Microbiological Research 227 (2019) 126309

Contents lists available at ScienceDirect

Microbiological Research

journal homepage: www.elsevier.com/locate/micres

Regulatory rewiring through global gene regulations by PhoB and alarmone (p)ppGpp under various stress conditions

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ARTICLE INFO

Keywords:
Alarmones (p)ppGpp
Gene network
Pho regulon
Phosphate solubilizing bacteria
Stringent response

ABSTRACT

The phosphorus availability in soil ranged from < 0.01 to 1 ppm and found limiting for the utilization by plants. Hence, phosphate solubilizing bacteria (PSB) proficiently fulfill the phosphorus requirement of plants in an eco-friendly manner. The PSB encounter dynamic and challenging environmental conditions viz., high temperature, osmotic, acid, and climatic changes often hamper their activity and proficiency. The modern trend is shifting from isolation of the PSB to their genetic potentials and genome annotation not only for their better performance in the field trials but also to study their ability to cope up with stresses. In order to withstand environmental stress, bacteria need to restructure its metabolic network to ensure its survival. Pi starving condition response regulator (PhoB) and the mediator of stringent stress response alarmone (p)ppGpp known to regulate the global regulatory network of bacteria to provide balanced physiology under various stress condition. The current review discusses the global regulation and crosstalk of genes involved in phosphorus homeostasis, solubilization, and various stress response to fine tune the bacterial physiology. The knowledge of these network crosstalk help bacteria to respond efficiently to the challenging environmental parameters, and their physiological plasticity lead us to develop proficient long-lasting consortia for plant growth promotion.

1. Introduction

Bacteria can survive under a diverse environment where they encounter a variety of conditions, for instance, amino acid deprivation, nutrient limitation, high temperature, oxidative stress, drought and osmotic shock (Sharma et al., 2013; DeAngelis et al., 2018; Uluşeker et al., 2018; Zhu et al., 2019). In response to the encountered adverse conditions, bacteria mount appropriate reactions by regulating gene expression leading to adaptability and balanced physiology. Bacterial systems engaged in C:N:P (carbon: nitrogen: phosphorus) metabolism must interact, but their coordination is not entirely understood (Santos-Beneit, 2015). Bacteria can respond to a diverse array of stresses simultaneously, the decision made against various stress response leads to crosstalk of the regulatory network. An intricate global regulatory network leads to an efficient and coordinated response. The living organism must survive the environmental perturbation by metabolic regulation; which is mediated through transcriptional regulation (Antiqueira et al., 2012; Shimizu, 2013). The property of this system is similar to that of ‘neural network,’ as it operates multiple signaling pathways simultaneously, and crosstalk occurs between pathways (Hellingwerf, 2005).

Phosphorus (P) is a vital nutrient necessary for the growth of all organism, including microbes, and plants. It is a crucial element for intracellular signaling, genetic materials, membrane integrity, and energy metabolism whereas in plants it plays an essential role in photosynthesis, cell division, development of excellent root system and utilization of carbohydrate (Santos-Beneit, 2015; Thuynsma et al., 2016; Sharma et al., 2017; Carstensen et al., 2018). Carstensen et al. (2018) carried out a study to describe the effect of P deficiency on the process of photosynthesis and the electron transport chain. The P deficiency results in a low concentration of orthophosphate in the chloroplast stroma. Hence, the thylakoids accumulate more protons and results in lumen acidification. Consequently, this situation inhibits photosystem II overexcitation and cause damage to leaf tissues. P stress not only affects the plant photosynthesis but it also adversely affect growth and photosynthesis in photosynthetic bacteria (Litchman et al., 2003).

Although ample amount of phosphorus (both organic and inorganic) present in nature, they exist in unavailable form, only a little amount of orthophosphate anion (PO_4^{3-}) also known as inorganic phosphate (Pi) is available for the direct utilization by microbes and plants (Hinsinger, 2001; Achat et al., 2009; Sharma et al., 2013; Santos-Beneit, 2015; Wang et al., 2015; Cooper et al., 2018; Gouda et al., 2018). The bacteria

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https://doi.org/10.1016/j.micres.2019.126309
Received 6 May 2019; Received in revised form 23 July 2019; Accepted 2 August 2019

always try to accumulate an excess of Pi in the form of polyphosphate (PolyP) and use as Pi reservoir under starvation/stress conditions whereas the modern agriculture mostly relies on the application of chemical fertilizers for increased crop productivity (Kaur and Reddy, 2015). There are various fungal strains known to solubilize inorganic phosphate through organic acid secretion but, their action of solubilization is selective for different phosphate source and may vary under different condition (Gaind, 2016). Thus, phosphate solubilizing bacteria (PSB) as a biofertilizer is the pronounced source for phosphorus availability to plants in an eco-friendly manner (Kucey et al., 1989; Sharma et al., 2013). The current focus is to have highly efficient rhizobacteria which not only support the growth promotion of sustainable crop but also able to tolerate environmental stresses, due to global concerns on the effects of climate change (Alexandre and Oliveira, 2016)

The current review discusses the gene networks involved in phosphorus homeostasis under the starvation condition and its interaction with the phosphorus solubilizing genes. We also review the crosstalk of the Pho regulon genes with the gene network involved in other stresses like high temperature, oxidative stress, nutrient limitation and acid stress, which usually encountered by PSB in the soil. This network interaction defines that under limited phosphorus level, the Pho regulon interacts with different gene network and decides the optimum physiological conditions for survival (Fig. 1).

