Review

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Biotechnological production and applications of phytases for removal of phosphorus from environment

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Abstract

Phytic acid (myo-inositol 1,2,3,4,5,6-hexakis dihydrogen phosphate) and its mixed cationic salts, termed as phytate, are naturally found in plants and accumulates in seeds. When monogastric animals take such plants based food, tremendous amount of organic phosphorus is released through excreta, causing several environmental problems and economic losses. Phytases are enzymes that dephosphorylate the phytate (myo-inositol hexakisinositol-phosphate to myo inositol) and release inorganic phosphate plus free inositol, makes phosphorus available for absorption. In recent years, microbial phytases are being applied to animal and human food stuffs to improve food processing and mineral bioavailability. For the production of phytases, variety of natural and recombinant expression systems employing bacteria, yeast and fungi are exploited to enhance the overall productivity. This paper summarizes the information on natural and genetically modified sources of phytases along with main focus on their relative productivity and their associated role towards removal of phosphorus from environment.

Keywords: Phytic acid; monogastric; dephosphorylate; phytase; expression systems; recombinant

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Introduction

Phytic acid and phytate are synthesized in plants and accumulated in ripening seeds. These are essential nutrient source of organic phosphorus in plants for proper growth. Natural phytases are present in plants to carry out the dephosphorylation of phytate complexes (Jorquera et al., 2008). Mono-gastric animals (e.g., pigs, poultry and fish) are unable to digest phytate because these animals lack the enzymes in gastrointestinal tract required for dephosphorylation of the phytate complex (Coffey and Cromwell, 1995) The phytate is an anti-nutrient which forms complex with a number of proteins and bivalent metallic cations, hence decreasing the availability of these nutrients in animals (Soetan and Oyewole, 2009).

Ultimately, phytate accumulates in animals manure which leads to phosphorus pollution in the environment. Plenty of phosphorus is released into the environment causing serious environmental issues, e.g., eutrophication and algal blooms in water bodies and consequential ecological problems (Olstorpe et al., 2009). Sustainable farming requires a reduction in the environmental burden caused by agricultural practices. Animals generate manure in large quantity, particularly phosphorus as major pollutant (Poutanen et al., 2009). Animal feed has to be supplemented with inorganic phosphate to meet the nutritional requirements (Greiner et al., 2013).

The enzyme industry today is the result of rapid development in the field of modern biotechnology (Beilen and Li, 2002). Since ancient times, naturally derived enzymes have been used for variety of purposes such as production of food products (e.g., cheese, wine, vinegar, beer, etc.), industrial products (e.g., manufacturing of leather, linen, etc.) and other items of household usage (Buchholz et al., 2012).

Recombinant DNA technology has further enabled the commercialization of these enzymes, playing a vital role in the improvement of overall yield (Lynd et al., 1999). This has been achieved by unraveling the effective catalytic properties of enzyme systems (Schallmey et al., 2004). In recent years, phytase industry has

