

Biodiversity, mechanisms of action, and potential biotechnological applications of phytate-solubilizing microbiome: A review

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ABSTRACT

In the 21st century, industrial applications of potential microbial enzymes have grown extensively and are still increasing to satisfy the requirements of the world's expanding population and to tackle the natural resources depletion. Due to the increasing demand of such enzymes, phytases have been extensively investigated to decrease the quantity of phytate in animal feed and human food. Phytases are a group of enzymes that are able to release phosphate from phytate, one of the superabundant forms of organic phosphate present in the natural environment. They comprise efficacious enzymatic groups that help in solubilizing phytate and therefore provide plants with a supportive environment. These enzymes can be obtained from different sources, for example, from animals, plants, and microbes. The microbial phytases have been recognized as more stable, efficient, and promising as compared to animal- and plant-based phytases. Phytate-solubilizing microbes use a sustainable and eco-friendly approach to reduce the consumption of chemically synthesized phosphate fertilizers that are widely used worldwide. These microbes have several biotechnological applications other than the agriculture sector, such as they can be used in the fish feeds, bioethanol production, biomedical sectors, and paper and pulp industries. Notwithstanding the renowned importance in biotechnology, investigation on phytases-producing microbes and microbial phytases is noticeably restricted, and more efforts are required to develop the knowledge of phytases present in microbes and their application.

1. INTRODUCTION

Phytate (salts of *myo*-inositol-1,2,3,4,5,6-hexakisphosphate) accounts for a huge amount of the total organic phosphorus (P) present in most soils. However, plants are unable to access this form of P due to its strong interactions with soil minerals and organic matter [1]. There are six inositol esters of phytates: mono-, bis-, tris-, tetrakis-, pentakis-, and hexakis-phosphates (IP1–6). Out of these six inositol

esters, IP6 is the predominant type, accounting for 83–100% of IP [2]. Since phytate was discovered, studies have indicated that it may support vital physiological processes and provide antioxidant, anti-inflammatory, anti-cancer, anti-diabetic, neuroprotective, and antimicrobial qualities. It also has the potential to prevent bone loss and reduce pathological calcification, including renal lithiasis and vascular calcification [3,4]. There is no evidence that plants directly take phytate from the soil. To aid in plant P nutrition, the soil phytate must first undergo phytase-mediated hydrolysis to dephosphorylate from phosphate ester, phosphoanhydride, or cysteine phosphatase (CP). Phytases do this by cleaving the phosphomonoester linkages in the phytate, which releases the inorganic P [5].

Since there is a lot of interest in using phytases, or phytate-degrading enzymes, to lower the amount of phytate in animal feed and human

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food, they have been the subject of extensive research in recent years. They are also useful for kinetic and physiological research since they can produce specific breakdown products [6]. Phytases have raised a lot of interest in both ecological and industrial research because of their various uses and ability to avoid pollution in the environment. Phytases are the main enzymes that dephosphorylate phytate and are suggested to be added to the diet of non-ruminant animals such as fish, pigs, and poultry. Phytases have gained significant interest from entrepreneurs and scientists in the area of environmental protection, nutrition, and biotechnology due to the diverse applications of phytases [7].

Phytases are widely distributed in nature. The main sources are animal tissues, plants, and microorganisms. Phytases of microbial origin are the most appropriate for use in commercial biotechnological production of enzymes because of their simplicity of enzyme production and catalytic properties. Low hydrolytic activity phytases that do not secrete phytase into the rhizosphere have been found in a small number of plant roots. Phytases are actively released by bacteria and, to a lesser degree, microscopic soil fungi [8]. Finding an economical and effective way to synthesize the enzymes is the primary challenge in producing plant phytases. Compared to microbial phytases, plant phytases are less stable in terms of pH and heat. Furthermore, the process of producing phytases from plants is expensive, time-consuming, and complex. In addition, this is not advantageous economically [9].

The extraction of phytases produced by plants requires the use of chemicals and takes longer than that of microorganisms because of the strong cell walls and phyto-depositions. In addition, the type of plant source can affect the cost of chemicals. However, microbes can be used for mass production if the right growth conditions, substrate, and manufacturing methods are used. Consequently, there is greater potential for phytase generation from microbial sources [10]. Furthermore, phytate-solubilizing and mobilizing microbes in agriculture can solve the issue of limited P supply without changing the ecology of the ecosystem, as the use of chemical-based P fertilizers has caused various harmful effects so far. These microbes are known to have various applications in the agriculture sector and industries for the production of food, bioethanol, paper and pulp, fish feeds, and can also be used in the biomedical field [8]. The present review compiled the biodiversity, mechanism of action, and biotechnology of applications of the phytate-solubilizing and mobilizing microbes.

2. BIODIVERSITY OF PHYTATE-SOLUBILIZING MICROBES

On the basis of phylogenetic profiling of phytate-solubilizing microbes, *Pseudomonadota* has been observed as the most dominant phylum, followed by *Bacillota*, *Ascomycota*, *Actinomycetota*, and *Bacteroidota*. *Pseudomonadota* consists of 62 diverse species belonging to 24 different genera, *Bacillota* consists of 42 species belonging to 15 genera, whereas *Ascomycota*, *Actinomycetota*, and *Bacteroidota* consist of 26, 6, and 1 species, respectively [Figure 1]. The most predominant genus among phytate-solubilizing microbes was *Pseudomonas* followed by *Bacillus* [Figure 2].

2.1. Plant-associated Phytate-solubilizing Microbes

Plants host phytate-solubilizing microbes in different regions, fostering a mutual beneficial relationship in which microbes achieve access to nutrients and a stable environment; in return, they provide solubilized P for plant growth.

Plants offer different regions to phytate-solubilizing microbes, and microbes in return they provide solubilized P. Rhizospheric (region around to roots), endophytic (internal space of the tissues), epiphytic (surfaces of the leaves, stem, flower, and tendrils) are the different regions where phytate-solubilizing microbes are present in plants. These three regions are very important for microbes as well as for plants, as they share a symbiotic relationship and benefit each other by providing nutrients, shelter, strength, and survival in the harsh conditions [Table 1].