2. Current scenario of phosphorus availability in the soil

Along with nitrogen, phosphorus also required for increased crop productivity. To meet the global agronomic requirement, farmers are critically using synthetic/chemical fertilizers for increased crop production (Corrales Ramírez et al., 2014). The application of these synthetic fertilizers provide the nutrient for plant growth, but still, a significant portion of the applied nutrients is not taken up by plants. The process of volatilization, nitrification (nitrogen), leaching, surface runoff, and mineralization (phosphate) or other means strive these nutrients and make fertilizer costlier and pollutes the environment on a large scale (Sharpley, 1993; Sharpley et al., 1995; Timilsena et al., 2015). Usually, it was seen that many soils have the phosphorus availability approximately 1 μmol l^{-1}, whereas plant needs approximately 30 μmol l^{-1} for its maximum production (Sashidhar and Podile, 2010; Adhya et al., 2015). According to the reports, soils have adequate total phosphorus reserve which nearly accounts for 0.05% of the dry soil weight, however, only 1–5% of total phosphorus reserve available in the soluble form for plant uptake (Wang et al., 2015). The current phosphorus soil status around various geographic regions showed the different distribution (Table 1) and signifies that most soils are soluble phosphorus deficient (Dey et al., 2017). The phosphorus status in the agricultural soil of different state of India like Maharashtra, Assam, Tamil Nadu and Odisha was analyzed, and sampling location mapped based on GPS/GIS soil fertility mapping (Table 1) (Basumatary et al., 2014; Mishra et al., 2015, 2016; Vijaya Kumar et al., 2015; Dey et al., 2017; Parhad et al., 2018). In China, based on soil P chemistry the arable land was divided into five management zones, out of which 15–92% of land have worse P status than the optimum agronomic values and 0.3–7.2% have threats of P leaching (Li et al., 2015). In the south-west of Siberia the concentrations of Pi in the solution (Qw - 2–22 at 5 cm and 0.1–0.4 μg g^{-1} at 100 cm), organic P (P_{org} - 389–774 at 5 cm and 37–79 μg g^{-1} at 100 cm) and total P (P_{tot} - 694–1095 at 5 cm and 319–694 μg g^{-1} at 100 cm) decreases along the 1 m depth in the studied grassland and forest sites. According to the global scale the total P concentrations in topsoil (initial 20 cm) was ranged between 62 - 2480 μg g^{-1}, 32 - 3548 μg g^{-1} and 19 - 3090 μg g^{-1} in croplands, grasslands and forests respectively. The measurements in SW Siberia ranged between 481-741 μg g^{-1} in grasslands and between 345-770 μg g^{-1} in forests. The mentioned values were between the upper and the median quartile for grasslands and virtually above the upper quartile for forests. According to the global cropland standards, these concentrations were mostly above the upper quartile (Brédoire et al., 2016).

3. The new trend for increased crop production: Phosphate solubilizing Microbes (PSM)

The use of PSM to the agricultural fields as a biofertilizer is known to be an improved strategy for increased food production without any

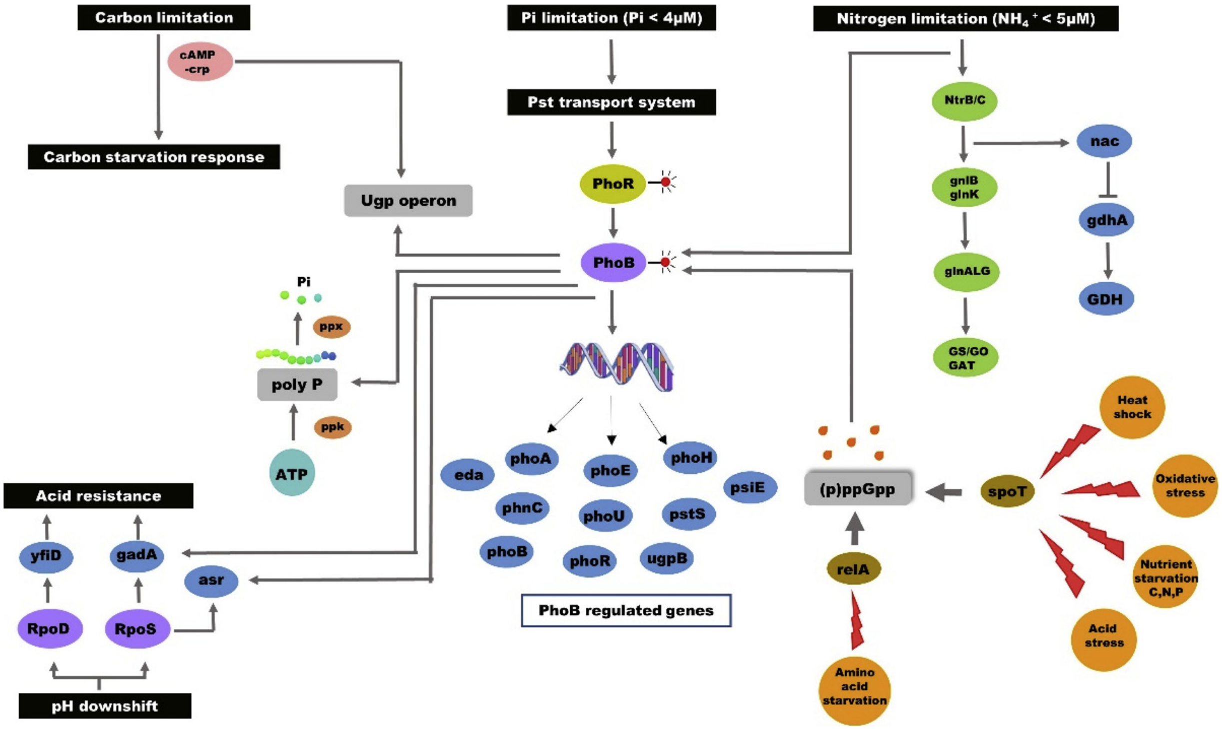

Fig. 1. An overview of network crosstalk between the response regulator PhoB and components involved in the other stressed conditions.

Table 1
The available phosphorus status of different geographic locations.

Sr. No	Area	Available phosphorus (kg ha^{-1})	Reference
1	Sindkheda (Maharashtra)	5.36 - 30.74	Parhad et al., 2018
2	Jorhat (Assam)	14.81- 39.49	Basumatary et al., 2014
3	Sivasagar (Assam)	10.54 - 34.2	Basumatary et al., 2014
4	Golaghat (Assam)	14.28 - 36.38	Basumatary et al., 2014
5	Theni (Tamil Nadu)	9 - 183	Vijaya Kumar et al., 2015
6	Puri (Odisha)	0.25 - 111.5	Mishra et al., 2015
7	Nayagarh (Odisha)	6.1 - 12.0	Mishra et al., 2016
8	Jimma zone (Ethiopia)	27 – 45.6	Nigussie et al., 2013
9	Wote town and Wamunyu market (Kenya)	4.5 - 490	Itabari et al., 2013
10	Western Ethiopia	9 - 198	Goshu et al., 2015

Table 2
Phosphate solubilizing activity of different plant growth promoting rhizobacteria (PGPR).