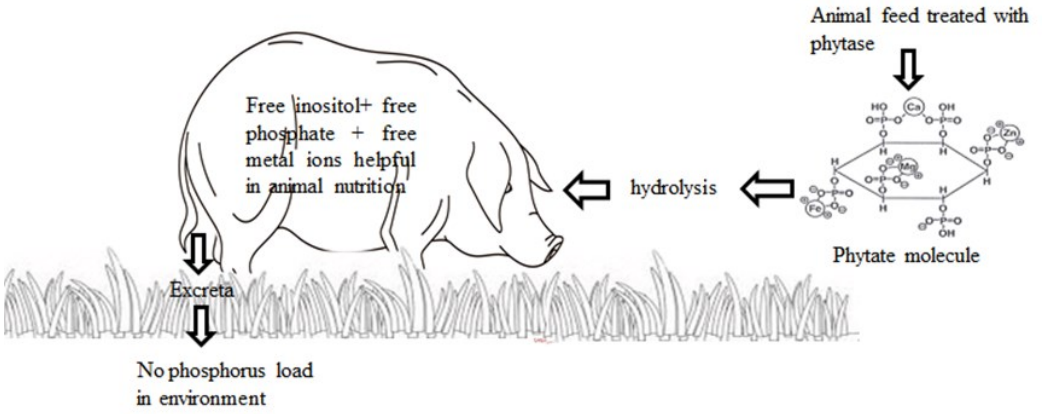

Figure 1: Dephosphorylation of phytate complex by phytase

grown significantly due to its importance in food biotechnology. Phytases, a subclass of phosphatases, are phosphomonoesterase enzymes that accomplish the hydrolysis of phytate into inorganic orthiophosphate (Nielsen et al., 2008). Nomenclature committee of the international Union of Biochemistry and Molecular biology has recognized two types of phytases namely 3-phytase (E.C. 3.1.3.8) and 6-phytase (E.C. 3.1.3.26) (Dvořáková, 1998). The differentiation is devised on their mode of hydrolyzing the phytate as well as their occurrence.

Briefly, the 3-phytase attacks on phytate at the 3rd position of carbon, while 6-phytase targets the 6th position in the ring (Turner et al., 2001). Moreover, phytase 3 belongs to the animal kingdom while phytase 6 is originated from the plants. The catalysis results into dephosphorylation and therefore, releases inorganic phosphate and lower inositol phosphate esters (myo-inositol hexakisinositolphosphate to myo-inositol) (Figure 1).

Animal feed, with the addition of phytase, decreases the phosphorus load upto 50% in the environment and increases the availability of phosphorus for animal digestion (Simons et al., 1990; Lei et al., 1993; Qian et al., 1996; Vohra et al., 2006). The release of inorganic phosphate however depends on the enzyme activity (Buchholz et al., 2012). The current review elucidates the phytase production from different sources by using natural and recombinant means along with its removal from the environment.

Phytase sources

The natural sources of phytases are quite diverse. Plants, animals, fungi as well as bacteria are the natural sources of phytases (Konietzny and Greiner, 2004).

Occurrence of phytase producing bacteria

The bacterial phytases possess several characteristics that make them important in enzyme industry. These include broad spectrum of temperature tolerance, wide range of pH functioning (even closer to the stomach pH of chicken and pigs), high catalytic efficiency, and greater resistance to pepsin. A good example is the phytase -associated class of *Escherichia coli,* that enhances the overall availability of phosphate from phytate (Santos, 2011). The strain BL21 (DE3) of *Escherichia coli* can produce phytase up to 20% of total soluble protein under T7 promoter (Kim et al., 1998). Similarly, wide range of *Bacillus* species are also identified with promising phytase production. Two strains of *Bacillus licheniformis* LH1 and LF1 can produce inorganic phytase quicker than average strains (Roy et al., 2009). Interestingly, the role of *Bacillus* species in phytase enzyme industry is not limited but has also been observed in the immobilization of enzymes on edible matrix. This helps in creating stabilized feed with the enzyme responsible for release of phosphate from phytate. The method displays an efficient food-grade safety (Cho et al., 2011).

Recombinant DNA technology is used to improve the working efficiency of the enzyme machinery especially on wide pH range and temperature (Miao et al., 2013). This technology has further enhanced the production rate in certain species. For example, cloning of the *E. coli* originated benzyl penicillin acylase gene increased phytase production up to 45-fold as compared to wild-type (Adrio and Demain, 2010). Likewise, lactic acid producing bacteria (LAB) such as *Lactobacillus reuteri*, *Lactobacillus panis, Pediococcus pentosaceus and Lactobacillus panis* were also tested for both intra and extra cellular activity; among which *Lactobacillus panis* appeared to have highest phytase activity (Nuobariene et al., 2015).

