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Review Article

Increasing the Bioavailability of Phosphate by Using Microorganisms

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Phosphorous (P) is a nonrenewable and one of the most important macronutrients for all living organisms. The formation of complexes with cations such as Al, Fe, and Ca reduces the solubility of P leading to limiting the absorption of P by plants. Therefore, we need to apply excessive amounts of P through conventional fertilizers. However, plants can use only a small portion of P of these added fertilizers whenever those become unavailable. Therefore, utilizing excess amounts of phosphate as fertilizers can lead to various environmental issues like eutrophication. Phosphate-solubilizing microorganisms (PSM) have the ability to solubilize soil phosphate through the production of organic acids, inorganic acids, enzymes, protons, siderophores, and exopolysaccharides resulting in the absorption of P by plants. The application of PSM has the potential to be used as an efficient, ecofriendly, and sustainable approach that can replace traditional fertilizers. This review aimed to give an overview of the diversity of PSM, methods of P solubilization, current trends, and technological advances that can assist in using PSM to achieve Sustainable Development Goals (SDGs).

1. Introduction

Phosphorous (P) is an essential macronutrient in biomass [1–3] and is the 11th most abundant element in the Earth's crust, representing 0.12% of its composition [4, 5]. P is available in organic and inorganic forms within P sources [3, 6–8] which are nonrenewable [5, 9, 10]. Among soil, clay, plant and animal matter, and other resources, rock phosphate (apatite) is the best P source [5], and the one which is commonly used for phosphate fertilizer production [11]. The less bioavailability of phosphates is the major issue to be used as fertilizer [11]. PSM has a huge potential to develop and a gap to address in developing as an efficient phosphate biofertilizer by increasing the bioavailability other than the currently used products. Therefore, the purpose of this review is to elaborate the details of PSM and its potential usage as an effective agent for sustainable utilization of phosphate.

2. Functions of Phosphorous in Biomass

Phosphorous is involved in common biological functions for all living organisms [2, 3, 12], as mentioned in Table 1. In particular, P is the second most limiting macronutrient for plant growth, representing 0.2% of plant dry weight [15, 18] and acting as a key element in the animal body [7, 13, 16]. Therefore, P has become a critical and essential element for the wellbeing of human beings [20].

The world population is expected to reach 9,400 million in 2050 [21] and global food production needs to be increased by 50% compared to the demand in 2012 [22]. Due to the low solubility of phosphate, its use has been severely limited [20]. Additionally, the wastage of phosphate that plants and animals cannot utilize causes additional problems such as eutrophication [14, 23]. Low bioavailability of phosphate is directed to the high utilization, and the peak extraction of phosphate will take place in 2030 [24]. Therefore, the sustainable utilization of phosphate is highly required by increasing its bioavailability to avoid wastage of phosphate [5, 24]. A new trend that is emerging is to use microorganisms to solubilize the insoluble forms of phosphates and increase its bioavailability [6, 14, 25]. This review is intended to provide a comprehensive description of the occurrence of lower bioavailability of phosphate, phosphate solubilizing potential of microorganisms and their diversity, and isolation techniques and phosphate solubilizing mechanisms of those microorganisms as well as future trends.

3. Reasons for Lower Bioavailability of Phosphate

Soil is a significant source of phosphate that contains around 400–1000 $mg \cdot kg^{-1}$ of total phosphates [26]. However, only around 1.00–2.50% of phosphate is available for plants due to the high insolubility of phosphate compounds [2, 26, 27]. Orthophosphate is the only soluble of the three types of phosphates contained in the soil while the insoluble organic phosphate and insoluble inorganic phosphates are unavailable for plants [4, 12, 14]. Therefore, orthophosphates such as HPO_4^{2-} and $H_2PO_4^-$ can be absorbed by plants [1, 14, 15, 17, 28, 29], while insoluble inorganic phosphates (PO_4^{3-}) and insoluble organic phosphates are reserved in soil without being absorbed by the plants [1]. Approximately 52.3 billion tons of phosphate-related fertilizers are added annually to maintain the optimum soluble phosphate level in soil. However, plants use approximately 0.2% of this vast amount through absorption via roots [30]. Around 80% of phosphates added into the soil are rapidly converted into an insoluble state and fixed in the soil due to its adsorption, precipitation, or conversion to organic compounds [2, 15, 27, 30, 31]. Phosphorous is highly reactive and not freely available in the elemental form [14]. Phosphate gets immobilized through precipitation or sorption by reactions with Fe^{3+} and Al^{3+} in acidic soils and Ca^{2+} in calcareous soils [2, 11, 14, 17, 21, 26, 28, 31] and forms ferrous phosphate ($FePO_4$), aluminium phosphate ($AlPO_4$), and calcium phosphate (Ca_3 $(PO_4)_2$), respectively [14, 17, 31]. Continuous addition of phosphates into the soil due to this immobilization is not sustainable as it rapidly depletes the natural phosphate resources [11] whilst causing environmental problems such as soil fertility depletion and eutrophication [14].

4. Phosphate Solubilizing Potential of Microorganisms

At present, P management is a necessity to minimize phosphate loss and increase agricultural production [2]. Using microorganisms to solubilize phosphate is cost-effective and eco-friendly compared to chemical and physical methods [31]. According to Shin et al., 2015 [32], chemically synthesized organic acids such as salicylic, citric, phthalic, and oxalic leach the phosphates from the mineral sources. That potential also holds microorganisms, which secrete organic acids [13, 33], such as citric, gluconic, ketogluconic, oxalic [31, 32] acetic, lactic, tartaric, succinic [31] phthalic, salicylic, and malic [32]. For example, Jones and Oburger, 2011 [34] explain that *Gluconacetobacter diazotrophicus* can immobilize phosphate because it produces gluconic and ketogluconic acids. However, the mutant strain of *Gluconacetobacter diazotrophicus* is unable to solubilize phosphate because those mutations would cause a loss of production of organic acids. Jones and Oburger, 2011 [34] reported that tricarboxylic anions such as citrate (salt of citric acid) have a higher potential to immobilize phosphate than dicarboxylic acids such as oxalate and gluconate (salts of oxalic and gluconic acids). Furthermore, various enzymes such as phytase [35] and phosphatase [2, 33, 35] that are secreted by microorganisms induce the PSM to produce exopolysaccharides under stress conditions such as phosphorous deficiency. Exopolysaccharides have an ability to form metal complexes (order of potential of ions to form complexes is $Al^{3+} > Cu^{2+} > Zn^{2+} > Fe^{3+} > Mg^{2+} > K^+$) in the soil and to induce the release of phosphates [34]. This phosphate solubilizing potential of microorganisms converts the insoluble phosphates into soluble form through biochemical processes such as mineralization and transformation [11, 36]. Phosphate solubilizing potential is affected by the applications of organic amendments including composts, plant residue, and animal manure through accelerating the phosphate immobilization process [31, 34] and promoting the phosphate absorption and growth of plants [12, 21, 29, 35].