Sr.no	Species	Media	Phosphate solubilizing efficiency		Target plant	Reference
			Solubilization index	Broth assay ^{a} (mgL^{-1})		
1	*Flavobacterium psychrophilum* IARI-HHS2-37	NBRIP	–	66.0 ± 0.7	Wheat (Triticum aestivum)	Verma et al., 2015
2	*Kocuria kristinae* IARI-HHS2-64		–	64.0 ± 1.0		
3	*Bacillus thuringiensis* IARI-HHS1-6		–	63.2 ± 1.4		
4	*Arthrobacter nicotinovorans* IARI-HHS1-1		–	61.9 ± 0.2		
5	*Pseudomonas extremorientalis* IARI-HHS2-1		–	57.7 ± 0.6		
6	*Bacillus altitudinis* BRHS/S-73	PKV	–	837.33 ± 9.41	Vigna radiata, Cicer arietinum, and Glycine max	Sunar et al., 2015
7	*Pseudomonas oryzihabitans* S6-242 Krome 37	NBRIP	2.74	523.69	–	Liu et al., 2015
8	*Pseudomonas aeruginosa* LP8 Krome3		2.30	511.78	–	
9	*Acinetobacter* sp. YZT101 Krome5		2.25	356.01	–	
10	*Bacillus circulans* CB7	PKV	2.7	828 ± 3.2	Tomato (Solanum lycopersicum)	Mehta et al., 2015
11	*Streptomyces* sp. BPSAC34	PKV and NBRIP	73^b	326	Chilli (Capsicum annuum L)	Passari et al., 2015
12	*Leifsonia xyli* BPSAC24		64^b	315		
13	*Pantoea* sp. Pot1	PKV	150	956 ± 6	Tomato (Solanum lycopersicum)	Sharon et al., 2016
14	*Burkholderia tropica* P4	NBRIY*	–	580.56 ± 13.38	(Lycopodium cernuum L)	Ghosh et al., 2016
15	*Burkholderia unamae* P9		–	517.12 ± 17.15		
16	*Burkholderia cepacia* P10		–	485.18 ± 14.23		
17	*Alcaligenes aquatilis* A4	PKV	4.48 ± 0.30	277.72 ± 1.45	Maize (Zea mays)	Pande et al., 2017
18	*Burkholderia cepacia* C1		4.88 ± 0.69	305.49 ± 10.72		
19	*Alcaligenes aquatilis* H6		4.64 ± 1.12	282.38 ± 11.81		
20	*Pseudomonas fluorescens* L228	NBRIP	–	1312 ± 4.1	Pisum sativum L	Otieno et al., 2015
21	*Pseudomonas* sp. L132		–	1024 ± 1.7		
22	*Pseudomonas fluorescens* L321		–	788 ± 0.4		
23	*Pseudomonas fluorescens* F113		–	649 ± 0.2		
24	*Pseudomonas aeruginosa* PSB 11	PKV	2.75	–	–	Sen and Joshi, 2017
25	*Pseudomonas aeruginosa* PSB 16		2.18	–	–	
26	*Pseudomonas aeruginosa* PSB 51		2.77	–	–	
27	*Pseudomonas oryzihabitans* PSB 55		3.50	–	–	
28	*Cronobacter universalis* PSB 91		3.12	–	–	

^{a}Numerical values are mean ± SD of three independent observations; ^{b} phosphorus solubilization index in percentage; NBRIP = National Botanical Research Institute Phosphate; *NBRIY = National Botanical Research Institute Phosphate medium devoid of yeast extract; PKV = Pikovskaya's.

environmental damages (Kucey et al., 1989; Sharma et al., 2013; Alori et al., 2017). The application of PSM to the soil can swap /partially reduce the use of inorganic phosphorus fertilizers. It could be one of the highly efficient, cost-effective, and sustainable approaches to circumvent phosphorus pollution and conserve phosphorus resources (Matsushita et al., 2002; Raj et al., 2005; Liu et al., 2015). There is a wide range of phosphate solubilizing fungi, reported and used as biofertilizers, known to be more efficient than bacteria having the solubilizing capacity (Khan et al., 2010; Gaind, 2016). It seems to be a novel area of work; hence, the capacity of bacteria for phosphate solubilization should target. There are some studies carried out for the development of PSBs as biofertilizer and use for a variety of crops, for example, sunflower, chilly, corn, rice (Table 2) (Panhwar et al., 2014; Amalraj et al., 2015; Thilagar et al., 2016). Mehta et al. (2013) in their study reported the isolation of 206 PSB from root endosphere (ER) and rhizosphere soil (RS) of apple trees from 4 different locations of Himachal Pradesh (Chamba, Kinnaur, Kullu, and Shimla). Amalraj et al. (2015) carried out their study on *Trichoderma viride* (CRITV01), *Azotobacter chrococcum* (AZB 29), *Azospirillum brasilense* (ASP20) and *Bacillus megaterium* var. phosphaticum (PSB037) to evaluate their ability of solubilizing nutrients and development of a microbial consortium for promotion of growth in sunflower. In a study, it was reported that the microbial inoculants *Bacillus sonorensis* and *Funneliformis mosseae* showed improvement of growth in chilly plants and reduced the use of chemical fertilizers by 50% (Thilagar et al., 2016). PSB help plants to acquire this nutrient by solubilizing the insoluble phosphorus source (Wang et al., 2015). PSB, both gram positive and gram negative, has the same mechanisms to solubilize the insoluble form of phosphorus (inorganic or organic); these mechanisms have different categories depending on their mode of action. Secretion of mineral dissolving or complexing compounds, e.g., organic acid, hydroxyl ions, protons, siderophores is the first applied option. Second is the secretion of extracellular enzymes (P mineralization), and the last one is the release of phosphorus during substrate degradation (Sharma et al., 2013; Prabhu et al., 2018). Organic acid production/chelation of cations bound to phosphorus, H_2S production, inorganic acid production, siderophores, lowering pH through the release of protons are some of the methods to solubilize the inorganic phosphorus source. Phosphatase (based on the optimum pH they are either acid phosphatase or alkaline phosphatase), phytase, phosphonatase/C–P lyases are the extracellular enzymes responsible for mineralization of the organic phosphorus sources (Sharma et al., 2013). Among these mentioned mechanisms, solubilization of phosphate by secretion of organic acids and extracellular enzymes is most widely studied and focused on developing efficient consortia.

4. Mechanism of phosphorus homeostasis under the starvation condition: Pho regulon

Pho regulon is a global regulatory mechanism responsible for Pi homeostasis. The environmental Pi- perturbance results in the inflection of the Pho regulon expression that provokes bacteria to regulate phosphate assimilation pathways accordingly (Monds et al., 2006). The Pho regulon comprises the following transcriptional units: *pstSCAB-phoU*, *phoBR*, *phoH*, *phoE*, *eda*, *psiE*, *phnCDEFGHIJKLMNOP*, and *ugpBAECQ* (Brzoska et al., 1994; Hulett et al., 1994; Wanner et al., 1996; Jochimsen et al., 2011; Shimizu, 2013; Chekabab et al., 2014). Along with these operons, the Pho regulon also activates extracellular enzymes, able to retrieve Pi from organic phosphates, and enzymes responsible for the storage of phosphorus in the form of polyP. The most commonly activated extracellular enzymes are alkaline phosphatases (PhoA), phospholipases (PhoD), phytases (PhyC), 5′-nucleotidases (UshA) and glycerophosphodiester phosphodiesterases (GlpQ and UgpQ) (Brzoska and Boos, 1988; Eder et al., 1996; Santos-Beneit, 2015). In order to store the excess amount of Pi bacteria express polyphosphate kinase (*ppk*) which forms a polyP chain as a Pi reservoir and when required use this Pi with the help of exopolyphosphatase (*ppx*).

