



Review

Increased understanding of the cereal phytase complement for better mineral bio-availability and resource management



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ABSTRACT

The present paper summarizes the current state of knowledge on cereal phytase that are particular relevant for improving mineral and phosphate bio-availability. Phytases can initiate the hydrolysis of phytate, the main storage form of phosphate in cereals and the major anti-nutritional factor for the bio-availability of micronutrients in human nutrition. The composition and levels of mature grain phytase activity (MGPA) in cereals is of central importance for efficient phytate hydrolysis. The MGPA varies considerably between species. Substantial activity is present in Triticeae tribe cereals like wheat, barley and rye whereas non-Triticeae cereals such as maize and rice have very little MGPA. Recent studies have determined the evolutionary relationships of phytases in Triticeae and non-Triticeae and highlighted the importance of the purple acid phosphatase phytases (PAPhys). In the Triticeae, PAPhys are synthesized during grain development (PAPhy_a) and during germination (PAPhy_b). In non-Triticeae species, only PAPhys that are mainly synthesized during germination were identified. The new knowledge provides new opportunities for modulating the MGPA in Triticeae cereals but also indicates that nutritionally relevant levels of MGPA are unlikely to be achieved in non-Triticeae by conventional breeding. Increasing MGPA in barley via cisgenesis is discussed.

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1. Introduction

Phytases (*myo*-inositol hexakisphosphate 3- and 6-phosphohydrolase; EC 3.1.3.8 and EC 3.1.3.26) are phosphatases that can initiate the stepwise hydrolysis of phytate (InsP₆, *myo*-inositol-(1,2,3,4,5,6)-hexakisphosphate). Increasing our understanding of cereal phytases has importance that extends far beyond purely scientific enquiry. Phytases can be viewed as tools for natural resource management and for increasing micro-nutrient bio-availability in food and feed. Future exploitation of the potential of cereal phytases will contribute to the development of sustainable phosphorous management strategies on a global scale and to overcoming micronutrient deficiencies in developing countries.

Around 70% of total seed P and 2–4% of the cereal seed dry weight is represented by phytate (Lott, 1984). In small grained cereals ~90% of the seed phytate is localized in the aleurone and the remaining 10% in the scutellum, whereas in maize 90% is in the

scutellum and 10% in the aleurone. Almost all of the phytate is present as phytin, a mixed salt, usually with K⁺, Ca²⁺, Mg²⁺, or Zn²⁺, and is deposited as globoid particles in single membrane vesicles together with protein (Lott, 1984).

Unfortunately, monogastric animals have only very limited phytase activity in their digestive tract. Similarly, many food and feed components including maize, rice and soybean have essentially no phytase activity in the mature seed. Consequently, phytate passes largely undigested through the digestive systems. To compensate for the lost phytate P, bio-available phosphate is added to feed. From an environmental perspective, this strategy has become critical in many regions of the world where intense livestock production and spreading of manure with high levels of undigested phytate P leads to run-off of phosphorus from oversupplied agricultural soils to aquatic ecosystems. The resulting eutrophication is a severe environmental risk.

Apart from the environmental perspective, phosphorus is a limited resource playing a critical role in the world production of cereals grains and legume seeds (Lott et al., 2011). The time point when phosphate becomes substantially depleted or otherwise inaccessible will depend largely on demand as market drivers should lead to the exploitation of further accessible reserves. However, phosphate consumption worldwide is increasing (Lott et al., 2011). Moreover, most global agricultural production

Abbreviations: BPP, β -Propellar phosphatase; BSE, bovine spongiform encephalitis; CP, cysteine phosphatase; HAP, histidine acid phosphatase; MBM, meat and bone meal; MGPA, mature grain phytase activity; MINPP, multiple inositol polyphosphate phosphatase; PAP, purple acid phosphatase.

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depends on mined phosphate supplies and the exploitation of new accessible reserves for food production will have tangible socio-economic impacts (Lott et al., 2011). This was already clearly demonstrated by two major events that took place at the beginning of the new millennium. The first event was the ban of meat and bone meal (MBM) as a feed additive in Europe as a control measure for bovine spongiform encephalitis (BSE). The consequence of the MBM ban was a profound change in P-management in Europe. MBM was removed from the production chain as a source of P for animal nutrition and cost-effective P-supply alternatives had to be found.

The second event was (and still is) the strong economic growth of China and India that, in conjunction with increases in oil prices, lead to increases and strong fluctuations in the world prices of many resources. Calcium phosphate prices were no exception, increasing the demand for alternative P-sources and efficient P-management technology around the world.

Phytate, at that time almost unexploited, became a valuable resource. The yearly global production of plant phytate in 2000 was estimated to be > 51 million metric tons, equivalent to almost 65% of the elemental P sold worldwide for use in mineral fertilizers (Lott et al., 2001).