Furthermore, this phosphate solubilizing potential of microorganisms is naturally applied in mineral weathering [35] and remediation of polluted sites such as heavy metal-contaminated water and soil [33, 37]. In addition, the phosphate-solubilizing potential of microorganisms is more important in the natural phosphorus cycle [33].

5. Diversity of Phosphate Solubilizing Microorganisms (PSM)

The basal habitat of PSM is soil [7, 14]. The average bacteria number in 1 gram of fertile soil is 101 to 1010 cells and their live weight may exceed 2,000 $kg \cdot ha^{-1}$ [14, 38]. The highest

Table 1: Functions of Phosphorous in biomass.

Functions of P in all living organisms	Functions of P in plants	Functions of P in animals
Energy metabolism and transmission [2, 3, 12]	Photosynthesis [2, 3]	Bone formation, eggshell formation, proper function of muscles [13]
Protein and nucleic acids (DNA and RNA) synthesis [1, 12, 14]	Nitrogen fixation [15, 16]	Nerve function associated with signal transduction [7, 13, 16]
Being key component of enzymes, coenzymes, and phospholipids [14, 17]	Improving the quality of crops [15, 18]	
Cell division [3]	Creating the resistant for diseases [7, 19], development of roots [4, 19], strengthening the stems and stalks [8, 17], formation of flowers and seeds [14, 17], transformation of sugar to starch [14], laying down the primordia of plant reproductive parts during the early phases of plant development [17, 18], proper stress mitigation and plant maturation [1, 14]	

number of PSM accumulates at the rhizosphere of plants, and those organisms are metabolically very active [14, 38]. The soil properties such as phosphate content, chemical/physical properties, and organic matter affect the population of the phosphate solubilizing bacteria [7, 38]. Those phosphate-solubilizing bacteria are coccus, bacillus, or spirillum in shape, while the bacillus is the most abundant and the spirillum is the least abundant form [7, 38]. In addition, phosphate-solubilizing bacteria represent 1–50% and phosphate-solubilizing fungi represent 0.1–0.5% of the whole population of PSM in the soil [14, 38]. However, there is a high diversity of PSM in the soil. Among these microbial species; *Bacillus* and *Pseudomonas* are the most abundant bacterial genera and *Penicillium* and *Aspergillus* are the notable fungal genera. The foremost PSM and the countries for relevant research studies are listed in Table 2.

6. Isolation and Characterization of Phosphate Solubilizing Microorganisms

6.1. Culture Media. Isolation of PSM is required for the sustainable utilization of phosphates. The two major culture media that are currently being used for the isolation process are known as the Pikovskaya (PVK) medium and National Botanical Research Institute Phosphate (NBRIP) medium [4, 15].

6.2. Isolation of PSM. The pour plate or spread plate methods on PVK or NBRIP media can be used in isolation [2, 13, 41]. The incubation period and temperature vary with research expectations and requirements whilst usually a temperature of 30°C [3, 21, 39] and 7 days incubation period are used [2, 13, 15, 27]. PSM form a clear zone (halo zone) by solubilizing phosphate around their colonies, reflecting their basic function [2–4, 21, 39, 41, 63]. Isolated halo zone-forming microorganisms can be picked and purified on solid media for several rounds to obtain purified sole microbial colonies [13].

6.3. Evaluation of the Phosphate-Solubilizing Ability. Qualitative and quantitative methods are used to evaluate the phosphate solubilizing ability of PSM. Qualitative evaluation is based on HD/CD value [13, 27, 64] and solubilization index (SI) [2, 3, 15, 16, 27, 41, 52, 63, 65]; while the measurement of phosphate concentration is a quantitative approach [2, 13, 23, 39, 41, 52, 64, 65].

6.3.1. Qualitative Evaluation

(1) HD/CD Value. The phosphate solubilizing ability of PSM is evaluated using the ratio between HD (halo zone diameter) and CD (colony diameter) [13, 27, 64]. If HD/CD ≥ 1.5, it indicates a strong ability. The HD/CD value between 1.0 and 1.5 indicates a weak ability to solubilize phosphate [13].

(2) Solubilization Index (SI). The ratio between the total diameter and colony diameter (Colony diameter + Halo diameter/Colony diameter) is also used in the evaluation of phosphate solubilizing ability [2, 3, 15, 16, 27, 41, 52, 63, 65].

6.3.2. Quantitative Evaluation

(1) Measuring the Phosphate Concentration. The phospho molybdate blue method is usually used to measure the solubilized phosphate concentration. Autoclaved NBRIP or PVK broth media are inoculated with PSM, and those broths that were not inoculated are used as controls. Broth media are incubated by shaking, while the usual incubation period and temperature are 7 days and 28 ± 2°C, respectively [2, 31, 41, 52, 64]. Each test and control broths are centrifuged at 10000 rpm for 15 min [23, 31] to obtain the supernatant, which is used to measure solubilized phosphate. The colorimetric method (molybdenum blue method) is used to measure optical density by using UV-VIS spectrophotometer [2, 31, 41, 52, 64]. In addition, ICP-MS and ICP-OES methods are used to measure the solubilized phosphate concentrations [66].

6.4. Identifying Isolated Strains

6.4.1. Morphological Characterization. Morphological identification is the basic step to characterize PSM [15, 21, 23, 67]. It is achieved by assessing the shape, color, edge, and elevation of the colony. Furthermore, the Gram staining test was used to observe the microbial cells [21, 63].