Pi uptake in bacteria occurs by two systems, inorganic phosphate transport (Pit system) and high-affinity phosphate specific transporter (Pst System). Under Pi excess condition, the constitutively expressed PitA and inducible PitB transferred Pi as metal phosphate complex by using the proton motive force (Santos-Beneit et al., 2008; Gonzalez et al., 2014). However, under the Pi limiting/stress condition, Phosphate starvation induced high-affinity Pst System transport phosphorus at the expense of ATP hydrolysis (Vershinina and Znamenskaya, 2002). The high-affinity Pst system is comprised of PstSCAB-PhoU proteins, in pst operon, *pstS* encodes for high-affinity periplasmic protein; *pstC* and *pstA* encode for transmembrane channel protein, and *pstB* encodes for the ATPase having nucleotide binding domain. The gene *phoU* encodes for a metal binding protein and not the component of Pst transport system, but regulates the Pi transportation through Pst system (Fig. 2A) (Amemura, et al., 1985; Vershinina and Znamenskaya, 2002; de Almeida et al., 2015; Neves et al., 2015; diCenzo et al., 2017; Jha et al., 2017; Jha et al., 2018). Under different environmental Pi concentrations, the two-component regulatory systems (TCS) comprises of sensor protein (PhoR) and response regulator (PhoB) control the Pho regulon by the phospho-relay mechanism (Hulett et al., 1994). The TCS switch ON the Pho regulon under the stressed condition as the histidine sensor kinase PhoR auto-phosphorylate on its conserved His- residue and transfer the phosphoryl group to Asp- residue of response regulator PhoB for its activation (Makino et al., 1989). The activated PhoB then binds to the consensus DNA sequence called PHO box, having GTTC ACC consensus sequence, present at the promoter region of the Pho regulon genes. The PHO box sequence is characterized by the two direct repeats comprised of seven highly conserved and four less conserved nucleotides in each repeat (Blanco et al., 2002; Sola-Landa et al., 2005; Apel et al., 2007; Sola-Landa et al., 2008; Diniz et al., 2011; Blanco et al., 2012; Chekabab et al., 2014; Santos-Beneit, 2015). Whereas, the presence of an ample amount of Pi makes the Pho regulon system switch OFF. Under this condition, the PhoU, Pst system and PhoR makes a repressor complex which turns on the phosphatase activity of PhoR and removes the activatory phosphoryl group from PhoB and thus prevents the further expression of the Pho regulon genes (Fig. 2B) (Amemura et al., 1985). Although the function of Pho regulon is conserved throughout the organism, there exist some contradictory findings. Variation in the genetic arrangement and copy number of Pho regulon genes among different bacteria signifies the evolutional adaptation towards environmental challenges (Jha et al., 2018). It was observed that phoU gene is missing in *Bacillus subtilis,* and the regulation of Pi-deficient response is mediated by the interconnection of three two-component systems (PhoP–PhoR system, Spo0 system, and ResD–ResE system) (Hulett, 1996). Recently, Lubin et al. (2016) have proposed a study carried out in *Caulobacter crescentus,* where the role of PhoU showed a marked difference from its well-known function of regulating the PhoB activity. The PhoU depletion does not affect the PhoB mediated gene expression; instead, it significantly increases the accumulation of polyphosphate granules, thus indicating its role in maintaining intracellular Pi accumulation. Apart from regulating the Pi transport via Pho regulon, the PhoU negatively modulates the expression of glpQ1 in *Streptomyces coelicolor*. It also plays an essential role in modulating the expression of genes responsible for spores pigment and production of actinorhodin and undecylprodigiosin antibiotics in *Streptomyces coelicolor* (Martín-Martín et al., 2018).

5. Inorganic and organic phosphorus utilization by bacteria

5.1. Molecular mechanism of inorganic phosphorus solubilization

The solubilization of inorganic phosphate is an essential technique of plant growth promotion via bacterial consortia. The inorganic form of phosphorus accounts for 35–70% of total phosphorus present in the soil (Harrison, 1987; Sharon et al., 2016). The readily available form, inorganic phosphate, often combined with the minerals present in the soil and become insoluble, thus unavailable for plant uptake. Numerous studies have reported that various bacterial species, particularly rhizobacteria, can solubilize insoluble Pi compounds such as hydroxyapatite, dicalcium, tricalcium, and rock phosphate (Otieno et al., 2015). The inorganic forms of P can be solubilized by microorganisms that secrete organic acids mainly, gluconic acid and to a lesser extent, α-keto-gluconic acid, to dissolve phosphate complexed minerals. As compared to Gram-positive bacteria, Gram-negative bacteria are known to secrete a large number of organic acids and have great potential to mineralize insoluble phosphates (Sashidhar and Podile, 2010). The direct oxidation pathway of glucose produces the organic acid in the periplasmic space of gram-negative bacteria with the help of glucose dehydrogenase (GCD/GDH) and gluconate dehydrogenase (GAD) which produce gluconic acid and α-keto-gluconic acid respectively (Miller et al., 2010; Sashidhar and Podile, 2010; Otieno et al., 2015). Glucose dehydrogenase (GDH) is the key enzyme of direct oxidation pathway, and it is of two types based on their cellular localization, i.e., GDH A and GDH B. GDH A is the membrane-bound enzyme attached to cytoplasmic membrane and orient towards the periplasmic space to oxidize the substrate. The membrane-bound GDH A reported from *Acinetobacter lwoffi, Escherichia coli, Gluconobacter suboxydans, Klebsiella aerogenes,* and *Pseudomonas aeruginosa* (Sashidhar and Podile, 2010; Otieno et al., 2015). Whereas, GDH B is the soluble enzyme, reported only from *Acinetobacter calcoaceticus* (Cleton-Jansen et al., 1988; Sashidhar and Podile, 2010). The bacterial glucose dehydrogenase enzyme required PQQ as a cofactor for its activity. Proteins encoded by *pqqABCDEF* operon are required for the synthesis of PQQ. PqqA is a short oligopeptide of 22–24 amino acids, a substrate for PqqE; PqqC is the key enzyme catalyzing the final step in PQQ biosynthesis; PqqD has