Despite the renowned importance in biotechnology, information regarding phytase-producing bacteria is not clearly defined and limited. Some major research insights are however required to improve the information about bacterial phytases and their utilization. Some bacteria that show quicker and high rate of phytase production are listed in (Table 1)

Occurrence of phytase producing Yeast

Yeast is a better source of phytases as compared to the bacteria due to the heterologous protein production (Macauley□Patrick et al., 2005). All yeast phytases have a broad temperature (55-75ºC) range and optimal pH (2-5). The molecular weight (MW) of yeast protein range is (40-490 kDa) while bacteria have (10-45 kDa) (Vohra and Satyanarayana, 2004). To analyze phytase production,

Table 1: Examples of a few phytase producing bacteria.

	References
Bacillus amyloqfaciens	(Ha et al., 1999; Idriss et al., 2002; Greiner, 2004a)
Bacillus subtilis	(Kerovuo et al., 1998; Kerovuo et al., 2000; Choi et al., 2001)
Bacillus sp.	(Kim et al., 1998; Choi et al., 2001; Greiner, 2004b)
Citrobacter braakii	(Kim et al., 2003)
Enterobacter sp.	(Yoon et al., 1996)
Escheria coli	(Greiner and Jany, 1991; Greiner et al., 1993; Golovan et al., 1999)
Klebsiella sp.	(Shah and Parekh, 1990; Sajidan et al., 2004)
Klebsiella aerogens	(Tambe et al., 1994)
Klebsiella oxytoca	(Jareonkitmongkol et al., 1997)
Klebsiella pneumonia	(Wang et al., 2004)
Lactobacillus amylovorus	(Sreeramulu et al., 1996)
Megasphaera elsdenii	(Yanke et al., 1998; Cheng et al., 1999)
Mitsuokella jalaludenii	(Lan et al., 2002)
Mitsuokella multiacidus	(Yanke et al., 1998; Cheng et al., 1999)
Obesumbacterium proteus	(Zinin et al., 2004)
Pantoea agglomerans	(Greiner, 2004a; Greiner, 2004b)
Prevotella sp.	(Yanke et al., 1998; Cheng et al., 1999)
Pseudomonas syringae	(Cho et al., 2005)
Pseudomonas fragi	(Jang et al., 2004)
Pseudomonas sp.	(Irving and Cosgrove, 1971; Richardson and Hadobas, 1997)
Selenomonas ruminantium	(Yanke et al., 1998; Cheng et al., 1999)
Treponema sp.	(Yanke et al., 1998; Cheng et al., 1999)
Yersinia intermedia	(Huang et al., 2006)

specific phytase assays were performed on different yeast strains. Two strains namely *Arxula adeninivorans* and *Pichia anomalareached* have been shown to possess highest phytase activity (Olstorpe et al., 2009). Some phytase producing species of yeast are listed in Table 2.

Occurrence of phytase producing fungi

The fungal sources of phytase production are recognized as most promising source due to three main reasons, i.e., (1) fungi is itself resistant to the harsh environment, (2) its growth rate is higher as compared to other sources, and (3) its products (enzymes) possess diverse functioning potential. An example is thermophilic fungi *T. lanuginosus* that secretes phytases, which are tolerant against high temperatures, wide pH range, possesses longer shelf life, and is protease resistant (Singh and Satyanarayana, 2006; Wang et al., 2007). This is the reason that thermophilic fungi have been widely exploited for commercial purposes, e.g., feed and food industries to tolerate acidic environment of intestine during digestion (Greiner and Konietzny, 2006; Maheshwari et al., 2000; Reilly, 1999; Suhairin et al., 2010, Kelly et al., 1986). Thermophilic fungi have an advantage to grow in solid-state fermentation, which is not possible for yeast and bacteria (Vohra and Satyanarayana, 2003), (Vats and Banerjee, 2004). As described earlier, many of the fungi originated phytases are stable in organic solvents and therefore, their functioning is not inhibited in majority of the cases (Gulati et al., 2007; Singh and Satyanarayana, 2009; Vats and Banerjee, 2005).