6.4.2. Biochemical Characterization. Biochemical tests such as Gram staining, starch hydrolysis capability, gelatin hydrolysis, catalase activity, IMViC test, casein hydrolysis, oxidase, carbohydrate fermentation (glucose and sucrose), urease activity, Hugh–Leifson (O/F) reaction, H_2S production, NO_3^- reduction, gelatine liquefaction, and growth at 5% NaCl are important in the characterization process of PSM, and the motility test is also required [3, 21, 67]. A combination of the results of all biochemical tests characterizes the microorganism up to a particular taxonomic level [21, 67]. The Bergey's Manual of Determinative Bacteriology is used for biochemical identification and morphological characterization [23].

6.4.3. Molecular Characterization. 16s rRNA gene sequencing technique is used to characterize and identify the exact bacterial species [3, 21, 23, 31, 41], and ITS sequence analysis is used for the characterization of fungal species [68] of PSM. Universal primers are used for the gene amplification [3, 39]. Agarose gel electrophoresis is used to check the amplified PCR product [3, 13, 21]. Sequencing of the PCR products of the genes is needed to compare the similarity levels with other reference sequences using BLAST to identify the PSM species [2, 3, 13, 31].

Table 2: Phosphate solubilizing microorganisms (PSM).

Microorganismns	Country and any other important character	Reference
Acetobacter aceti	Germany	[33]
Achromobacter xylosoxidans	Israel and Thailand	[39]
Acinetobacter sp.	China	[40]
Acorus calamus	China	[28]
Aeromonas ichthiosmia	China	[15]
Aeromonas veronii	China	[15]
Arthrobacter ramosus	India	[41]
Arthrobacter sp.	India	[42]
Aspergillus aculeatus	India	[43]
Aspergillus amowari	Mali, India	[44, 45]
Aspergillus clavatus	India	[42, 43]
Aspergillus flavus	India, commercially available strain	[42, 46]
Aspergillus foetidus	India	[43]
Aspergillus fumigatus	India	[42, 43]
Aspergillus niger	India, Indonesia, Ethiopia, Brazil, Thailand, China, commercially available strain	[42, 45–50]
Aspergillus ochraceus	Brazil	[47]
Aspergillus tamarii	India	[43]
Aspergillus terreus	India	[43]
Aspergillus terricola	India	[43]
Aspergillus tubingensis	Thailand	[48]
Aspergillus ustus	Commercially available strain	[46]
Azospirillum sp.	Indonesia	[51]
Azotobacter sp.	India	[52]
Azotobacter chroococcum	Egypt	[45]
Bacillus albus	Morocco	[21]
Bacillus altitudinis	China	[15]
Bacillus amyloliquefaciens	India	[3]
Bacillus aryabhattai	China, Morocco	[15, 21]
Bacillus caribensis	Brazilian region	[53]
Bacillus cereus	China, India	[3, 15, 54]
Bacillus endophyticus	India	[41]
Bacillus ferrariae	Brazilian region	[53]
Bacillus filamentosus	Morocco	[21]
Bacillus firmus	China	[15]
Bacillus flexus	China, India	[15, 41]
Bacillus halotolerans	Morocco	[21]
Bacillus idriensis	China	[15]
Bacillus indicus	China	[15]
Bacillus jianyang sp.nov	China	[15]
Bacillus licheniformis	India, Brazil, Morocco	[21, 43, 47]
Bacillus macerans	Brazil	[47]
Bacillus megaterium	Germany, India, Brazil, Morocco, Jordan, United Kingdom	[11, 21, 33, 41, 47]
Bacillus niacin	India	[41]
Bacillus paralicheniformis	Morocco	[21]

Table 2: Continued.

Microorganismns	Country and any other important character	Reference
Bacillus paramycoides	Morocco	[21]
Bacillus polymixa	India	[43]
Bacillus proteolyticus	China	[15]
Bacillus pseudomycoides	Morocco	[21]
Bacillus siamensis	Morocco, India	[3, 21]
Bacillus simplex	Ethiopia	[55]
Bacillus subtilis	India, Brazil, India, Argentina	[3, 41, 45, 47, 56]
Bacillus tequilensis	Morocco	[21]
Bacillus thuringiensis	India	[3, 45]
Bacillus toyonensis	Morocco	[21]
Bacillus wiedmannii	Morocco, India	[3, 21]
Burkholderia ambifaria	China	[40]
Burkholderia cenocepacia	India	[3]
Burkholderia cepacia	China, India, South-eastern Venezuelan region	[3, 40, 45, 57]
Burkholderia contaminans	India	[3]
Burkholderia gladioli	Indonesia	[45]
Burkholderia paludis	India	[3]
Burkholderia pyrrocinia	China	[40]
Burkholderia tropica	Israel and Thailand	[39]
Burkholderia vietnamiensis	South-eastern Venezuelan region	[57]
Candida montana	Ethiopia	[58]
Citrobacter freundii	China	[40]
Citrobacter gillenii	Ethiopia	[55]
Cochliobolus lunatus	Jordan, United Kingdom	[11]
Colleotrichum sp.	India	[59]
Corynibacterium freneyi	Ethiopia	[55]
Cryptococcus luteolus	Ethiopia	[58]
Cupriavidus basilensis	China	[40]
Curvularia sp.	India	[60]
Cylindrocadium sp	Commercially available strain	[46]
Enetrobacter cloacae	India, Ethiopia	[1, 41, 55]
Enterobacter ludwigii	South Korea	[35]
Enterobacter aerogenes	Ethiopia	[55]
Enterobacter asburiae	China	[54]
Enterobacter bugandensis	Morocco	[2]
Enterobacter hormaechei	India	[41]
Enterobacter mori	China	[54]
Enterobacter sp.	China, Indonesia	[40, 51]
Erwinia sp.	Indonesia	[51]
Eupenicillium shearii	Brazil	[47]
Fusarium solani	Commercially available strain	[46]
Glomus fasciculatum	India	[45]
Gordonia amicalis	Ethiopia	[55]
Gordonia terrae	China	[15]

Table 2: Continued.