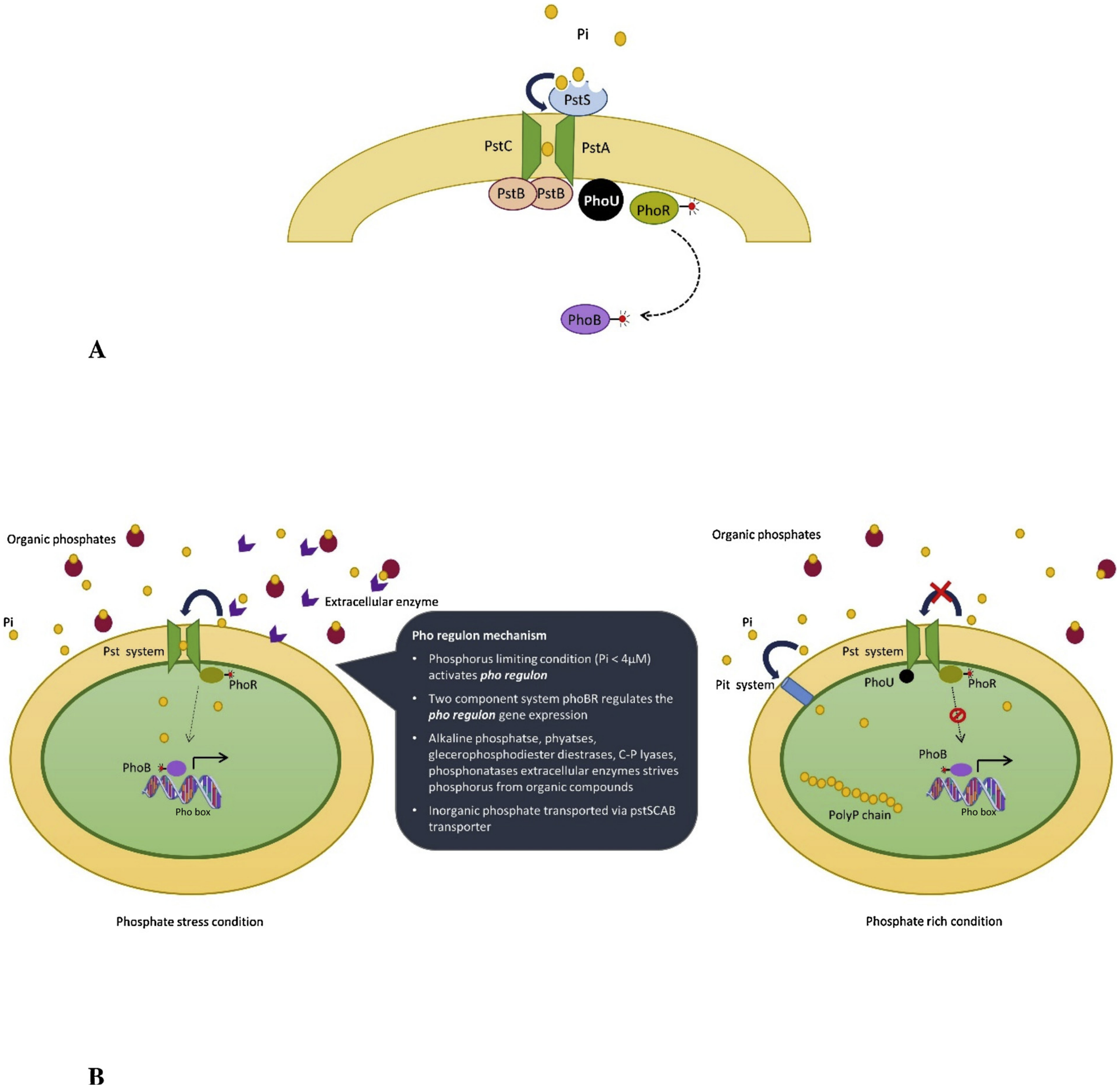

Fig. 2. The generalized mechanism of signal transduction by phoBR two-component system and Pi transport by high-affinity Pst system under the Phosphate starvation condition.

A. Components of the Pst and Two-component system. **B.** The dotted arrow depicts the activation event of the Pho regulon by bacteria in order to elicit a response to the stimulus. Extracellular enzymes produced for utilizing phosphorus-containing organic compound.

a function to interact with PqqE physically. PqqE catalyzes a reductive cleavage of SAM to 5′-deoxyadenosine and methionine. The two non-essential proteins PqqB and PqqF is a suspected member of the Metallo-β-lactamases family of proteins and a peptidase, respectively (Shen et al., 2012). The distribution of PQQ-dependent GDH is ubiquitous in bacterial species, many of them synthesize their PQQ co-factor whereas others viz., *E. coli* and *Klebsiella pneumoniae* produce PQQ-dependent GDH but incapable of producing PQQ, hence, require an external supply of this cofactor (Neijssel et al., 1983; Hommes et al., 1984; Sashidhar and Podile, 2010).

There are various studies reported about the relatedness of the direct oxidative pathway and phosphorus starvation. The network of the direct oxidation pathway mediated phosphorus solubilization genes (*gcd* and *pqqABCDEF*) showed interaction with Pho regulon genes. In a study by Gyaneshwar et al., the GDH enzyme from *Enterobacter asburiae* exhibited a fivefold increase in its activity under phosphate starvation condition (Gyaneshwar et al., 1999). Similarly, another study on phosphate solubilization potential of *Burkholderia tropica* reported that the direct oxidative pathway has a non-constitutive nature and it is induced under limited P and N availability (Bernabeu et al., 2016). Other than the gene of GDH, genes involved in the biosynthesis of PQQ also can be induced under nutrient limitation (Choi et al., 2008). Zeng et al. (2016) studied the effect of different soluble phosphate concentration (0, 0.5, 1.0, 5.0, 10.0 and 20.0 mmol L^{-1}) on the phosphate solubilizing capacity and *gcd* gene expression of *Pseudomonas frederiksbergensis* JW-SD2. They found that the phosphate solubilizing potential of *P. frederiksbergensis* JW-SD2 was decreasing along with the increasing soluble Pi concentration. As compared to the colony diameter, the clear zone diameter was 1.8 folds greater in 0, 0.5, and 1.0 mmol L^{-1} soluble Pi concentration, whereas no zone was observed at 20.0 mmol L^{-1}. The results of RT-qPCR showed that *gcd* expression is 5.89 and 3.42 folds higher in the case of 0 and 5.0 mmol L^{-1} respectively as compared to the gene expression at 20 mmol L^{-1}. Similar results found in case of *Rhizobium leguminosarum* D600 and *Sinorhizobium meliloti* D163 and the phosphate solubilization potential is repressed at the soluble phosphate concentration of 15 and 25 mmol L^{-1}

respectively (Mikanova and Novakova, 2002). These findings suggest the induction of phosphate solubilization potential subjecting upon low soluble Pi concentration is a universal phenomenon among the microorganisms. The possible explanation of the induction and high activity of PQQ dependent GDH under phosphorus starvation condition might be that gluconic acid-mediated phosphorus solubilization made phosphorus available to the bacterial cell and glucose can now be phosphorylated and sent to the glycolytic pathway. The exact molecular mechanism of low phosphate concentration mediated higher production of organic acids and solubilization of insoluble phosphate form is not known. Hence, it represents a new area of future research towards the development of PSB as biofertilizers.