2.1.1. Phytate-solubilizing microbes in the rhizospheric region

Rhizosphere is an important region of the soil ecosystem where soil microbiota and plant roots interact with each other. These interactions are beneficial for the plant health, improving soil fertility and degrading toxic chemicals. An enormous diversity of microbes is associated with the rhizospheric region. These plant-associated microbial communities are also known as the plant's second genome, as it is crucial for their growth and health [11]. Plant growth-promoting (PGP) fungi and rhizobacteria reside around the plant root soil, improving health and augmenting plant growth. Majority of PGP rhizobacteria and fungi belongs to different genera, including *Agrobacterium*, *Acinetobacter*, *Arthobacter*, *Aspergillus*, *Azospirillum*, *Azotobacter*, *Bacillus*, *Bradyrhizobium*, *Burkholderia*, *Penicillium*, *Pseudomonads*, *Rhizobium*, *Serratia*, *Trichoderma*, and *Thiobacillus* [12,13]. PGP microbes enhance plant growth by diverse methods, including the production of plant growth regulators, siderophores, hydrolytic enzymes, HCN, ammonia, antibiotics, 1-aminocyclopropane-1-carboxylate deaminase, and solubilization of insoluble macro and micronutrients [14]. Many phytate-solubilizing microbes have been reported from rhizospheric soil. In an investigation, phytate-solubilizing *Pseudomonas* sp. have been isolated from alpine grassland [15]. In another investigation, Ghorbani Nasrabadi *et al.* [16] reported the isolation of phytate-degrading rhizospheric *Streptomyces*. Ghorehshizadeh *et al.* [17] reported the isolation of two phytate-degrading rhizospheric bacteria, namely *Pseudomonas taetrolens* and *Pseudomonas* sp., from hop plants.

2.1.2. Phytate-solubilizing microbes in the endophytic region

Endophytes are a prevalent group of microbes that invade intracellular and extracellular gaps in all recognized plant sections but do not harm the host or significantly alter its morphology. Endophytes mainly colonize to the plants internal tissues, where they are capable of participating in several kinds of associations, including mutualistic, commensalistic, symbiotic, and trophobiotic [18]. A huge diversity of endophytic phytase producing microbiome has been reported from the phylum *Actinomycetota*, *Ascomycota*, *Bacillota*, and *Pseudomonadota*. These microbiomes have been reported from cereal crop such as wheat, rice, soybean and sugarcane. In a report, phytase-producing endophytic *Microbacterium foliorum* was isolated from leaves of *Phaseolus vulgaris* [19]. In another report, Yue, Shen *et al.* [20] revealed that endophytic *Bacillus altitudinis* decreases low-P stress in wheat by production of phytases that degrades phytate. Zhu *et al.* [21] reported the identification of endophytic phytases producing yeasts from rice seedlings. In a similar finding, phytase producing endophytic bacteria, *Rahnella aquatilis* was sorted out from Masson pine [22]. In an investigation, [23] demonstrated that two endophytes including *B. altitudinis* and *Pseudonocardia alni* was able to solubilize phytate by the production of phytases.

2.1.3. Phytate-solubilizing microbes in the epiphytic region

Microbes have a main habitat on the surfaces, where they are always greater than in other areas of the biosphere. Plant surface is one of the

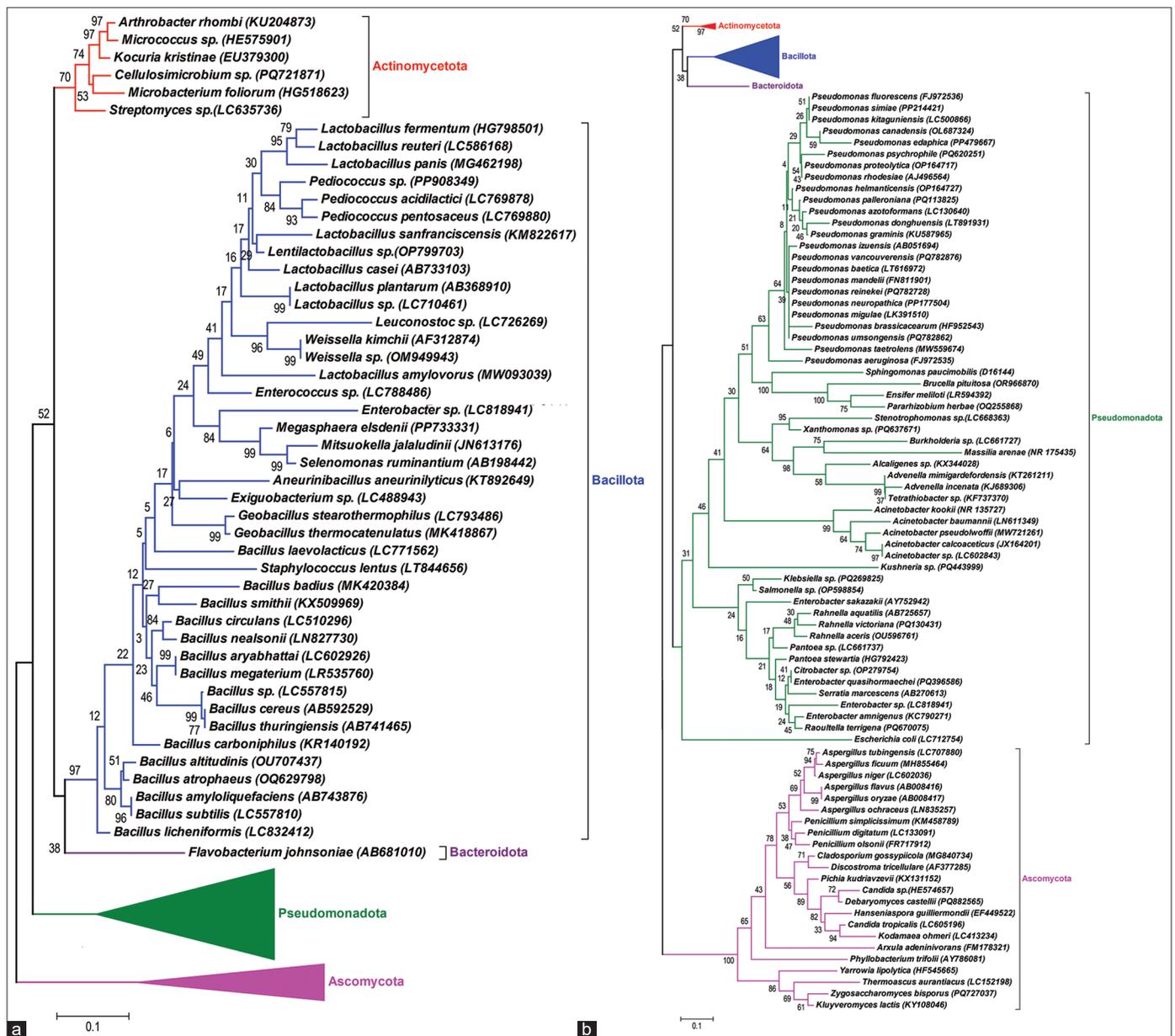


Figure 1: (a) Phylogenetic tree showing the relationships among different species of the phylum Actinomycetota and Bacillota and Bacteroidota listed, (b) Phylogenetic tree showing the relationships among different species of the phylum Pseudomonadota and Ascomycota listed.