Microorganismns	Country and any other important character	Reference
Iris tectorum	China	[28]
Klebsiella oxytoca	India	[41]
Klebsiella variicola	Israel and Thailand	[39]
Leclercia adecarboxylata	China	[37]
Mesorhizobium ciceri	Germany	[33]
Microbacterium invictum	China	[15]
Micrococcus leteus	India	[41]
Micromonosporaceae jiansan sp.nov	China	[15]
Mortierella nana	Commercially available strain	[46]
Mucor sp.	Jordan, United Kingdom	[11]
Mycobacterium confluentis	Ethiopia	[55]
Neosartorya fisheri var. fischeri	Ethiopia	[58]
Ochrobactrum pseudogrignonense	Israel and Thailand	[39]
Paecilomyces marquandii	India	[9]
Paenibacillus agaridevorans	China	[15]
Paenibacillus polymyxa	India	[41]
Paenibacillus populi	China	[15]
Paenibacillus provencensis	China	[15]
Paenibacillus thiaminolyticus	India	[41]
Pantoea agglomerans	China, South-eastern Venezuelan region, Morocco	[2, 40, 57]
Pantoea ananatis	South-eastern Venezuelan region	[57]
Pantoea calida	China	[12]
Pantoea rodasii	China	[12]
Pantoea stewartii	Morocco	[2]
Paraburkholderia tropica	India	[41]
Penicicllium variabile P16	Commercially available strain	[61]
Penicillium aculeatum	China	[45]
Penicillium chrysogenum	Mali	[44]
Penicillium daleae	Jordan, United Kingdom	[11]
Penicillium implicatum	Brazil	[47]
Penicillium minioluteum	Brazil	[47]
Penicillium nigricans	India	[43]
Penicillium oxalicum	India	[62]
Penicillium purpurogenum	Brazil, Ethiopia	[47, 58]
Penicillium solitum	Brazil	[47]
Penicillium veridicatum	Brazil	[47]
Providenci arettgeri	India	[41]
Pseudomonas aeruginosa	Israel and Thailand, Ethiopia, India, Taiwan	[23, 39, 45, 55, 56]
Pseudomonas asiatica	China	[15]
Pseudomonas brassicacearum	Morocco	[2]
Pseudomonas cepacia	Brazil	[47]
Pseudomonas cichorii	Ethiopia	[55]
Pseudomonas fluorescens	Germany, Ethiopia, India	[33, 55, 56]
Pseudomonas frederiksbergensis	China	[12, 54]

Table 2: Continued.

Microorganismns	Country and any other important character	Reference
Pseudomonas koreensis	India	[1]
Pseudomonas lactis	Morocco	[2]
Pseudomonas mosselii	China	[40]
Pseudomonas putida	Germany, China, Japan	[33, 37, 45]
Pseudomonas rhizosphaerae	Germany	[33]
Pseudomonas striata	India	[45]
Pseudomonas tolaasii	Ethiopia	[55]
Pseudomonas vancouverensis	China	[12]
Ralstonia picketii	South-eastern Venezuelan region	[57]
Rhizobium sp.	Indonesia, India, Jordan, United Kingdom	[11, 51, 52]
Rhizobium tropici	Colombia	[45]
Rhodococcus aetherivorans	China	[15]
Rhodococcus rhodnii	Ethiopia	[55]
Rhodotrula aurantiaca	Ethiopia	[58]
Roseateles sp.	Indonesia	[51]
Saccharomyces occidentalis	India	[60]
Sclerotium rolfsii	Commercially available strain	[46]
Serratia marcescens	South-eastern Venezuelan region	[57]
Serratia rubidaea	Morocco	[2]
Solibacillus isronensis	China	[15]
Sphingobacterium thalpophilum	Israel and Thailand	[39]
Stenotrophomonas maltophilia	Ethiopia	[55]
Trichoderma sp.	India	[60]
Trichosporon beigelii	Ethiopia	[58]
Verticillium alboatrum	Commercially available strain	[46]
Zygo ascus hellenicus	Ethiopia	[58]

7. Phosphate Solubilizing Mechanisms of Microorganisms

Due to the high reactivity of phosphorous, it is available in the soil as organic and inorganic compounds that are unavailable for plants [69]. Microorganisms immobilize these insoluble phosphates through solubilizing via secreting complex compounds such as protons, organic acid anions, exopolysaccharides, siderophores, and hydroxyl ions, secreting extracellular enzymes, or releasing the phosphates by the degradation of substrates [70] (Figure 1). The phosphate-solubilizing mechanism can be discussed under two major forms, namely, inorganic phosphate solubilization and organic phosphate solubilization based on the substrate [4].

7.1. Inorganic Phosphate-Solubilization Mechanisms. The inorganic phosphates solubilizing process involves organic acids, inorganic acids, siderophore and exopolysaccharide production. and proton extrusion by the PSM [4]. These mechanisms can be described as follows:

7.1.1. Organic Acid Production. Secretion of the organic acids that result from the metabolic activities of PSM is the key mechanism of phosphate solubilization [4, 38]. These organic acids decrease the pH and chelate the cations (such as Al^{3+}, Fe^{3+}, Ca^{2+}) bound to phosphate ions to release the phosphate [4, 38, 45]. Here, organic acids compete with the phosphate-binding sites of the medium and allow phosphates to be available in free form (as HPO_4^{2-} and HPO_4^{-3} [14, 17]. Among the all-organic acids released by PSM, gluconic acid is the most prominent one [4, 14, 17, 38, 69]. Most common organic acids secreted by PSM are listed in Table 3.

7.1.2. Inorganic Acid Production. Some PSMs act as nitrifying and sulfur-oxidizing bacteria that produce inorganic acids such as sulfuric acid, nitric acid, carbonic acid [4], and hydrochloric acid [38] in the process of phosphate solubilization. Nitric acid-producing bacteria such as *Nitrosomonas*, *Nitrobacter*, *Nitrosovibrio*, *Nitrosospira* [75], and sulfuric acid-producing bacteria such as *Thiobacillus thiooxidans* [76] may have a considerable ability to solubilize phosphate. Further studies on these abilities are highly warranted. The released inorganic acids may cause the acidification of the media and H^+ substitution reactions to release the phosphates by converting insoluble phosphates to soluble form [38]. However, the effectiveness of phosphate immobilization by inorganic acids is lower than the efficiency of organic acids [4, 38, 45].

7.1.3. Proton Extrusion. Solubilization of the phosphate without the secretions of acids is also a possibility [4]. In excretion of H^+ through H_2CO_3 production, NH^{4+} assimilation and liberation of organic acid anions are other options for the solubilization of phosphates by acidifying the media [4, 14, 38, 45]. *Pseudomonas fluorescens* [77], *Pseudomonas sp.*, *Bacillus sp.*, and *Azospirillum sp.* [78] significantly exhibit this mechanism of proton extrusion in the process of phosphate solubilization.