5.2. *Molecular mechanism of the utilization of various organic phosphorus forms under Pi stressed condition*

Apart from inorganic phosphorus bacteria can use an organic compound having phosphorus, e.g., phosphonates, phytic acid (Phytate) and glycerophosphodiesters (Vershinina and Znamenskaya, 2002; Singh and Satyanarayana, 2011; de Almeida et al., 2015; Otieno et al., 2015). The utilization of these organophosphates is under the control of the Pho regulon TCS PhoBR. The assimilation of the phosphorus-containing compound consists of two steps, first: Transport of compound into the cell and second incorporation of phosphorus into ATP (Vershinina and Znamenskaya, 2002). Uptake of these compounds occurs through additional transporters, for example, Ugp (i.e., glycerophosphodiesters uptake), and Phn (i.e., phosphonate uptake) which are under the control of TCS PhoBR (Yang et al., 2009a, 2009b; Jochimsen et al., 2011; Chekabab et al., 2014; Santos-Beneit, 2015). The utilization of Glycerol-3-phosphate (G3P) and glycerophosphodiester are carried out by the proteins encoded by the *ugpBAECQ* operon. Herein, *ugpB* encodes for periplasmic G-3-P binding protein; *ugpA* and *ugpE* encode for the integral membrane proteins; *ugpC* encodes for the nucleotide binding permease protein, and *ugpQ* encodes for the glycerophosphodiester phosphodiesterases (Vershinina and Znamenskaya, 2002; Yang et al., 2009a, 2009b; Lidbury et al., 2017). Another operon a *glpQT* encodes for glycerophosphodiester phosphodiesterase, and glycerol-3-phosphate permease is known to be responsible for the utilization of glycerophosphodiester (Vershinina and Znamenskaya, 2002; Lidbury et al., 2017).

The other unusual organic source of phosphorus is phosphonates used by bacteria under Pi scarcity. Phosphonates have a characteristic stable carbon-phosphorus (C–P) bond, which is found difficult to be metabolized. Hence, bacteria evolve with the different pathways involving C–P lyase or phosphonatase enzymes, depending on their catalytic C–P bond cleavage and substrate specificity, to break down and utilize phosphonates as a phosphorus source. The C–P lyase pathways breakdown simple unsubstituted phosphonates like methyl phosphonate, using radical-based cleavage mechanism whereas, the phosphonatase use hydrolytic cleavage mechanism to break down the complex phosphonates having the 2-carbonyl group (Vershinina and Znamenskaya, 2002; Morais et al., 2004; Manav et al., 2018). The C–P lyase known to utilize a wide range of substrates including phosphite, saturated as well as unsaturated alkyl and aryl phosphonates. The C–P lyase pathway involves 14 genes arranged in phn operon; *phnCDEFGHIJKLMNOP* is forming a membrane attached multienzyme complex (Vershinina and Znamenskaya, 2002; Morais et al., 2004). The products of the three genes, viz., *phnD, phnE*, and *phnC,* constitute the Phn transport system. Herein, *phnD* encodes for the periplasmic binding protein, *phnE* encodes for the transmembrane protein, and *phnC* encodes for the ABC transporter nucleotide binding protein (permease). The protein product of *phnG*, *phnH*, *phnI*, *phnJ*, *phnK*, *phnL*, and *phnM* forms a multienzyme C–P lyase complex. *phnN* and *phnP* encode for auxiliary proteins, namely ribosyl bisphosphate phosphokinase, and phosphoribosyl cyclic phosphodiesterase. Lastly, the two remaining genes encode for the proteins involved in the regulatory function, *phnF*, and *phnO*, encodes for a transcriptional regulator and aminoalkylphosphonate N-acetyltransferase respectively (Vershinina and Znamenskaya, 2002; Jochimsen et al., 2011; Manav et al., 2018).

Phytate (myo-inositol hexa kis phosphate) is the next alternative source of organic phosphorus for bacterial utilization. Organic phosphorus accounts nearly 80% of total soil phosphorus and phytate constitute the principal organic phosphorus source in soil (Singh and Satyanarayana, 2011; Jorquera et al., 2018; Liu et al., 2018). Bacteria employed phytase (myo-inositol(1,2,3,4,5,6) hexakisphosphate phosphohydrolase) enzyme to break down the complex phytate molecules (Sharma et al., 2013; Jorquera et al., 2018; Samaddar et al., 2019). The activity of the phytase enzyme is under the control of the Pho regulon, under the phosphorus-deficient condition the higher abundance of 3-phytase gene was reported, the less P availability shown to increase mineralization of phytate by bacteria (Zhang et al., 2014; Samaddar et al., 2019).