essential surfaces for the survival and growth of microorganisms. The epiphytic or phyllosphere of plants is a habitat to some of the most diverse and abundant groups of bacteria, fungi, cyanobacteria, viruses, nematodes, and protozoans [24]. Therefore, epiphytic bacteria play a significant role in influencing a number of beneficial characteristics, including cellular and biological protection, N_2 fixation, and the acceleration of phytohormone biosynthesis. The majority of epiphytic microorganisms are bacteria, which are also the most prevalent, while archaea and fungus are far less prevalent [25]. Epiphytic bacteria are able to adapt to a variety of abiotic challenges including high temperatures, low humidity, damaging ultraviolet (UV) radiation, and osmotic stress. These stressors fluctuate throughout the day and have a significant effect on the communities of epiphytic microbes. The pigmentation of several bacteria found on the phyllosphere, including *Methylobacterium*, *Pseudomonas*, and *Sphingomonas*, aids in shielding from the harmful UV radiation [26]. The phytase producing

microbiomes belong to phylum Actinomycetota, Bacteroidota, Bacillota, and Pseudomonadota. Most common phytase producing bacterial genera belong to *Enterococcus* sp., *Lentilactobacillus* sp., *Lactobacillus plantarum*, *Leuconostoc* sp., *Pediococcus* sp., and *Weissella* sp., In a report, phytase producing epiphytic bacteria namely *Bacillus subtilis* was isolated from rice [27]. In another report, *Acinetobacter* sp, *Exiguobacterium* sp., *Pseudomonas fluorescens*, and *Stenotrophomonas* sp., were isolated from cereal crop and showed phytase production [28].

2.2. Phytate-solubilizing Microbes from Extreme Habitats

2.2.1. Halophilic microbes

Halophiles are extremophiles that can tolerate extreme saline conditions in a range of habitats. Halophiles can be observed in hypersaline settings such as salt marshes, saline soils, salty lakes, and salt pans, which are

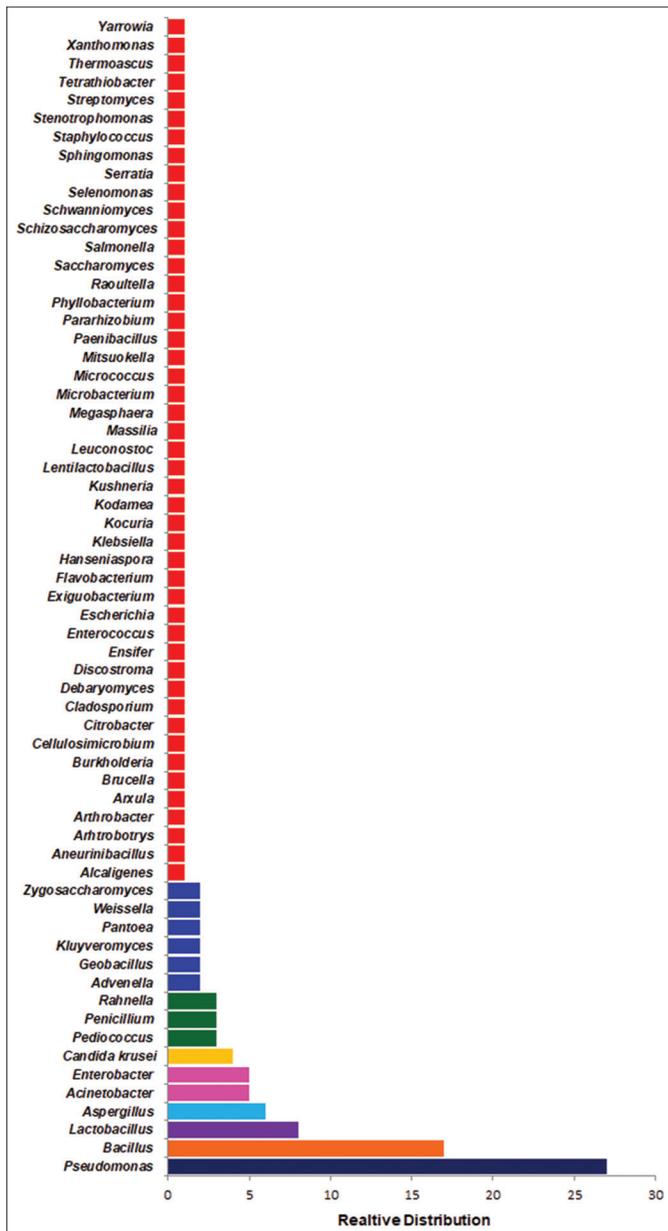


Figure 2: Diversity and distribution of different predominant genera of phytate solubilizing microbes.

widely spread worldwide. These microbial species (archaea, bacteria, and eukarya) are characterized by their high salt requirements for growth [29]. Microbes present in naturally saline habitat are thought to have evolved a technique for surviving in high salt concentrations and several adaptations for keeping them lively under severe conditions. On the basis of genetic standpoint, these microbial species exhibit an under-or over-expression of specific genes and metabolites that enable them to survive with osmotic stress [30]. Various phytase producers are reported from different saline sites include *Aspergillus niger*, *Aspergillus oryzae*, *Bacillus amyloliquefaciens*, *Bacillus megaterium*, *Bacillus licheniformis*, *B. subtilis*, *Enterobacter* sp., *Kushneria* sp., *Kocuria kristinae*, *Micrococcus* sp., *Schizosaccharomyces pombe*, *Sphingomonas paucimobilis*, and *Xanthomonas* sp. [31-34]. In an investigation, [35] reported phytate-solubilizing halotolerant *Bacillus safensis* and *Cytobacillus firmus* from mangrove soil for ecological

and agricultural benefits. In another investigation, [36] revealed the isolation of phytase producing halophilic *Cobetia marina* for animal food supplement.

2.2.2. Marine microbes

The phytates make up around 20–80% of the organic P in manure and soil. The phytic acid is released into the environment through decaying matter and feces. A huge amount of phytic acid also enters into aquatic systems through land subsurface flow, surface runoff that ultimately enters the ocean. Thus phytate is the main source of biophosphorous input from terrestrial runoff into aquatic systems [37]. Although the majority of phytases that have been identified come from terrestrial organisms, a small number have been discovered from marine microbes. Farha and Hatha [38] reported the isolation and identification of phytase producing fungal strain, *Penicillium* sp. from marine sediment. A phytase producing *Curtobacterium luteum* strain was isolated from seagrass meadow sediment [39].