7.1.4. Exopolysaccharide Production. Microorganisms release exopolysaccharides under stress conditions that exhibit an ability to promote the phosphate solubilization [4, 79]. Exopolysaccharides bind with the metal ions in the soil, which formed the complexes with phosphates and subsequently resulted in the release of those phosphates. Exopolysaccharide concentration has a positive correlation with the rate of phosphate solubilization [4].

7.1.5. Siderophore Production. Siderophore production is a common ability of microorganisms, although it is used by PSM as the another alternative method to solubilize the phosphates [4, 14, 17, 45]. Siderophores have a strong affinity with chelated iron and release phosphate. Furthermore, it contributes to the release of phosphates from organic phosphates [4].

7.2. Mechanisms of Organic Phosphate Solubilization

7.2.1. Enzyme Production. Organic compounds in the soil such as phosphonates, phytic acid, polyphosphonates, sugar phosphates [4], phosphomonoesters, phosphodiesters, phosphotriesters [45], and phospholipids and nucleic acids [4, 45] are high molecular-weight compounds and are resistant to chemical hydrolysis. Therefore, these organic phosphates should be converted into a soluble form by a biological method such as microbial solubilization [45].

PSM secretes the enzymes to solubilize the organic phosphate [45]. There are three groups of enzymes that are secreted by PSM [4, 45, 69, 70]. These enzymes are as follows:

(1) Nonspecific phosphatases

(2) C-P Lyases and Phosphonatases

(3) Phytases

Phosphatase enzymes cause the hydrolysis of ester phosphate bonds and convert high-molecular-weight organic phosphates into low-molecular-weight compounds to ease off the release of phosphate ions. Phytic acid or myo-inositol phosphate compounds are hydrolyzed by phytase enzyme while ester bonds of phosphonates (e.g., phosphoenolpyruvate, phosphonoacetate) are hydrolyzed by phosphonatase and CeP lyase to form phosphate ions [4, 45, 70].

8. Current Trends and Advances Related to Phosphate Solubilizing Microorganisms

Due to the potential to solubilize organic and inorganic phosphates, there is a trend to use and improve PSM as biofertilizers [7, 14, 45]. Biofertilizers are microbiologically active, eco-friendly, low-cost products, and are applied to soil for growth promotion of plants [14, 17]. Though currently used chemical fertilizers fulfill the phosphate requirement of plants, it damages the soil health and fertility.

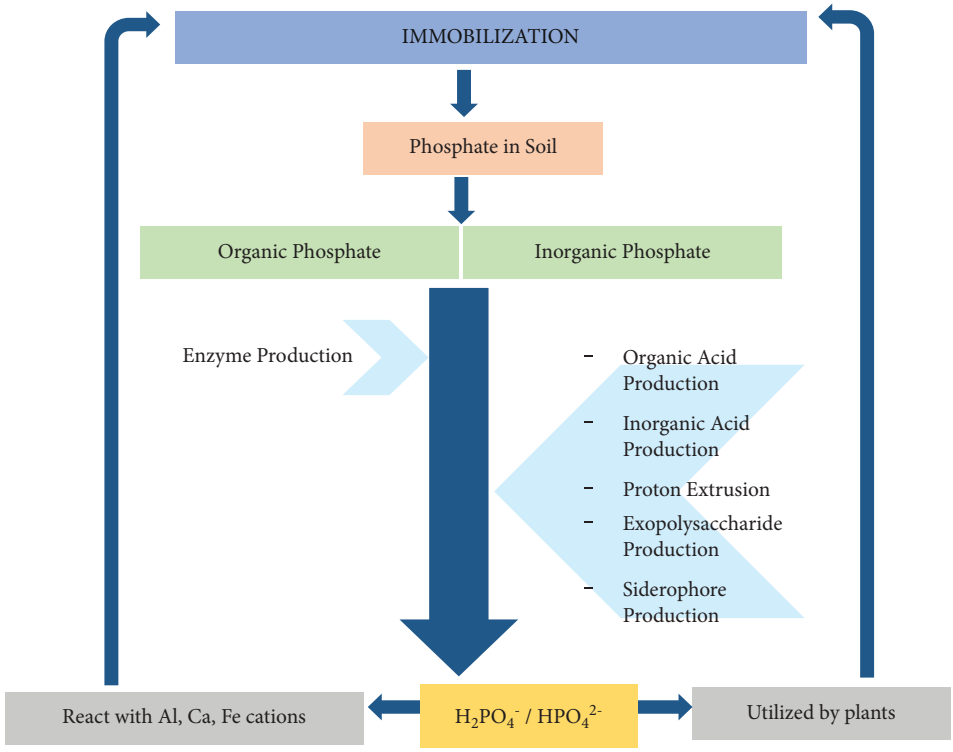

Figure 1: Phosphate solubilizing mechanisms of microorganisms.

Nevertheless, the PSM increases the available phosphates in the soil without harming its biochemical composition [14, 17]. Furthermore, these biofertilizers are not crop-specific and can be used for any type of plant, expecting the increment of growth, yield, and crop quality through the high phosphate absorption [14].

According to Satyaprakash [17], biofertilizers can substitute 50% of chemical fertilizers without any reduction of the yield. However, some other studies report that biofertilizers sometimes increase the yield. For example, it was reported that there was a 12.6% yield increment of sugarcane and 30% increment of wheat with *Azotobacter* and *Bacillus* inoculants [14]. Furthermore, the combinations of PSM with other PSMs give a better output of the yield. For example, there was a 10–20% yield increment with the combination of *Bacillus megaterium* and *Azotobacter chroococcum*. The *Bacillus circulans*, *Bacillus megaterium*, *Bacillus subtilis*, and *Pseudomonas striata* have been recognized as common and effective biofertilizers [14].

The utilization of biofilm inoculants and nano-bio inoculants are the newest techniques in the biofertilizer formulation technology. Biofilm inoculants are a combination of two microorganisms; one microorganism (usually used bacteria) colonizes over the other microorganism (bacteria or fungi can be used). The second microorganism can be a biotic surface to the first microorganism to form a metabolically enhanced biofilm rather than to a single culture [4, 80]. The density of these biofilms is very low in the soil, although it affects high phosphate solubilization and promotes growth in plants [4, 81]. Therefore, utilization of these biofilms as biofertilizers through artificial formulation is beneficial in agriculture [4]. Bahu et al., 2017 explained that *Pleurotus ostreatus*, *Xanthoparmelia mexicana*, and *Penicillium spp*. could be used in biofilms to achieve a significant output.