6. Stress and alarmone mediated responses to maintain the balanced physiology

Guanosine tetra- or pentaphosphate molecule, collectively referred to as (p)ppGpp, is a phosphate-containing alarmone, involved in stringent stress response during the starvation condition. It acts as a modulator of global regulatory response in bacteria by binding to RNA polymerase and causes an essential alteration in the expression profile of the cell, which required for stationary phase survival. The binding of alarmone (p)ppGpp to RNA polymerase redirects its activity to up-regulate the expression of stress response genes and down-regulate the expression of genes responsible for translation like ribosomes and cell building (Spira et al., 1995; Spira and Yagil, 1998; Konberg et al., 1999; Chatterji and Ojha, 2001). In addition to the phosphate starvation, (p)ppGpp accumulation also reported under various stress conditions like carbon, nitrogen and amino acid starvation, iron limitation, fatty acid starvation, as well as osmotic stress and heat shock (Dalebroux and Swanson, 2012; Dasgupta et al., 2016; Köhler et al., 2016; Potrykus and Cashel, 2016; Zhu et al., 2019). It was reported that alarmone (p)ppGpp plays a crucial role in antibiotic tolerance and biofilm formation in many bacteria (Ghosh et al., 2019). There are two ppGpp synthase reported in beta- and gamma-proteobacteria, RelA, and SpoT produce ppGpp by transferring pyrophosphate (PPi) moiety to ATP or GTP under the amino acid starvation and carbon/phosphorus starvation respectively. Whereas, in many others, including some gram-positive bacteria, single Rel Spo homolog (RSH) dedicated to the same function (Mittenhuber, 2001; Sharma, 2016). (p)ppGpp controls the general gene expression pattern during the stress condition by up-regulating the stress survival genes like many molecular chaperones, cold and heat shock genes (*csp*, *dnaJ*, *grpE*, *hdeA*, and *usp*) and down-regulating the bacterial growth and rRNA synthesis. (p)ppGpp required for efficient transcription of *E. coli* and *Pseudomonas putida*, sigma factors like σ^{38}, σ^{32}, σ^{24} and σ^{54} required during the different growth phase and stress conditions respectively (Sharma and Chatterji, 2010; Sharma, 2016). Study on *Pseudomonas aeruginosa* antioxidant defense reported that, in Δ*relA* Δ*spoT* mutant, the total SOD and catalase activity significantly reduced by approximately 75 and 60%, respectively. The *relA* and *spoT* genes complementation restored the effect of reduced activity. The Δ*relA* Δ*spoT* mutant also showed significantly reduced basal expression of *ahpC* as compared to the wild-type. (p)ppGpp indirectly controls the expression of antioxidant, and several of the regulators involved, merged into an intricate network that allows it to respond to different environments. The reduced expression of *katB* and *ahpCF* in the Δ*relA* Δ*spoT* mutant may be the result of impaired expression/activity of OxyR, but this needs more experimental validation (Sampathkumar et al., 2016). Several consecutive acid resistance response genes, encoding glutaminase, glutamate decarboxylase A, and hdeA were induced by Rel Spo Homolog (RSH) in response to acid resistance under stress (Occhialini et al., 2012; Damiano et al., 2015; Köhler et al.,

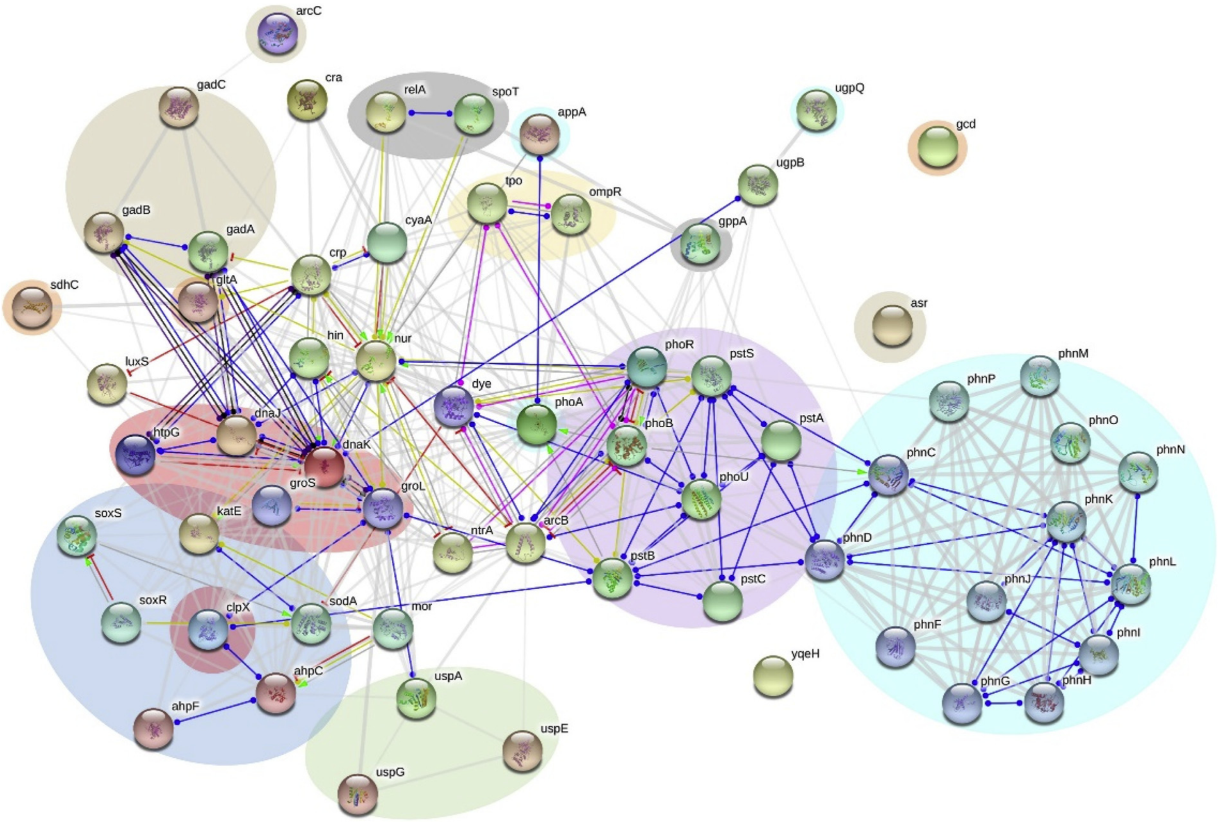

Fig. 3. Gene network crosstalk between the PhoB (response regulator of Pho regulon) with the genes involved in other metabolic pathway and various stress response. Genes involved in different stress response depicted with different colored regions; heat shock – red, acid stress – brown, salt stress – yellow, oxidative stress – blue, stringent response – grey, universal stress response – green, phosphate solubilisation – orange and cyan for inorganic and organic phosphorus respectively, phosphorus limitation - purple.

2016). In *E. coli* cells it was reported that under amino acid starvation the serine hydroxamate (SHX) induce (p)ppGpp synthesis and provides tolerance to high salt condition (Tarusawa et al., 2016). These findings suggest the vital role of (p)ppGpp to maintain the survival of bacterial cell under a variety of stress condition.

7. Crosstalk between Pho regulon, alarmone biosynthesis, and other stress response genes

The molecular interaction network of the selected genes involved in phosphorus homeostasis under Pi stress, phosphate solubilization and various stress response viz., heat shock, salt, acid, and oxidative stress constructed by string software (Mering et al., 2003). Parameters of the network construction were as follows; confidence level kept to medium (0.400) and interaction score kept to query protein only (Fig. 3). The network of the weighted protein interactions offers a sophisticated observation of functional linkages and facilitates the scrutiny of modularity in biological processes. Protein or gene interactions were not only bound to the direct physical interactions or binding, but they also interact indirectly by regulating each other transcriptionally, by using substrate in a metabolic pathway, or by contributing in a multi-protein complex.