2.2.3. Thermophilic and psychrotrophic microbes

Thermophilic microorganisms are thought to be effective producers of thermostable enzymes that exhibit high catalytic activity, increased resistance to denaturing agents, and decreased contamination rates. Thermostable enzymes are gaining a lot of attention due to their ability to catalyse a variety of enzymatic industrial activities at high temperatures [40]. The extensive substrate specificity exhibited by the phytases of thermophilic moulds is a crucial characteristic for application in the food and feed industries to enhance the nutritional content of food and feed. Thermophilic mould phytases, due to their thermostability, acid stability, and lack of sensitivity to proteases, may find application as supplements to food and animal feed and as well as in the soil amendment to encourage plant growth [41]. Therefore, thermostability is of major importance for phytases which are utilized especially in the feed industry, where the enzymes are exposed to high temperatures range during processing of feed to prevent the contamination caused by pathogenic microbes [42]. Promising thermostable phytases tolerating temperatures beyond 80°C from diverse microbes includes *Thermoascus aurantiacus* [43], *Bacillus nealsonii* [44], and *Geobacillus stearothermophilus* [45]. Zhang et al. [46] characterized thermostable phytases from *B. licheniformis*. Puppala et al. [47] characterized novel thermostable and acidic phytase secreting *Streptomyces* sp. for PGP characteristics.

Phytase have also been found to be produced by the cold tolerant microbes and promotes the agricultural productivity [48]. In a report, reported the ability of phytase-producing *Tetrathlobacter* sp. and *Bacillus* sp. from Himalayan soils were sorted out and they have the ability to improve the growth of Indian mustard [49]. *Bacillus aryabhatai* from low temperature area was reported for producing phytase [50]. Bulk soil collected from Laiyang Experimental Station, which is a low temperature area were reported for having various phytate-solubilizing microbes including *Acinetobacter*, *Bacillus*, *Cupriavidus*, *Arthrobacter*, *Massilia*, *Ochrobactrum*, *Pseudomonas*, and *Stenotrophomonas* [51]. Another study reported that *Pseudomonas azotoformans* from Indian Himalaya higher altitude was found to have phytase activity which helps in the solubilization of soil P [52]. *Pseudomonas mandelii* from alpine grassland growing in Qinghai-Tibetan Plateau was reported for produce phytase and have ability to solubilize phytate in soil and release solubilized P [15].

2.2.4. Acidophilic and alkaline microbes

The microbial enzymes' robust nature with pH stability, thermostability, and multi-functionality makes them potential for efficient

Table 1: Biodiversity of phytase producing microbes for phytate solubilization.

Microorganism	Isolated from	Sample collected	References
<i>Bacillus aryabhathi</i>	Volcanic areas	Soil sample	Sajidan <i>et al.</i> [130]
<i>Bacillus cereus</i>	Volcanic areas	Soil sample	Sajidan <i>et al.</i> [130]
<i>Bacillus coagulans</i>	Hot springs	Water and sediment samples	Irwan <i>et al.</i> [131]
<i>Bacillus licheniformis</i>	Hot springs	Water and sediment samples	Irwan <i>et al.</i> [131]
<i>Bacillus psychrotolerans</i>	Volcanic areas	Soil sample	Sajidan <i>et al.</i> [130]
<i>Bacillus safensis</i>	Tea garden	Rhizospheric soil	Ghosh <i>et al.</i> [132]
<i>Bacillus siamensis</i>	Tea garden	Rhizospheric soil	Ghosh <i>et al.</i> [132]
<i>Bacillus</i> sp.	Hot springs	Water sediments	Jorquera <i>et al.</i> [133]
<i>Bacillus stearothermophilus</i>	Hot springs	Water and sediment samples	Irwan <i>et al.</i> [131]
<i>Bacillus</i> sp.	Indian timber bamboo	Rhizospheric soil	Gauchan <i>et al.</i> [134]
<i>Burkholderia lata</i>	Maize	Endophytic region	Hafsan <i>et al.</i> [135]
<i>Enterobacter quasihormaechei</i>	Spinach	Endophytic region	Misra <i>et al.</i> [136]
<i>Geobacillus</i> sp.	Hot springs	Water sediments	Jorquera <i>et al.</i> [133]
<i>Nocardiopsis</i> sp.	Orchard	Rhizospheric soil	Sharma <i>et al.</i> [137]
<i>Paenibacillus</i> sp.	<i>Mikania micrantha</i>	Rhizospheric soil	Qu <i>et al.</i> [138]
<i>Penicillium daleae</i>	<i>Taxus wallichiana</i>	Endophytic region	Adhikari and Pandey [139]
<i>Proteus</i> sp.	Cabbage fields	Rhizospheric soil	Motamedi <i>et al.</i> [140]
<i>Raoultella terrigena</i>	Cabbage fields	Rhizospheric soil	Motamedi <i>et al.</i> [140]
<i>Streptomyces</i> sp.	Orchard	Rhizospheric soil	Sharma <i>et al.</i> [137]
<i>Talaromyces purpurogenus</i>	Maize	Rhizospheric soil	Sun <i>et al.</i> [141]

biotechnological processes under different physicochemical conditions. The need for sustainable substitutes to various environmental challenges has further surged the industrial enzymes demand [53]. Phytases have been categorized as the alkaline phytases, which are known as the histidine acid phytases. The histidine acid phosphatase (HAP) class shows broad substrate specificity, whereas the alkaline phytase class exhibits substrate specificity [54]. Acid and alkaline phytases have been characterized and purified from diverse microbes. de Oliveira Ornela and Guimarães [55] purified and characterized alkalistable phytase from *Rhizopus microsporus* in submerged fermentation. Rocky-Salimi *et al.* [27] characterized a novel phytase with high pH tolerance from *B. subtilis*. The enzyme showed optimum activity at pH 7.3 and maximum activity at a wide ranges pH (6.3–8.0). Zhang *et al.* [56] characterized a new alkaline β -propeller phytase from *Janthinobacterium* sp. on biochemical and molecular basis. The purified enzyme exhibited maximal activity at 8.5 pH and 45°C and is highly active over a wider range of pH (6.0–9.0). These results indicated the enzyme to be β -propeller phytase with potential in aquaculture feed. Zhang *et al.* [57] identified two phytase types in *Serratia* sp., including HAP (acidic) and β -propeller phytase (alkaline), with maximal activities at pH 5.0 and 7.5–8.0, respectively. Soni *et al.* [58] purified and characterized two extracellular acidic phytases, i.e., Phy I and Phy II, from *A. niger*. The study revealed that Phy I was highly acidic with an optimum pH of 2.5 and was stable over a broad range of pH (1.5–9.0), while Phy II showed an optimum pH of 5.0 with stability in the range of 3.5–9.0 pH. SEO, KIM [59] purified and characterized novel alkaline extracellular phytases from *Aeromonas* sp.

