*. *Biol. Control* 80, 89–95.
- Redmile-Gordon, M.A., Evershed, R.P., Hirsch, P.R., White, R.P., Goulding, K.W.T., 2015. Soil organic matter and the extracellular microbial matrix show contrasting responses to C and N availability. *Soil Biol. Biochem.* 88, 257–267.
- Rybakova, D., Rack-Wetzlinger, U., Cernava, T., Schaefer, A., Schmuck, M., Berg, G., 2017. Aerial warfare: a volatile dialogue between the plant pathogen *Verticillium longisporium* and its antagonist *Paenibacillus polymyxa*. *Front. Plant Sci.* 8, 1294.
- Saha, M., Maurya, B.R., Bahadur, I., Kumar, A., Meena, V.S., 2016. Can potassium-solubilizing bacteria mitigate the potassium problems in India? In: Meena, V.S., Maurya, B.R., Verma, J.P., Meena, R.S. (Eds.), *Potassium Solubilizing Microorganisms for Sustainable Agriculture*. Springer, New Delhi, pp. 127–136.
- Shaheen, M., Li, J., Ross, A.C., Vederas, J.C., Jensen, S.E., 2011. *Paenibacillus polymyxa* PKB1 produces variants of polymyxin B-type Antibiotics. *Chem. Biol.* 18, 1640–1648.
- Shi, L., Du, N., Shu, S., Sun, J., Li, S., Guo, S., 2017. *Paenibacillus polymyxa* NSY50 suppresses Fusarium wilt in cucumbers by regulating the rhizospheric microbial community. *Sci. Rep.* 7, 41234.
- Tambadou, F., Caradec, T., Gagez, A., Bonner, A., Sopéna, V., Bridiau, N., Thiéry, V., Didelot, S., Barthélémy, C., Chevrot, R., 2015. Characterization of the colistin (polymyxin E1 and E2) biosynthetic gene cluster. *Arch. Microbiol.* 197, 521–532.
- Timmusk, S., Nicander, B., Granhall, U., Tillberg, E., 1999. Cytokinin production by *Paenibacillus polymyxa*. *Soil Biol. Biochem.* 31, 1847–1852.
- Timmusk, S., Copolovici, D., Copolovici, L., Teder, T., Nevo, E., Behers, L., 2019. *Paenibacillus polymyxa* biofilm polysaccharides antagonise *Fusarium graminearum*. *Sci. Rep.* 9 Article number: 662.
- Tiwari, G., Duraivadevi, P., Sharma, S., Hariprasad, P., 2018. 1-Aminocyclopropane-1-carboxylic acid deaminase producing beneficial rhizobacteria ameliorate the biomass characters of *Panicum maximum* Jacq. by mitigating drought and salt stress. *Sci. Rep.* 8, 17513.
- Vater, J., Niu, B., Kristin, D., Borriss, R., 2015. Characterization of novel fusaricidins produced by *Paenibacillus polymyxa* M1 using MALDI-TOF mass spectrometry. *Am. Soc. Mass Spectrom.* 26, 1548–1558.
- Vater, J., Herfort, S., Doellinger, J., Weydmann, M., Lasch, P., Borriss, R., 2018. Genome mining of lipopeptide biosynthesis of *Paenibacillus polymyxa*. *Chembiochem* 4 (7), 744–753 19.
- Vijayaraghavan, P., Vincent, S.G.P., Arasu, M.V., 2016. Purification, characterization of a novel fibrinolytic enzyme from *Paenibacillus* sp. IND8 and its in vitro thrombolytic activity. *South Indian J. Biol. Sci.* 2, 434–444.
- Wang, C., Huang, T., Liang, T., Fang, C., Wang, S., 2011. Production and characterization of exopolysaccharides and antioxidant from *Paenibacillus* sp. TKU023. *N. Biotech.* 28, 559–565.
- Weller, D.M., Thomashow, L.S., 1994. Current challenges in introducing beneficial microorganisms into the rhizosphere. In: O'Gara, F., Dowling, D.N., Boesten, B. (Eds.), *Molecular Ecology of Rhizosphere Microorganisms*. Academic Press, NY, pp. 1–18.
- Wen, F.Y., Liao, F.P., Lin, J.R., Zhong, Y.S., 2010. Cloning, expression and application of B-1,3-1-4-glucanase gene from *Paenibacillus polymyxa* CP7. *J. Integr. Agric.* 43, 4614–4623.
- Wesulowski, B., Nathoo, N., Eastman, A.W., Macdonald, J., Yuan, Z., 2016. Isolation, identification and characterization of *Paenibacillus polymyxa* CR1 with potential for biopesticide, biofertilization, biomass degradation and biofuel production. *BMC Microbiol.* 16, 244–254.
- Xu, S., Bai, Z., Jin, B., Xiao, R., Zhuang, G., 2014. Bioconversion of wastewater from sweet potato starch production to *Paenibacillus polymyxa* biofertilizer for tea plants. *Sci. Rep.* 4, 4131.
- Yadav, R.K., Saini, P.K., 2018. Plant Hormones: their nature occurrence and functions: A chapter. *Eur. J. Biotechnol. Biosci.* 6 (6), 13–17.
- Yadav, B.K., Sidhu, A.S., 2016. Dynamics of Potassium and their bioavailability for plant nutrition. In: Meena, V.S., Maurya, B.R., Verma, R.P., Meena, R.S. (Eds.), *Potassium Solubilizing Microorganisms for Sustainable Agriculture*, pp. 187–201 16.
- Yasin, M., Munir, I., Faisal, M., 2016. Can *Bacillus* spp. enhance K<sup>+</sup> uptake in crop species. In: Meena, V.S., Maurya, B.R., Verma, J.P., Meena, R. (Eds.), *Potassium Solubilizing Microorganisms for Sustainable Agriculture*. Springer, New Delhi, pp. 163–170.
- Yegorenkova, I.V., Tregubova, K.V., Matora, L.Y., Burygin, G.L., Ignatov, V.V., 2011. biofilm formation by *Paenibacillus polymyxa* strains differing in the production and rheological properties of their exopolysaccharides. *Curr. Microbiol.* 62, 1554–1559.
- Zhao, L., Yang, X., Li, X., Mu, W., Liu, F., 2011. Antifungal, insecticidal and herbicidal properties of volatile components of *Paenibacillus polymyxa* strain BMP-11. *Agric. Sci. China* 10, 728–736.
- Zhao, K., Xu, R., Zhang, Y., Tang, H., Zhou, C., Cao, A., Zhao, G., Guo, H., 2017. Development of a novel compound microbial agent for degradation of kitchen waste. *Braz. J. Microbiol.* 48, 442–450.
- Zhou, C., Guo, J., Zhu, L., Xiao, X., Xie, Y., Zhu, J., Ma, Z., Wang, J., 2016. *Paenibacillus polymyxa* BFKC01 enhances plant iron absorption via improved root systems and activated iron acquisition mechanisms. *Plant Physiol. Biochem.* 105, 162–173.