Extracellular phytases are secreted by a cell and functions outside it. These have simple nutritional environment than bacteria and yeast (Wodzinski and Ullah, 1995), (Vohra and Satyanarayana, 2003), (Maheshwari et al., 2000). Extracellular secreted phytase can be purified easily by down streaming process, which is cost effective as compared to the purification of the intracellular enzymes. Different strains of *Aspergillus niger* have been employed to produce a bulk amount of extracellular phytase with subsequent cultivation on solid-state substrates economically (Ramachandran et al., 2007).Some fungal sources of phytase are given in Table 3.

Table 2: Examples of a few phytase producing yeast species.

Yeast	References
Arxula adininivorans	(Sano et al., 1999)
Fellomyces fuzhouensis	(Sano et al., 1999)
Pichia anomala	(Vohra and Satyanarayana, 2004)
Pichia farinose	(Sano et al., 1999)
Rhodotorula gracilis	(Bindu et al., 1998)
Schwanniomyces occidentalis	(Lambrechts et al., 1993)
Schwanniomyces occidentalis	(Sano et al., 1999)
Sporidiobolus johnsonii	(Sano et al., 1999)
Sporobolimyces sp.	(Sano et al., 1999)
Sterigmatosporus polymorphum	(Sano et al., 1999)

Table 3: Examples of a few phytase producing fungi.

Fungi	References
Aspergillus fumigatus	(Pasamontes et al., 1997; Wyss et al., 1999)
Aspergillus candidus	(Samson, 1994)
Aspergillus niger	(Ehrlich et al., 1993; Yoon et al., 1996)
Aspergillus parasiticus	(Aseri et al., 2009; Reese et al., 2011)
Aspergillus rugulosus	(Samson, 1994; Singh and Satyanarayana, 2011)
Aspergillus terreus	(Mitchell et al., 1997; Wyss et al., 1999)
Penicillium rubrum	(Yadav and Tarafdar, 2003; Awad et al., 2014)
Pseudeurotium simplicissimum	(Summerbell, 2005)
Trichoderma harzianum zonatum	(Aseri et al., 2009; Yadav and Verma, 2012)
Trichoderma viride	(Nevalainen et al., 1998; Aseri et al., 2009)
Saccharomyces cerevisiae	(Andlid et al., 2004)
Saccharomyces uvarum	(Olstorpe et al., 2009; Loponen and Sibakov, 2013)
Rhizpous oryzae	(Bogar et al., 2003; Vohra and Satyanarayana, 2003)
Rhizpous oligosporus	(Casey and Walsh, 2004)
Rhizpous stolonifer	(Guimarães et al., 2006)
Rhizpous arrhizus	(Haefner et al., 2005)
Mucor racemosus	(Singh and Satyanarayana, 2008)
Botrytis cinerea	(Murphy et al., 2008)
Geotrichum candidum	(Fredrikson et al., 2002)
Cladosporium	(Olstorpe et al., 2009)
Rhodotorulla	(Pandey et al., 2001)
Cladosporoides	(Moubasher et al., 2016)

Genetically modified sources of phytases

The natural sources of phytases are quite diverse but the rate of production is quite low to meet up demand of food industry (Singh and Satyanarayana, 2008a). Bacterial genera *Xinnthomonas, Psettdomonas, Xanthomonas campestri, Pseudomonas syringae, Xanthomonas oryzae,* produces various types of phytases (Jorquera et al., 2008). But the rate of prodution is quite low, moreover downstreaming processing is costly due to intracellular prodution. To overcome this problem, different approaches of genetic and protein engineering are carried out for phytase production (Lei and Stahl, 2001). Facultative methylotrophic yeasts such as *Hansenula polymorpha* and *Pichia pastoris* are considered as high yield expression systems (genetic constructs, designed to produce an RNA or protein either inside or outside a cell (Macauley□Patrick et al., 2005) in another host system) for phytase production (Gellissen, 2000). Methanol utilization pathway associated with expression system (methanol is used as an inducer for gene expression) in *Pichia pastoris* is used for phytase production (Mayer et al., 1999).