2.3. Biodiversity of Phytate-solubilizing Microbes on the Basis of Types of Phytase

Phytase are classified into four classes, including HAPs, purple acid phosphatases (PAPs), cysteine phytase, and β -Propeller phytase, on the

basis of catalytic mechanism, distinctive sequence characteristics, and 3-D structure [57]. Microbes producing phytases, including bacteria, yeasts, moulds, and archaea, have been recognized as efficient, stable, and promising bioinoculants in comparison to plant and animal-based phytase [60]. Several reports have exposed the diversity of phytase-secreting microbes such as *Escherichia coli*, *Candida otropicalis*, *Candida krusei*, *Zygosaccharomyces bisporus*, *Zygosaccharomyces priorionus*, *Arxula adenivorans*, *B. licheniformis*, *Debaryomyces castellii*, *B. subtilis*, *Kluyveromyces fragilis*, *K. lactis*, *Lactobacillus sanfranciscensis*, *Selenomonas ruminantium*, *Schwanniomyces castellii*, *Megasphaera elsdenii*, *L. amylovorus*, *P. mandelii*, and *P. spartinae* from different hosts [8,61,62].

2.3.1. β -Propeller phytase

The six-bladed beta-propeller structure known as β -propeller phytase is considered to be the most extensively dispersed in nature and is anticipated to be a vital component in the phytate-P cycling in soil and water [63]. β -Propeller phytase is the sole phytase class that has been shown to exhibit activity in both neutral and alkaline pH environments [60]. Despite the fact that phytase from yeast, bacteria, and fungi have been reported in numerous studies, their identification and commercial production are severely limited by their low thermo stability at higher temperatures and potential to modify other metabolic pathways due to their broad substrate specificity [64]. In light of these constraints, β -propeller phytase offers an excellent alternative to existing commercial phytases due to its superior thermostability, proteolytic resistance, and complete substrate specificity [65]. While there have been a number of studies focusing on β -propeller phytases, a thorough examination of the untapped variety, present developments, and particular uses of this class of phytase is still missing. This is extremely important for the effective utilization of this phytase class. A study documented that rPhyPB13, a recombinant β -propeller phytase produced by *B. licheniformis*, has several desirable properties that make

it a useful feed enzyme. Therefore, it would be an appropriate choice for aquatic feed dietary supplementation, as well as would be more effective in aquatic application [66]. A study reported first time a new fungal-derived β -propeller phytases from *Arhthrobotrys oliogospora*. The ideal temperature was found to be 50°C, and the ideal pH value was approximately 7.5. The release of P_i from soybean meal was greatly enhanced by r-Aophytase, and the absorption of water-soluble minerals from finger millet flour and durum wheat flour was also improved [67]. Another study reported that β -propeller phytase produced by *P. mandelii* exhibited the highest activity at 40°C temperature and pH 6 [15].

2.3.2. HAPs

HAPs are the most studied phytase, having a two-step process for phytase hydrolysis and a common active site motif (RHGXRXRP) [68]. The majority of HAPs found in filamentous fungi and yeasts have been documented. HAP phytases are divided into two categories according to their catalytic characteristics [69,70]. The substrate binding locations of the two varieties of HAP phytases differed. A study documented that PA0335 encodes Hol-Pase, and genetic and biochemical techniques were used to examine the enzyme's role and enzymatic activity. The functions of 12 other putative genes implicated in *P. aeruginosa* histidine biosynthesis were investigated in addition to PA0335 [71]. A study reported the histidine acid phytase-producing microbes identified as *Pantoea* sp. using methylotrophic yeast *Pichia pastoris* [72].

2.3.3. PAPs

PAPs receive a colorful nomenclature because of the peculiar purple or pink color in solution [73]. This is an indication of an electrical transition occurring at approximately 560 nm between the metallic ligand Fe(III) and the metal-coordinating tyrosine. Along with phosphoprotein phosphatases and exonucleases, PAPs are metallophosphoesterase superfamily members [74]. The seven metal ligating residues found in members of the PAP family form dimetallic active sites and are highly conserved among PAPs found in bacteria, mammals, and plants [75]. Plant PAPs usually have a Fe(III)-X(II) active site, where X is either one Mn^{2+} or Zn^{2+} , but mammalian PAPs contain a Fe(III)-Fe(II) active site despite conservation of metal legating residues [76]. These metals are present in plant or mammalian cells, indicating that functional PAPs specialization could be provided by divalent metal cation specificity [77]. When it comes to catalyzing the P_i hydrolysis from a wide range of Pi-esters, the majority of PAPs that have undergone biochemical characterization are categorized as non-specific acid phosphatases [78]. However, it is believed that the Fenton reaction involving the active site's Fe(II) and the expression of mammalian PAPs in macrophages and spleen cells upon phagocytosis contributes to the reactive oxygen species production [79].

2.3.4. Cysteine phytases

Another type of phytases seen in anaerobic ruminal bacteria is CP. The CP superfamily and *S. ruminantium* share similarities in their structures and suggested catalytic mechanisms [7,80]. The deeper and broader niche of *S. ruminantium* phytase allows it to carry the substrate, phytic acid. This phytase ultimately hydrolyses phytic acid to produce inositol-2-monophosphate [81]. The ruminal cysteine phytases diversity, abundance, and enzymatic characteristics highlight their significant role, most likely in the terrestrial cycle of P [72]. A study reported that *Mitsuokella jalaludinii* has been isolated from rumen and having the ability to produce the CPs [82].