Whereas resource and environmental consequences of undigested phytate are mostly of concern for agriculture, human nutritionists are mostly concerned about the consequences of chelation of nutritional important minerals by phytate in the digestive tract. Phytate, and to some extent the lower isomers of inositol phosphate $InsP_5$, $InsP_4$ and $InsP_3$, are strong chelators and bind positively-charged proteins, amino acids and minerals in insoluble complexes in the digestive tract (Brinch-Pedersen and Hatzack, 2006; Kies et al., 2006; Sandberg and Andlid, 2002). Upon passing from the stomach (pH 2–5) to the small intestine (pH 6.5–7.5), the phytate becomes more ionized and begins to bind cations (for a review of pH effects on phytate–mineral interactions see (Champagne and Phillippy, 1989). The decreasing order of stability of mineral phytate complexes *in vitro* is Zn^{2+} , Cu^{2+} , Ni^{2+} , Co^{2+} , Mn^{2+} , Ca^{2+} and Fe^{3+} (Cheryan, 1980). Phytate is considered the major anti-nutritional factor for the bio-availability of micronutrients and contributes to mineral depletion and deficiencies in human populations that rely on whole grains and legume-based products as staple foods. It is estimated that >2 billion people, primarily children and women in developing countries, suffer from iron and zinc deficiencies (Bouis, 2000).

1.1. Strategies for improving phytate P and micro nutrient bio-availability

The issues summarized above have led to increased interest in improved phytate P utilization from plant feed stuffs and on reducing the anti-nutritional effect of non-hydrolyzed phytate on micronutrients in the digestive tract. Five strategies have been proposed to solve these problems. (1) Addition of microbial phytases to food and feed (i.e. up to 2500 FTU/kg, where 1 FTU is the amount of enzyme that liberates 1 μ mol orthophosphate/min from phytate) significantly enhances the release of phosphate and minerals from phytate (Kornegay, 2001; Troesch et al., 2009). (2) Crops can be genetically engineered for increased phytase production in their seeds (Brinch-Pedersen et al., 2002). (3) Pigs have been engineered to produce heterologous phytases in their saliva glands (Golovan et al., 2001). (4) Grains can be soaked in water, germinated or fermented whereby endogenous grain or exogenous phytase is activated (Egli et al., 2002; Marero et al., 1991; Svanberg et al., 1993). (5) Impairing phytate biosynthesis has proved to be useful in

cereals such as maize, barley, rice and wheat (Raboy, 2009). Phytase is central to four out of five of the strategies and we believe that phytase will also prove to be the most versatile solution in the long run.

However, until recently very little was known about plant phytase enzymes, their genes, genetics and potential exploitation in plant breeding and biotechnology. This has changed dramatically over recent years to a situation where the necessary knowledge for reaching towards cereals with a high grain phytase activity (i.e. 6000 FTU/kg) has been provided. In this review we summarize and address issues on cereal phytases that are particularly relevant for improving mineral and phosphate bio-availability in food and feed, and for reducing the environmental load of phosphorus. Genetic engineering of crops with various microbial phytases has been reviewed extensively and will not be repeated here. Likewise it out of scope to review the complex issue of nutrient uptake in the digestive tract.

2. Types of phytases

Currently, four classes of phosphatase enzymes are known to include representatives that can degrade phytate: (1) Histidine Acid Phosphatase (HAP), (2) Purple Acid Phosphatase (PAP), (3) Cysteine Phosphatase (CP) and (4) β -Propellar Phytase (BPP). However, not all classes can effectively utilize phytate as a substrate. Each phytase type has unique structural features due to their distinct catalytic apparatus that allows them to utilize phytate as a substrate in various environments. In plants, only phytases belonging to the HAP and PAP groups have been identified and the current review will only discuss the major features of these phosphatases. Detailed descriptions about the CP and BPP phytase can be found elsewhere (Lei et al., 2007).

2.1. Purple acid phosphatase phytases (PAPhys)

All members of the purple acid phosphatase metal-lophosphoesterases contain a unique set of seven amino acid residues (D, D, Y, N, H, H, H) necessary for metal chelation. These seven metal-ligands are contained in a shared pattern of five common consensus motifs (DxG/GDx₂/GNH(E,D)/Vx₂H/GHxH) (Schenk et al., 2000). A binuclear metallic center containing two iron ions is found in animal PAPs, while in plant PAPs the second iron ion is replaced by either a zinc or manganese ion (Olczak et al., 2003). At a first glance plant PAPs can be divided into two classes: 1) small monomeric (~ 35 kDa) and 2) large homodimeric proteins (~55 kDa). Plant small PAPs are phylogenetically close to bacterial and mammalian enzymes while plant large PAPs are phylogenetic related to homologues in fungal and mycobacteria. The adaptation of PAPs in plants to degrade phytate may be a unique case. To our knowledge no microbial PAPs with significant phytase activity has been identified. This indicates that PAPhys may have evolved to fill this role as a phytase in plants. However, unlike HAPhys, BPPhys and CPPhys, no X-ray crystallography studies have been performed on PAPhys and no information are available on the adaptation of the PAPhys active site to phytate as a substrate. The wheat TaPAPhys is glycosylated with different site-specific N-glycans (Dionisio et al., 2011a). Phylogenetic analysis of several plant PAPs distinguished five types of PAPs where the PAPhys group, in addition to the five PAP metal coordinating motifs, contained a consensus of four consensus motifs (Dionisio et al., 2011b). PAPhys possessing these motifs all have a high specific phytase activity (50–200 μ mol min⁻¹ mg⁻¹) (Dionisio et al., 2011b). The precise catalytic mechanism needs to be determined by future research.

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