Genetically modified plant phytase expressed in canola and tobacco is better source of phytase than microbial sources. The phytase gene can easily be transferred and expressed in plants without the danger of contamination by animal pathogen. Phytaseed is genetically produced from canola seed having phytase activity (Zhang et al., 2000). Table 4 show sources strain and production strain for phytase while comparison of phytase sources at optimum conditions along with their efficacy are shown in Table 5.

Commercially available phytases

As far as its commercialization, some of bacterial and fungal phytase are available in market. Phyzyme (Danisco Animal Nutrition, Carol Stream, IL) a bacterial phytase from *Esherichia coli* and produced by *Schizosacchromyces pombe* is also commercialized phytase used as feed supplement (Wu et al., 2006). Natuphos (BASF Corp., Mt. Olive, NJ) is an aspergillus niger phytase used as animal feed along with soyabeen meal (Augspurger et al., 2003). Ronozyme (Roche Vitamins, Parsippany, NJ) is a fungal phytase naturally derived from Peniophora lyci and expressed in Apergillus oryzae through gene technology and used as phytase source in poultry industry (Nielsen and Wenzel, 2007). Similarly,

Table 4: Genetically modified microbial sources of phytases

Source strain	Production strain	References
Bacillus amyloliquefaciens	*Bacillus subtilis*	(Fukuda et al., 1999)
Bacillus licheniformis	*Bacillus subtilis*	(Sarangi and Tye, 2002; Rocky-Salimi et al., 2016)
Escherichia coli	*Streptomyces lividans*	(Kuhn and Stahl, 2003)
Escherichia coli	*Pichia pastoris*	(Rodriguez et al., 1999)
Escherichia coli	*Pichia pastoris*	(Rodriguez et al., 2000)
Escherichia coli	*Pichia pastoris*	(Chen et al., 2004)
Aspergillus fumigatus	*Pichia pastoris*	(Mullaney et al., 2000)
Aspergillus fumigatus	*Aspergillus awamori*	(Yadav and Tarafdar, 2003)
Aspergillus fumigatus	*Hansenula polymorpha*	(Gellissen, 2000)
Aspergillus niger	*Escherichia coli*	(Gellissen, 2000)
Aspergillus niger	*Saccharomyces cerevisiae*	(Han et al., 1999)
Aspergillus niger	*Pichia pastoris*	(Xiong et al., 2004)
Aspergillus niger	*Pichia pastoris*	(Han et al., 1999)
Aspergillus terreus	*Hansenula polymorpha*	(Pandey et al., 2001)
Consensusd	*Hansenula polymorpha*	(Chen et al., 2004)

Table 5: Comparison of phytase from different sources at optimum conditions

Phytase source	Phytase activity (U/mg) (37◦C)	pH optimum	Temperature optimum (◦C)
Bacteria			
Escherichia. Coli	811-1800	4.5	55-60
Bacillus. Subtilus	9.0 -15	6.5-7.5	55-60
Pantoea agglomerans	23	4.5	60
Pseudomonas syringae	769	5.5	4.0
Yeast			
Candida krusei	1210	4.6	40
Pichia anomala	NA[b]	4	60
Fungi			
Aspergillus niger	50-103	5.0-5.5	55-58
Aspergillus oryzae	11	5.5	50
Peniophora lycii	1080	5.5	58
Thermomyces lanuginosus	110	6	65
Plants			
Barley P1	117	5.0	45
Barley P2	43	6.0	55
Mung bean	0.5	7.5	57
Maiz root	5.7	5.0-5.1	35-40
Oat	307	5.0	38
Rye	517	6.0	45
Tomato roots	205	4.3	45

two phytases from the fungal source, one from basidiomycete, *Peniophora lycii*, and the other from a deuteromycete, *Aspergillus ficuum*, have been commercialized (Lei and Porres, 2003). Some commercially available genetically modified phytases are shown in Table 6.

Classical examples on application of phytases

In recent years, addition of feed enzymes in diets of pigs and poultry enhances the nutrient utilization. Exogenous enzymes are capable of degrading non-starch polysaccharides (NSP) in broiler feed based on grains; including barley and wheat initiated this study practice (Yin et al., 2001). However, phytate-bound phosphorus and its partial availability are found in all chick diets (Nelson, 1967). A general application of phytase enzymes is its presence in poultry and pig feed that economically enhances bioavailability of P and reduces the P load on the environment (Cao et al., 2007).