3. MECHANISMS OF PHYTATE-SOLUBILIZING MICROBES

In soil, phytate has a very high affinity; therefore, it gets

accumulated in comparison to other P esters. The availability of P is bare minimum, so phytate esters bond cleavage is needed. To access the phytate by the plants, it can be solubilized through two different approaches, i.e., desorption and solubilization with the use of phytase enzymes. Desorption can be achieved by the release of protons, organic acids, and phenolic acids, and among all organic acids, production is known to solubilize maximum P. Organic acid contains a carboxylate group, which can mobilize phytate through substitution of P with the carboxylate anion and results in the desorption of P anion in soil. Moreover, the carboxyl group lowers the pH of soil, which releases more P than dibasic oxalate, and oxalate degrades faster. Carboxylates can remove P by solubilizing Fe, and Al through H^+ ion and further dissolve organic matter that binds to P through Fe and Al-bridges, releasing P from this complex. Phytate solubilization can also be improved by chelating metals bound with metal-phytate complex and releasing the binded P [8]. Through the mechanism of phytate solubilization, phytate breaks down into inositol pentaphosphate, inositol tetraphosphate, inositol triphosphate, inositol diphosphate, inositol monophosphate, and finally to inositol, which could release soluble P in the soil, and it is utilized by the plants. The phytate solubilization by microbes is governed by the particular gene, i.e., *phy* [83]. Gene, *phy* has been widely distributed among the diverse microbial species, including bacteria, yeast, and other fungal species. In a report, *Pichia kudriavzevii* was reported for having the *PHYPk* expression [84]. Yeast, *Pichia pastoris*, was reported for having a gene responsible for the production of β -propeller phytase [85]. In another report, *Saccharomyces cerevisiae* were reported for having *PhySc*, which is responsible for the release of HAP [86].

4. BIOTECHNOLOGICAL APPLICATIONS OF PHYTATE-SOLUBILIZING MICROBES

The solubilization of phytate in the soil is mostly dependent on microbial phytases. Phytases catalyze the transformation and mineralization of P_o from phytate to P_i , which can be readily utilized by plants [87]. Due to the possible utility of phytases for enhancing the utilization of P efficiently, biotechnology led the quick advancement of the field to its present stage. The heterologous gene expression development enabled the rapid and comparatively inexpensive production of a huge number of enzymes [88]. Phytase is produced in transgenic plants or microorganisms by the use of genetic engineering techniques or fermentative processes. This innovative technology aims to increase agricultural output and efficiency [89]. Through the usage of genetic engineering and contemporary molecular technologies, new phytase genes have been discovered, making commercial manufacturing easier and expanding its possible uses [90] [Table 2 and Figure 3].

4.1. Agriculture Applications of Phytate-solubilizing Microbes

Phytase enzymes are advantageous in many ways when it comes to environmentally friendly and sustainable agriculture practices [91]. Strategies based on plants and microbes may improve phytate-P utilization by the plant. This is especially important for organic farming because industry regulations limit the use of soluble-P fertilizers. Thus, additional investigation is required for effective phytate-P absorption by plants through growing plants that can synthesize phytase and/or produce organic acids, which are resistant to soil sorption or maintain activity when incorporated into soil [5]. Due to its ability to provide farmers with necessary support, a wide range of commercially accessible microbial phytases have been on the market for almost two decades [92].

Table 2: Biotechnological applications of phytase solubilizing and mobilizing microbes.

Microbes	Source	Application	References
<i>Tetrathlobacter</i> sp.	Himalayan soil	Enhanced P-content, biomass, and growth of <i>Brassica juncea</i>	Kumar <i>et al.</i> [49]
<i>Bacillus</i> sp.	Bulk soil	Increased P levels in maize seedling	Liu <i>et al.</i> [142]
<i>Klebsiella</i> sp.	Poultry field soil	Improves nutritional status of feed and combat environmental pollution	Mittal <i>et al.</i> [143]
<i>Pediococcus acidilactici</i>	Neonatal feces	Dephytinization activity	Sharma and Shukla [144]
<i>Lactobacillus panis</i>	Sourdoughs	Phytate degradation and wheat dough fermented	Nuobariene <i>et al.</i> [145]
<i>Lactobacillus fermentum</i>	Sourdoughs	Phytate degradation and wheat dough fermented	Nuobariene <i>et al.</i> [145]
<i>Pseudomonas rhodesiae</i>	Agricultural soil	Increases P content in soil	Horii <i>et al.</i> [146]
<i>Flavobacterium johnsoniae</i>	Agricultural soil	Increases P content in soil	Horii <i>et al.</i> [146]
<i>Advenella incenata</i>	-	Improved P content and growth of <i>Brassica juncea</i>	Singh <i>et al.</i> [66]
<i>Advenella mimigardefordensis</i>	-	Improved P content and growth of <i>Brassica juncea</i>	Singh <i>et al.</i> [66]
<i>Pseudomonas mandelii</i>	<i>Avena sativa</i> L.	Increased root/shoot ratio of <i>Lolium perenne</i> L.	Li <i>et al.</i> [15]
<i>Bacillus amyloliquefaciens</i>	plant-pathogen-infested soil	Improves growth of maize seedlings under phosphate limitation	Idriss <i>et al.</i> [147]
<i>Bacillus subtilis</i>	Common bean	Antifungal activity against phytopathogens and enhances common bean	Kumar <i>et al.</i> [148]
<i>Streptomyces</i> sp.	Soil	Increment in tomato plants root, shoot and total height	Puppala <i>et al.</i> [47]
<i>Bacillus subtilis</i>	Potato	Increased root/shoot length and weight of potato	Hanif <i>et al.</i> [149]
<i>Pseudomonas proteolytica</i>	Himalayan soil	Improved growth, rosette diameter, leaf area, and biomass of <i>Arabidopsis thaliana</i>	Adhikari <i>et al.</i> [52]
<i>Pseudomonas azotoformans</i>	Himalayan soil	Improved growth, rosette diameter, leaf area, and biomass of <i>Arabidopsis thaliana</i>	Adhikari <i>et al.</i> [52]
<i>Citrobacter</i> sp.	Soil	Increased dry shoot/root ratio of <i>Cajanus cajan</i>	Patel <i>et al.</i> [150]
<i>Pantoea</i> sp.	Soil	Increased dry shoot/root ratio of <i>Cajanus cajan</i>	Patel <i>et al.</i> [150]
<i>Enterobacter</i> sp.	Soil	Dephytinizing animal feeds	Chanderman <i>et al.</i> [151]
<i>Candida</i> sp.	Rice	Enhanced shoot-root length, and weight of rice plants	Zhu <i>et al.</i> [21]
<i>Rahnella aquatilis</i>	Pine	Improves the growth of poplar and Masson pine	Li <i>et al.</i> [152]
<i>Pseudomonas fluorescens</i>	Pine	Improves the growth of poplar and Masson pine	Li <i>et al.</i> [152]
<i>Bacillus megaterium</i>	Poultry waste	Improved root length and P-content in maize plants	Kumar <i>et al.</i> [153]
<i>Candida tropicalis</i>	-	Dephytinization potential and enhances maize plant growth	Puppala <i>et al.</i> [154]
<i>Serratia marcescens</i>	Soil	Improves P-content and growth of barley plants	El Ifa <i>et al.</i> [99]
<i>Bacillus aryabhatai</i>	Chickpea	Improves germination and growth of chickpea seedlings	Pal Roy <i>et al.</i> [50]
<i>Burkholderia</i> sp.	Himalayan yew	Enhanced physico-chemical and plant growth parameters of soybean and rice plants	Adhikari and Pandey [155]
<i>Hanseniaspora guilliermondii</i>	Sugarcane juice	Promoted rice plant growth	Narayanan <i>et al.</i> [156]
<i>Enterobacter quasihormaechei</i>	<i>Spinacia oleracea</i>	Enhanced the nutrient levels and growth of <i>Spinacia oleracea</i>	Misra <i>et al.</i> [136]
<i>Pseudomonas taetrolens</i>	Common hop	Increased P uptake and accumulation of P in stems, petioles, and leaves of hop plants	Ghoreshizadeh <i>et al.</i> [17]

