ISSN 0026-2617, Microbiology, 2018, Vol. 87, No. 6, pp. 745–756. © Pleiades Publishing, Ltd., 2018.
Original Russian Text © N.P. Balaban, A.D. Suleimanova, E.V. Shakirov, M.R. Sharipova, 2018, published in Mikrobiologiya, 2018, Vol. 87, No. 6, pp. 635–648.

REVIEWS

Histidine Acid Phytases of Microbial Origin

N. P. Balaban[a], *, **A. D. Suleimanova**[a], **E. V. Shakirov**[a], [b], **and M. R. Sharipova**[a]
[a] *Kazan (Volga region) Federal University, Kazan, 420021 Russia*
[b] *The University of Texas at Austin, Texas, 78712 United States*
**e-mail: Nellybalaban@yandex.ru*

Received April 21, 2018

Abstract—This review is focused on analysis of the biological diversity of phytase-producing microorganisms capable of degrading phytate to inorganic phosphate. General approaches to microbial phytase classification are discussed, with a particular emphasis on histidine acid phytases (HAPs), which catalyze specific cleaving of *myo*-inositol hexakisphosphate. The effect of glycosylation and various effectors on enzyme thermostability and activity of phytases are described. The data on the biosynthesis of histidine acid phytases, their substrate specificity, and on the mechanism of *myo*-inositol hexakisphosphate hydrolysis are considered. A conclusion is made concerning the biotechnological potential of this group of microbial enzymes.

Keywords: histidine acid phytases, microorganisms, *myo*-inositol hexakisphosphate, biochemical properties, substrate specificity, phytate hydrolysis

DOI: 10.1134/S0026261718060024

Microorganisms—archaea, bacteria, yeasts, and microscopic fungi—inhabit various ecological niches and have a high hydrolytic potential. They can use various hardly accessible compounds even in highly polluted soils. Phosphorus is one of the essential macronutrients necessary for all organisms. On the Earth surface, phosphorus is present in the form of minerals that are components of natural phosphates: apatites and phosphorites, most of which are being used in the production of phosphate fertilizers. While plants take up phosphorus from soil almost solely as phosphate anions, mainly, as HPO_4^{-2} and $H_2PO_4^-$, these forms are characterized by low availability for land plants and high sorption capacity (Secco et al., 2017; Farias et al., 2018). At the same time, natural replenishment of soil with phosphate compounds is rather negligible and the addition of phosphate fertilizers to soil is therefore highly important for increasing crop yield. The major part of phosphorus in soil is often present in the form of phytates, and their low solubility is the cause of limited uptake of this phosphorous compound by plants (Haefner et al., 2005; Singh and Satyanarayana, 2011). Phytate is a *myo*-inositol hexakisphosphate, a strong chelating polyanionic agent capable of forming insoluble complexes with metal cations, proteins, peptides, and amino acids in soil and feeds, which results in decreased bioavailability of phosphorus and other components of the phytate complex. Phytates are the components of grain feeds, but they are not assimilated by monogastric animals and are considered as an antinutritional factor, due to which agricultural producers suffer considerable damage (Bohn et al., 2008). In addition, the limited ability of such animals to assimilate phytate complexes contributes to enhanced excretion of undigested mineral-phytate salts and environmental pollution, which leads to the growth of toxin-producing microorganisms, algae bloom on the water surfaces of lakes and rivers, and nitrogen oxide formation (Roy et al., 2016; Cangussu et al., 2018).

With respect to the chemical structure, inositol is a cyclic derivative of a hexabasic alcohol, and its conformation varies depending on the positions of hydroxyl groups with axial or equatorial spatial orientation. The interaction between hydroxyl groups and six phosphoric acid residues results in the formation of nine stereo isomers of inositol phosphate, the predominant residues being *myo*-inositol hexakisphosphate (phytate, *myo*-$InsP_6$). Each hydroxyl group of phytate binds to only one phosphate residue, and the phosphate group bound with the second carbon atom of inositol (position d-2) is axially oriented in space (Fig. 1) (Kerovuo et al., 2000; Balaban et al., 2016).

The monoester bonds of organic compounds are hydrolyzed by enzymes of a large class of phosphomonoesterases (phosphatases), and their hydrolysis is associated with metabolic regulation and with the regulatory network of cell signal transduction (Shin et al., 2001). In spite of the great diversity and broad distribution of phosphomonoesterases, many enzymes of this class cannot hydrolyze phosphomonoester bonds in inositol phosphate molecules. The enzymes that can hydrolyze phytate and its complexes are distinguished into a separate class of phytases in the vast phosphohydrolase family.