The genes which were in association encounter same selection pressure and need to be maintained together so that its encoded protein will function in harmony. The network interaction showed different modules highlighted with different colored regions, in which these genes interact with each other. These different modules are assigned as the genes involved in different stress response and metabolic pathways clustered together. There was a strong interaction observed between different modules, and different colored edges represent a different mode of interactions between the connecting nodes, like light green for activation; red for inhibition; blue for binding; violet for catalysis and golden for transcriptional regulation (see Fig. 3). There was a molecular interaction present, where *phoB* and *phoR* transcriptionally regulate itself and the other genes of that module. Activation, inhibitions, transcriptional regulation, and binding interactions observed between *phoR* and *phoB*. As expected, there was activation interaction observed in alkaline phosphatase gene (*phoA*) and phosphonate (*phn*) genes by *phoB* response regulator. The *phoB* carried out activation and post-transcriptional modification of *envZ* (*tpo*), the two-component system involved in osmoregulation in an unspecified manner. Expression, inhibition, and expression with inhibition interaction observed between *arcB* and *phoB*.

The regulation of ugp operon in *E. coli* via two separate promoters under both C- and Pi-limiting conditions is the example of Pi and carbon interaction (Kasahara et al., 1991). The upregulation of *phoB* and several other Pho regulon genes in *E. coli* under N limitation condition indicated a link between N and Pi interaction (Marzan and Shimizu, 2011). The expression of poly P kinase (*ppk*), an enzyme responsible for polyP synthesis when plenty of phosphorus present, is known to be under the control of PhoR/PhoB two-component regulatory systems (Kato et al., 1993; Ghorbel et al., 2006). In the absence of cognate sensor protein PhoR, acetyl phosphate, or CreC (PhoM) phosphorylate the PhoB, which further regulates the gene expression (Wanner, 1993).

Under different ecological conditions, the relevance of Pho regulon has demonstrated. The relation of the Pho regulon with biofilm formation was discussed in case of some organisms viz., *E. coli*, *Proteus mirabilis, Pseudomonas,* and *V. cholerae* (Monds et al., 2001, 2007; O'May et al., 2009). While, biofilm formation was abolished in Pst mutant organisms like *P. aerofaciens* and *P. fluorescences* (Monds et al., 2001). Many bacterial species use quorum sensing as a phenomenon to synchronize gene expression according to the density of their resident population (Miller and Bassler, 2001). These signaling molecules from the stationary phase known to repress some genes of Pho operon, i.e., *phoB*, *phoU*, *phoA*, *phoR*, *phoH*, and *phoE* (Ren et al., 2004). Although there are not direct physical interactions between the Pho regulon and alarmone biosynthesis genes, there were many studies present which reported their association with each other. Spira and Yagil (1998) reported the accumulation of *spoT*-dependent ppGpp in Pi starving *E. coli* cells and resulted in the induction of the Pho regulon genes. In the case of *phoB* mutants, the accumulation of ppGpp hampered during Pi starvation, this suggests that PhoB or one of the PHO products results in the control of ppGpp accumulation. The *E. coli* Δ*relA* and Δ*spoT* mutants were unable to accumulate ppGpp as a result, have repressed Pho regulon (Spira and Yagil, 1998; Santos-Beneit, 2015). The link between alarmone and the phosphorous solubilizing gene can be placed by the fact that extracellular enzymes like alkaline phosphatase, phosphonatase were required to mineralize the organic phosphorous compounds by the PSBs. It was reported that ppGpp synthesis is essential for the proper induction of *phoA* and *pstS* genes (Spira et al., 1995). A recent study report that biofilm formation by potential PSB (*Burkholderia tropica* P4 and *B. unamae* P9) on insoluble P granules constructs an environment in its vicinity for better the functioning of organic acids secreted under P deficient conditions by *Burkholderia* strains. As it is known that ppGpp required for biofilm formation; thus, it aids in the process of phosphate solubilization by the *Burkholderia* strains (Ghosh et al., 2019).

8. Outlook and future perspective of gene network crosstalk

As the application of chemical fertilizer has an antagonistic effect on the environment, the use of biofertilizers is encouraged nowadays. The application of individual bioinoculants seems to be expensive and insufficient. Therefore, the development of consortia with environmental stability and long shelf life will aid to commercialize the technology (Amalraj et al., 2015; Gupta et al., 2015). Recently studies are carrying out in the rhizospheric modification, a study of plant growth promoting rhizobacteria (PGPR) diversity, colonization ability, mechanisms of action, application and treir ability to withstand the adverse environmental conditions. Growth promotion or enhancement is not the job of a single gene; a group of genes performed a function to achieve plant growth. It is essential to understand the performance of the single gene and their performance in a cluster and how they interrelate with each other to achieve this goal. The future scenario of the study involves the understanding of the genetics of the potential strains, their ability to withstand the environmental stress condition. It can be answered with the aid of genomic exploration of the gene network involved in the phosphate metabolism, solubilization, and stress responses in bacteria. The current research will be dedicated to the study of microbe-plant interactions, especially in its mode of actions and adaptability to extreme environmental conditions. The researchers must be able to address some critical questions, like how to improve the efficiency of biofertilizers and how to stabilize the microbes in soil systems (Sharma et al., 2013; Mahanty et al., 2017). In order to combat these issues, it is essential to know the metabolic and the functional relationship among the genes involved in the phosphate homeostasis, solubilization, and stress responses.

9. Conclusion

The challenging environmental conditions lead to crosstalk between not only the global regulators but also the signaling molecule (p)ppGpp, to maintain the physiological plasticity of bacteria. The nutritional stress resulted due to the limitation of an essential nutrient and encounter with adverse stress condition elicits a response that directs the cell to enter a differential process of shifting its regulatory and metabolic circuitry. As a result, bacteria evolve with the fittest selection and mount an appropriate response to cope up with the adverse situation. The phenomenon of crosstalk act as a "neural system" that intelligently decide the expression and regulation of a particular set of genes required for survival. It helps the bacteria to surpass the irreversible metabolic wreck that will result into accidental cell death. However, the current understanding of gene network crosstalk is in its starting phase, and detail knowledge of the fine-tuning of the crosstalk with other components involved in it required, which will be unfolded by the omics studies in future.

Declaration of Competing Interest

None.

Acknowledgments

Varsha Jha is grateful to University Grant Commission (UGC) for Senior Research Fellowship (SRF) and also acknowledges the Director, CSIR-National Environmental Engineering Research Institute (CSIR-NEERI) for providing facilities for this work. The manuscript has been checked for plagiarism by Knowledge Resource Centre, CSIR-NEERI, Nagpur, India, and assigned KRC number is CSIR-NEERI/KRC/2017/AUG/EBGD/2.

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