4.1.1. Plant growth promotion

Reduced amounts of synthetic chemical fertilizers and crop production expenses are the foundation of high agricultural efficiency. Bioinoculants may be used for plant development due to their potential agronomic ability and inherent value for plant growth during extended P deficiency [93]. It is believed that microbial phytases are a precise way to increase plant productivity and growth worldwide. Since biofertilizers are easy to use, safe for the environment, inexpensive, and non-toxic, they are seen as highly successful substitutes for synthetic fertilizers [94]. Microbial phytase are desirable target for

biofertilizers because they are very important to the soil P nutrient cycle [95]. Phytate-mineralizing microbes with PGP abilities can be regarded as a promising biofertilizer for plant nutrition [96]. Recent research has shown that adding phytase or a microbial strain that produces phytase to the soil increases the P amount that is available for plant uptake. Enhancing the natural P supplies in the soil ecosystem can be accomplished using this practical and long-lasting approach [97,98].

In an investigation, El Ifa *et al.* [99] reported that phytase producing rhizobacteria increases the P availability and growth of barley

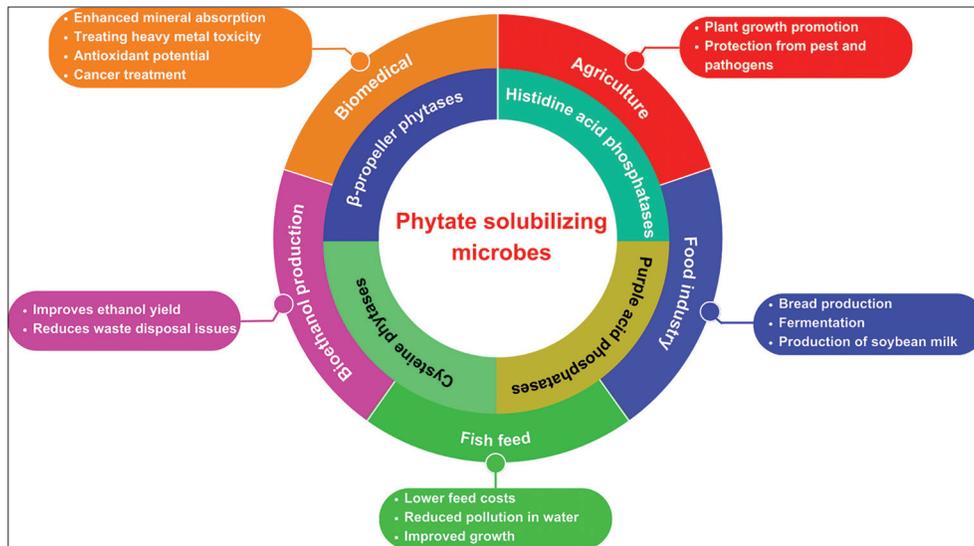


Figure 3: Biotechnological applications of phytate-solubilizing microbes.

plants. In another investigation, Suleimanova *et al.* [100] revealed that the inoculation of phytate-hydrolyzing *Pantoea brenneri* increases the growth of potato under greenhouse conditions. In a report, phytate-solubilizing bacteria, including *B. subtilis*, *B. safensis*, *Pantoea vagans*, *Pantoea agglomerans*, and *Pseudomonas psychrotolerans* were reported to considerably enhance tall fescue growth under *in vitro* conditions. The inoculation of *P. agglomerans* and *P. psychrotolerans* significantly enhances the growth of pepper and tomato plants [101]. In another report, *R. aquatilis* increases the growth of maize plants directly by producing IAA and indirectly by producing phytase Li *et al.* [22].

4.1.2. Plant protection

To ensure sustainable food production worldwide, particularly in developing nations, it is imperative to prioritize the identification, characterization, and biotechnological applications of biological control agents in field and post-harvest crops. This will enable the long-term generation of sustainable agriculture [102]. Production of phytase could be an advantage for microbes that have capability to protect economically imperative crops against phytopathogens. A combination of PGP, phytase and antagonistic activities might lead to the increased performance of commercial biocontrol inoculants under open field conditions. Some plant-associated isolates of *Serratia* sp., mostly *S. plymuthica* and *S. marcescens* have been reported as biocontrol substances for fungal phytopathogens [103-105]. Similarly, Xue *et al.* [106] demonstrated the potential of phytate-solubilizing *Bacillus velezensis* to serve as PGP rhizobacteria and biocontrol agent for management of gray mold on pepper and tomato.

4.2. Industrial Applications of Phytate-solubilizing Microbes

4.2.1. Fish feed

P is an essential nutrient for reproduction, and skeletal development of fish. However, the P uptake from water is negligible by fish and dietary sources play essential role to fulfill the P demands of fish. In the meantime, the extreme concentrations of P are the most common eutrophication cause in water bodies [107]. The microbial phytases inclusion in the diets of fish was prompted by the need to reduce the excretion of P and its loss into the environment, where pollution of P is a hazard to the quality of water [108]. Feeding trials have shown the effectiveness of supplementing microbial phytases for the augmented

utilization of phytate-bounded minerals and phytate-P by fish [109]. Supplementary phytase feed enhances the mineral absorption by chelating the P present in the feed and reduces the P pollution through its faecal excreta. Numerous reports are suggesting the environmental benefits of P release, which has been achieved by the supplementary phytase feed [110]. A study revealed a 60% reduction of P excretion among the phytase-fed catfish [111]. The phytase usage offers environment-related advantages such as minimal mineral supplement lesser excretion of P_o in their faeces, and hence vast reduction of P pollution in aquaculture [92,112].