PSM integrates with nanoparticles or nanostructures to form nano-bio inoculants that can be regarded as another novel technique in the production of biofertilizers. PSM encapsulating with micronutrient nanoparticles or nanoparticles used as delivery agents is the strategy that is used in the formulation of nano-bio inoculants. These nano formulations resist UV inactivation, heat, and desiccation, which allow an efficient application [4]. Silver, copper, gold, platinum, iron, and lead are the commonly used nanoparticles to formulate nano-bio inoculants [4, 82]. According to Shukla et al. [82], significant growth promotion is exhibited by the nano-bio inoculants using gold nanoparticles with *Pseudomonas putida*, *Pseudomonas fluorescens*, *Paenibacillus elgii*, and *Bacillus subtilis*.

Another remarkable trend of PSM is the ability to utilize for bioremediation and phytoremediation. Phytoremediation is an efficient, eco-friendly and economical method that removes metal contaminations from soil [4]. PSMs such as *Enterobacter, Pseudomonas,* and *Klebsiella* have an ability to bioremediate metals by phytostabilization or by phytoextraction in metal contaminated soil [83]. Using a consortium of PSM than single cultures is more efficient in bioremediation. During the process of bioremediation, PSM produces organic acids, protons, siderophore, and exopolysaccharides [4, 84].

PSM has the potential to be used as biological substances to promote plant growth, yield, and crop quality and to be used for bioremediation. Therefore, the development and the application of these eco-friendly biological methods are required to limit the usage of chemical fertilizers and other

Table 3: Organic acid secreting PSM.

Organic Acid	PSM	Reference
Lactic Acid	*E. freundii, A. niger, Penicillium sp., P. trivialis*	[7]
	Escherichia freundii, Aspergillus niger, Penicillium sp., Bacillus megaterium, Pseudomonas sp., Bacillus subtilus, Arthrobacter sp., Bascillus sp., Bacillus firmus B-7650, Bacillus amyloliquefaciens, B. licheniformis, B. atrophaeus, Penibacillus macerans, Vibrio proteolyticus, Xanthobacter agilis, Enterobacter aerogenes, E. taylorae, E. asburiae, Kluyvera cryocrescens, Pseudomonas aerogenes, Chryseomonas luteola, P.trivialis	[71]
Glycolic	*Aspergillus niger, Penicillium sp.*	[7]
	Aspergillus, Penicillium sp.	[18, 72]
Citric	*Penicillium rugulosum, Arrhrobacter, Enterobacter, P. trivialis, Aspergillus flavus, A. niger, Penicillium canescens, A. niger FS 1, Penicillium canescens FS23, Eupenicillium ludwigii FS 27, Penicillium islandicum FS 30*	[7]
	Aspergillus niger, Penicillium sp., Arthrobacter sp., Bascillus sp., Bacillus firmus B-7650, Aspergillus sp., Chaetomium nigricolor, A. japonicus, A. foetidus, Enterobacter agglomerans, Penicillium rugulosum, Aspergillus flavus, Penicillium canescens, P.fluorescens	[71]
	Bacillus sp., Pseudomonas sp., Proteus sp., Aspergillus sp., Azospirillum sp., Penicillium sp.	[18, 72–74]
Gluconic	*Penicillium rugulosum, Enterobacter intermedium, Aspergillus flavus, A. niger, Penicillium canescens, P. fluorescens, Arrhrobacter, Enterobacter, Enterobacter sps Fs 11, A. niger FS 1, Penicillium canescens FS23, Eupenicillium ludwigii FS 27, Penicillium islandicum*	[7]
	Aspergillus niger, Penicillium sp., A. japonicus, A. foetidus, P. radicum, Penicillium rugulosum, Aspergillus flavus, Penicillium canescens, P.fluorescens, B.pumilus var.2, B.subtilis var.2, Actinomadura oligospora, Citrobacter sp.	[71]
	Bacillus sp., Pseudomonas sp., Proteus sp., Aspergillus sp., Azospirillum sp., Penicillium sp., Erwinia herbicola	[18, 72–74]
2-Keto Gluconic	*Enterobacter intermedium*	[7]
	Enterobacter intermedium, Aspergillus sp., Penicillium sp., Chaetomium nigricolor	[71]
	Pseudomonas, Erwinia herbicola	[18, 71, 74]
Oxalic	*Aspergillus flavus, A. niger, Penicillium canescens, A. niger FS 1, Penicillium canescens FS23, Eupenicillium ludwigii FS 27, Penicillium islandicum*	[7]
	Aspergillus niger, Penicillium sp., Aspergillus sp., Chaetomium nigricolor, A. japonicus, A. foetidus, Enterobacter agglomerans, Aspergillus flavus, Penicillium canescens, B.pumilus var.2, B.subtilis var.2, Actinomadura oligospora, Citrobacter sp.	[71]
	Aspergillus sp., Penicillium sp.	[18, 72]
Succinic	*Aspergillus flavus, A. niger, Penicillium canescens*	[7]
	Aspergillus niger, Penicillium sp., Aspergillus sp., Chaetomium nigricolor, A. japonicus, A. foetidus, Aspergillus flavus, Penicillium canescens, B.pumilus var.2, B.subtilis var.2, Actinomadura oligospora, Citrobacter sp.	[71]
	Bacillus sp. , Pseudomonas sp., Proteus sp., Aspergillus sp., Azospirillum sp., Penicillium sp.	[18, 72–74]
Malic	*P. fluorescens, Arrhrobacter sp., Enterobacter sps Fs 11*	[7]
	Bacillus megaterium, Pseudomonas sp., Bacillus subtilus, P.fluorescens	[71]
	Bacillus sp. , Aspergillus sp., Penicillium sp.	[18, 72, 73]
Tartaric	*P. trivialis, Arrhrobacter, Enterobacter*	[7]
	A. japonicus, A. foetidus, P.fluorescens	[71]
	Bacillus sp.	[18, 73]
Funaric	*Enterobacter*	[7]
Formic	*P. trivialis*	[7]
	P.trivialis, B.pumilus var.2, B.subtilis var.2, Actinomadura oligospora, Citrobacter sp.	[71]
Indole Acetic Acid	*Psedomonas nitroreducens*	[7]
Acetic	*Bacillus amyloliquefaciens, B. licheniformis, B. atrophaeus, Penibacillus macerans, Vibrio proteolyticus, Xanthobacter agilis, Enterobacter aerogenes, E. taylorae, E. asburiae, Kluyvera cryocrescens, Pseudomonas aerogenes, Chryseomonas luteola*	[71]
Isobutyric	*Bacillus amyloliquefaciens, B. licheniformis, B. atrophaeus, Penibacillus macerans, Vibrio proteolyticus, Xanthobacter agilis, Enterobacter aerogenes, E. taylorae, E. asburiae, Kluyvera cryocrescens, Pseudomonas aerogenes, Chryseomonas luteola*	[71]

Table 3: Continued.