In human foodstuffs, the negative influence of phytate on the bioavailability of Calcium and trace elements zinc has been comprehensively investigated. In certain aspects, however, human diets containing phytate contents have potential paybacks, e.g. anticarcinogenic properties (Selle and Ravindran, 2007). The application of phytases is in the manufacture of food supplements and

Table 6: General Information about the phytase Products Used and their enzymatic properties

	EC1	EC2	EC3	BSP	CB	PL	AN
Trade mark	Quantum	Quantum Blue	Phyzyme XP	AxtraPHY	Ronozyme Hiphos	Ronozyme NP	Natuphos
Supplier	AB Vista	AB Vista	Danisco	Danisco	Novozymes/ DSM	Novozymes/ DSM	BASF
Donor organism	*Escherichia coli*	*Escherichia coli*	*Escherichia coli*	*Buttiauxella sp.*	*Citrobacter braakii*	*Perriophora lycii*	*Aspergillus niger*
Production organism	*Trichoderma reesei*	*Trichoderma reesei*	*Schizosaccharomyces pombe*	*Trichoderma reesei*	*Aspergillus oryzae*	*Aspergillus oryzae*	*Aspergillus niger*
formulation	liquid	Liquid	Liquid	liquid	liquid	Liquid	solid
pH range	4.0- 5.0	3.5-5.0	3.0- 5.0	3.0	3.0- 4.5	4.5- 5.5	4.5- 5.5
Phytase activity at pH 3	92.5	101.3	82.8	235.1	145.7	12.5	64.2
Phytase activity at pH 7	0.8	2.2	1.7	0.5	0.6	7.8	7.0
at pH 5 and 37 ºC	228	142	285	272	364	75	35
at pH 3 and 37 ºC	257	178	302	311	427	98	142
Optimal ionic strength (mM Nacl)	50-100	50-200	100-200	50-200	50-200	50-200	50-600

Table 7: Summary of the potential applications of phytases

	Main functions	Characteristics	Limitations
Inoculation of organic residues with phytase-producing bacteria	Increased P availability; decreased P pollution in water bodies	Resistance to physico-chemical changes during the stabilization process (changes in pH and temperature); capacity to utilize recalcitrant P forms	Low survival/activity during stabilization; rapid adsorption of Pin soil after application
Phytases as feed additives	Increased P utilization and metal bioavailability; decreased P concentration in excrements	Resistance to low pH and peptidase	Low effectiveness; cost
Inoculation of roots with phytase-producing bacteria	Increased uptake of P from organic forms by plants	P liberation should be greater than P requirements; rhizosphere competence	Low survival/activity in rhizosphere, sorption of phytases

functional foods in human consumption (Greiner and Konietzny, 2006). Phytases are used in long shelf life products, liquid and dry enzyme preparations. Enzymes worked well by retaining their activity at high temperatures (Haefner et al., 2005).

Conclusions

Phytases not only have application in diets for mono-gastric animals as feed additive, but also have great potential in enzymes processing and manufacturing for human food consumption. Complete removal of phytate from food digestion in upper small intestine and human stomach results in the bioavailability of essential minerals like (Fe and Zn). Animal feed, with the addition of phytase, decreases the phosphorus load upto 50% in the environment and increases the availability of phosphorus for animal digestion.

Moreover, phytate removal could be cost effective for production, purity and yield of the final products like bread making; corn wet milling, production of plant protein isolates and fractionation of cereal bran. Further research is required to identify metabolically active myo-inositol phosphate or a mixture of phosphatases and phytases. Still one ideal phytase does not exist for complete food degradation. Intrinsic phytases, their catalytic properties should be used for phytate dephosphorylation and to optimize phytate degradation in food product.

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Compliance with ethical standards

Conflict of Interest

The authors declare that they have no conflict of interests.

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