4.2.2. Biomedical application of phytase

Phytase and phytate have a prominent role in biomedicine. Phytase acts as a neuroprotective, anticancer, antioxidant agent, reduces inflammation, and acts as a chelators. Phytate has been known to act as an anti-carcinogenic, as the diet based on a plant-enriched with phytate demonstrated a lesser prevalence of cancer [113]. In addition, phytases also have various other health benefits such as physiological presence of phytate in body, close association of high-phytate diet with reduced frequency of many diseases and vice versa [114]. They have the potential to lower blood glucose and regulate the insulin secretion in human system and are known to reduce the levels of triglycerides and cholesterol and are also known to inhibit the renal calculi development.

4.2.3. Food industry

Enzymes are of great significance in the food industry. They are vital ingredients in several products and food production processes. Since the first commercial product of phytase Natuphos[®], the global phytase market is estimated at around \$350 million per year [115]. The utilization of microbial phytases in the food industry has various benefits. The addition of microbial phytases to animal feedstuff enhances P availability, which results in enhanced nutrient utilization and growth in animals. This also results in decreased environmental pollution caused by P released from animal waste. In addition, they also improve the nutrient assimilation and mineral bioavailability in plant-based food products, neutralizing the adverse effects of phytic acid on human health. They can also enhance the functional properties and taste of food and release bioactive substances that have advantageous health effects [98]. These enzymes are of great significance in the food industry. Phytase is an excellent breadmaking improver. In addition to reducing the content of phytate in fresh breads and doughs, the

time of fermentation has been shortened by phytases addition without disturbing the pH of dough. An improvement in the crumb texture and bread volume has also been observed. Reduction in the hardness of the bread has been observed with phytase supplementation [116]. The alkaline phytase extracted from *B. amyloliquefaciens* reduced phytate in the preparation of whole-wheat bread and increased the mineral availability [117]. Supplementation with phytase extracted from *E. coli*, ascorbic acid and citric acid reduced the phytate content in the whole-wheat bread and enhanced the iron dialysability [118].

Different strains of *Bifidobacterium* with novel phytate-degrading enzymes used as starters in the fermentation process of whole-wheat dough led to a progressive fall in the content of phytic acid within a short period of fermentation [119,120]. Phytate-free corn steep liquor was obtained by the addition of phytases together with the cell wall of plant-degrading enzymes [121]. Phytate-free corn steep liquor is easier to concentrate, and this is further used in the fermentation industry for the amino acids, antibiotics, polysaccharides, enzymes, and high-energy liquid animal feed ingredients production. Molds used in oriental food fermentation have been demonstrated to produce phytase [122]. Thus, the phytase application in the food industry has great benefits nutritionally and economically. However, the phytase efficacy of commercially available phytase must be tested before applying it in food applications.

4.2.4. Bioethanol production

Currently, biofuels development as a substitute fuel has gained considerable attention due to environmental challenges. Bioethanol is the predominant biofuel, and its production using cassava and corn as raw materials has become a prominent technology. However, phytate content of the raw material declines the ethanol production efficiency and increases the discharge of P, thus influencing the environment [123]. Recently, the utilization of thermostable phytases, which break down the phytic acid in corn and are indirectly related to the bioethanol production, has been increasing. This elimination of phytic acid creates a higher value-added ethanol coproduct, and improves the overall ethanol production efficiency [124,125]. Chan *et al.* [126] presented the genome sequence of *P. kudriavzevii*. The genome sequence revealed genes encoding enzymes involved in the utilization of xylose and the pentose P pathway for the production of bioethanol, along with the genes for phytase production. Phytase from thermophilic mould, *Thermomyces lanuginosus* reduced phytate content in *Colocasia esculenta* starch which resulted in an improvement in the fermentable sugars availability with a concomitant reduction in viscosity and 1.59 fold improvement in production of ethanol [127].

5. CHALLENGES AND FUTURE PERSPECTIVES

Phytate can produce insoluble metal complexes and bond firmly to mineral surfaces, particularly clays. These attributes may provide phytate resistance to mineralization by microbial attack, which could lead to its buildup in soils [128]. Laboratory-to-field translation is still a significant impediment. As a result, it is necessary to design microbial inoculants for stability, shelf life, and compatibility with agricultural operations. Future studies should concentrate on identifying resilient phosphate-solubilizing and phytate-degrading microorganisms that can flourish in a variety of soil types and climates [129]. Transgenic animals and plants producing phytase and low phytate crops are gaining interest nowadays. The development of more application-oriented phytases will usher in a new era of bioprocessing, expanding its range of effectiveness and usefulness. In addition, it highlights the utilization of genetic engineering and sophisticated molecular methods to generate microbial phytase genes for phytase synthesis. The most recent gene enhancement approaches can be used in the future to create more effective next-generation phytases for certain uses [90].

6. CONCLUSIONS

Microbial phytases are the need of present situation because these enzymes have multifarious advantages such as they are environmentally safe, easily accessible, non-toxic and have minimum production cost. They have received an increased amount of interest for use in the food and feed industries as a way of enhancing nutritional attributes and decreasing the levels of P pollution. The industrial application of phytases is indeed hindered due to their decreased activity under high temperature conditions. Therefore, the investigation of the biological attributes of microbial phytase is crucial and can assist researchers in accelerating the levels of phytase stability and activity for industrial application. The increasing demand for thermostable phytases with elevated residual activity could be achieved by the protein engineering techniques, combinatorial application of effective phytase sources, thermoprotective coatings, or heterologous expression hosts. The advancement in phytase research can result to its economical production with a simultaneous reduction of different environmental challenges, including global warming, eutrophication, and greenhouse gas emission. In conclusion, the phytate-solubilizing microbes can be utilized in different sectors, and more microbes having high phytase producing capacity must be identified that are more stable under extreme conditions.

7. AUTHORS' CONTRIBUTIONS

All authors made substantial contributions to conception and design, acquisition of data, or analysis and interpretation of data; took part in drafting the article or revising it critically for important intellectual content; agreed to submit to the current journal; gave final approval of the version to be published; and agree to be accountable for all aspects of the work. All the authors are eligible to be author as per the International Committee of Medical Journal Editors (ICMJE) requirements/guidelines.

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This study does not involve experiments on animals or human subjects.

11. DATA AVAILABILITY

All the data is available with the authors and shall be provided upon request.

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13. USE OF ARTIFICIAL INTELLIGENCE (AI)-ASSISTED TECHNOLOGY

The authors declare that they have not used artificial intelligence (AI)-tools for writing and editing of the manuscript, and no images were manipulated using AI.

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