Organic Acid	PSM	Reference
Itaconic	*Bacillus amyloliquefaciens, B. licheniformis, B. atrophaeus, Penibacillus macerans, Vibrio proteolyticus, Xanthobacter agilis, Enterobacter aerogenes, E. taylorae, E. asburiae, Kluyvera cryocrescens, Pseudomonas aerogenes, Chryseomonas luteola*	[71]
Isovaleric	*Bacillus amyloliquefaciens, B. licheniformis, B. atrophaeus, Penibacillus macerans, Vibrio proteolyticus, Xanthobacter agilis, Enterobacter aerogenes, E. taylorae, E. asburiae, Kluyvera cryocrescens, Pseudomonas aerogenes, Chryseomonas luteola*	[71]
Propionic	*B.pumilus var.2, B.subtilis var.2, Actinomadura oligospora, Citrobacter sp.*	[71]
Valeric	*B.pumilus var.2, B.subtilis var.2, Actinomadura oligospora, Citrobacter sp.*	[71]
Isovaleric	*B.pumilus var.2, B.subtilis var.2, Actinomadura oligospora, Citrobacter sp.*	[71]
Heptonic	*B.pumilus var.2, B.subtilis var.2, Actinomadura oligospora, Citrobacter sp.*	[71]
Caproic	*B.pumilus var.2, B.subtilis var.2, Actinomadura oligospora, Citrobacter sp.*	[71]
Isocaproic	*B.pumilus var.2, B.subtilis var.2, Actinomadura oligospora, Citrobacter sp.*	[71]
Oxalacetic	*B.pumilus var.2, B.subtilis var.2, Actinomadura oligospora, Citrobacter sp.*	[71]
Malonic	*B.pumilus var.2, B.subtilis var.2, Actinomadura oligospora, Citrobacter sp.*	[71]
Fumaric	*Bacillus sp., Pseudomonas sp., Proteus sp., Azospirillum sp.*	[18, 73, 74]

remediating chemicals as well as to promote the sustainable utilization of available phosphates on Earth [17].

9. Drawbacks in Using PSM

The major drawback that can occur in the usage of PSM as biofertilizers is competition with native microbial species and reduction of PSM population in biofertilizers. Among other constraints, there are insufficient nutrient amounts in the soil to produce adequate amounts of organic acids and enzymes, incompatible nature around the rhizosphere that is specific to particular plant species, the survival of PSM in biofertilizers [85], and necessity of aseptic conditions during packaging of manufactured biofertilizers [86]. Though the microorganisms perform well under laboratory and greenhouse conditions, it would not be performed in the field due to the harsh environmental conditions [30, 87].

Furthermore, the poor quality and less consistency are other issues of biofertilizers. Most of the biofertilizers are local productions, and information of the production process is rare. The production cost of biofertilizers also must be competitive compared to chemical fertilizers [30].

Several particular minerals associated with natural phosphate resources also mobilize parallelly with phosphate during the solubilization process. Among those minerals, F^{-}, Cl^{-}, Al^{3+}, and Ca^{2+} limit the solubilization of phosphate and naturally decrease the rate of phosphate solubilization [66].

Gluconic acid has a major responsible role in phosphate solubilization. However, recovery and purification of gluconic acid in conventional production methods are big challenges [88]. Not only that, undesirable by-products and unsatisfactory yields result in chemical methods are even under carefully controlled and optimized conditions [89].

Phytoremediation is an additional advantage of PSM. However, there are some drawbacks in practical applications. Limitations of stress tolerating [90], slow and seasonally applicable treatment due to the changing environmental conditions [91], and limitations of applicable compounds according to the degradation ability are some of them [90].

10. How to Improve PSM

There are various PSM that are found in the soil. In order to utilize the resource at the maximum level, it is necessary to explore phosphate-solubilizing ability by using biotechnology. At present, the scientific knowledge of phosphate solubilization is limited. Thus, it is essential to conduct new studies to explore this area. It is believed that several genes are related to phosphate solubilization. Thus, it is necessary to characterize these genes by genetic engineering and molecular biotechnological studies to obtain highly efficient PSM. At the initial stages, the napA phosphatase gene was transferred to *Burkholderia cepacia* IS-16 strain from *Morganella morganii* strain to produce an effective biofertilizer [92].

As previously described, gluconic acid is the frequently produced organic acid by PSM, which performs the major phosphate solubilizing mechanism. Oxidative glucose, catalyzed by glucose dehydrogenase enzyme, results in gluconic acid when pyrroloquinoline quinine (PQQ) acts as a cofactor [85]. Thus, there is a potential to clone the gene that causes the synthesis of PQQ and transfer to other microbial strains to produce highly efficient PSM with the ability to produce gluconic acid. Especially, most abundant microorganisms associated with the rhizosphere are able to be used for this gene transformation, because those strains are the most competent organisms (*Rhizobium spp., Pseudomonas spp.*) around the rhizosphere which decrease the phosphate solubilization of applied biofertilizers in some cases. Improving the phosphate solubilizing ability of PSM by using biotechnology needs to be essentially focused, because pesticide usage in agriculture has also been limited by microbial biotechnology [92]. In addition, the microorganisms, expected to be used as biofertilizer must have vast potential to tolerate harsh environmental conditions in the field application. Selecting the most tolerable PSMs for harsh conditions and improving the gene compositions to increase the phosphate solubilizing ability is far better to obtain expected outcomes. The genes responsible for phosphate solubilizing enzymes and organic acids have to be considered here.

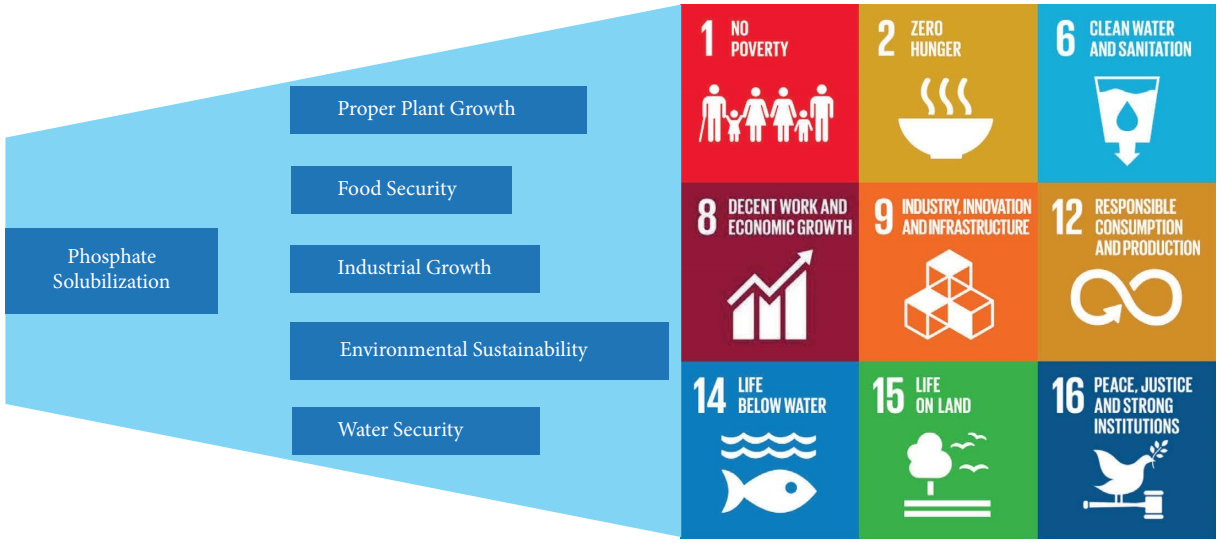

Figure 2: SDG related to Phosphate solubilization.

Further research studies are open to developing stress tolerating, which is highly efficient PSMs.

Selecting a carrier material that provides required nutrients and a favorable environment for the PSM while producing biofertilizers would enhance effectiveness up to the expected higher outcomes. In addition, it will strengthen the PSM to compete with native microorganisms and reflect the result of high-quality biofertilizers [30, 86]. High quality and low-cost phosphate biofertilizers still have a huge gap to fulfil in the international market [30]. An internationally recognized strong quality control framework has to be established to improve the quality of phosphate biofertilizers to achieve the economic goals.

Furthermore, parallel solubilization of associated minerals that decrease the phosphate solubilization has to be declined or to mask those minerals. Further research studies are needed to investigate a method to solubilize only phosphate or limit the solubilization of other interfering minerals.

Moreover, some essential macro and micronutrients for plants such as Mg, K, Cu Mn, and Zn parallelly mobilize during the phosphate solubilization process [12, 30]. This added advantage has to be considered in the biofertilizer production and price decision process.

Aspergillus sp., *Penicillium sp*, and *Gluconobacter sp.* [89, 93, 94] are adaptable to commercial production of gluconic acid as phosphate biofertilizer due to their huge potential for the natural synthesis of gluconic acid. There is a gap in developing a method to synthesize gluconic acid with high purity by using an eco-friendly and cost-effective substrate. Abovementioned microbial species have a huge opportunity to represent the frontline.

As the option for the issues of phytoremediation, a combination of other remediation methods with phytoremediation may give a significant positive outcome, and this also needs to be studied further.

11. Contribution of PSM for Achieving Sustainable Development Goals (SDG)

Increasing bioavailability of phosphate by microorganisms contributes towards sustainable development in a broad range of key areas (Figure 2). Proper plant growth, food security, industrial growth, environmental sustainability, and water security are directly affecting key areas with the microbial solubilization of phosphate [95].

Continuous addition of phosphate fertilizers to provide optimum requirement of phosphate for crops due to the low bioavailability is not the proper way and it is a waste of the resource [96]. Potential of PSM to solubilize available phosphate in soil makes responsible consumption of the resource (SDG 12). It creates the pathway to reduce the addition of excess phosphate with associated other chemicals as fertilizers to soil and contribute to build up sustainable terrestrial ecosystems with reverse land degradation to halt biodiversity loss (SDG 15) [85, 97]. On the other way, excess addition of phosphate to soil causes eutrophication by disrupting valuable aquatic resources and polluting the water [98]. Development of PSM as bio fertilizers by reducing the excess utilization of phosphate fertilizers ensures the sustainable conservation of aquatic resources (SDG 14) and of sustainable management of available clean water (SDG 06) [99]. Bioavailability of phosphate accelerates the proper growth of plants with sufficient production of food [100]. Contribution of PSM for food security through sustainable agriculture promotes public nutrition and end hunger (SDG 02) [101]. Development of crop production by PSM promotes the sustainable agricultural industry (SDG 09) which ensures the sustainable economic growth (SDG 08) with moving forward to reduction of poverty (SDG 01) [102]. Economically developed society with less poverty, zero hunger, and better living environment promotes sustainable peaceful society, which provides access to justice (SDG 16) [103]. In this context, PSM contributes significantly to achieve SDG directly and indirectly within the framework of the 2030 agenda of the United Nations.

12. Conclusion

The application of PSM to solubilize phosphate is an efficient and eco-friendly method. *Bacillus* and *Pseudomonas* are the

frequent bacterial genera while *Penicillium* and *Aspergillus* are the major fungal genera of PSM. A consortium of PSM other than single cultures improves the output significantly. Among the different solubilizing methods followed by PSM, organic acid production is notable, and gluconic acid is the foremost organic acid involved in the phosphate immobilization process. Because of this potential, there is a new trend to use more diverse and much more potent PSM for the formulation of biofertilizers. Genetic engineering and molecular biotechnology can be used to develop the phosphate solubilization of PSM. These applications and developments in methods would sustainably enhance the utilization of phosphate. Therefore, PSM contributes directly and indirectly to achieve the SDG, especially the goals of no poverty, zero hunger, clean water and sanitation, decent work and economic growth, industry innovation and infrastructure, responsible consumption and production, life below water, life on land and peace justice, and strong institutions.

Conflicts of Interest

The authors declare that they have no conflicts of interest.

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