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Phosphate dynamics: From plant physiology to human health and environmental impact

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Abstract
The phosphate cycle, which involves the movement of phosphorus through the lithosphere, hydrosphere, and biosphere, significantly affects its availability to plants. Factors such as soil characteristics, microbial activity, and agricultural practices are critical, emphasizing the need for optimizing phosphorus use in agriculture for sustainable crop production. Due to limited phosphorus availability in soils, phosphate fertilizers are often necessary. This review paper discusses the inefficiency of phosphorus utilization in plants and environmental concerns related to runoff, exploring physiological, genetic, and biotechnological approaches to enhance phosphorus utilization efficiency (PUE), including root architecture changes, symbiotic relationships, gene manipulation, and innovative biotechnological interventions. Additionally, it explores the role of phosphates in food technology, detailing their applications in improving food quality, safety, and nutritional value, as well as addressing regulatory aspects and potential health implications associated with phosphate use in food products.

Keywords: Phosphorus utilization, root phen, phosphate transporter, phosphate cycle

1. Introduction

Phosphate (PO_4^{3-}) is a key inorganic molecule involved in numerous biological functions. Approximately 85% of the body's phosphate is found in bones and teeth, 14% in cells, and 1% in extracellular fluid [1]. Phosphate homeostasis is tightly regulated by the interplay of intestinal absorption, bone storage, and renal excretion. This paper reviews the mechanisms regulating phosphate balance, its physiological roles, and the clinical consequences of phosphate dysregulation.

Phosphorus is an essential element for plant growth and development, playing a critical role in processes such as energy transfer (ATP), genetic information storage (DNA, RNA), and structural integrity (phospholipids). Despite its abundance in the Earth's crust, phosphorus availability to plants is often limited due to its complex cycle and interactions with soil components [2]. Phosphorus is vital for various plant functions, including energy transfer, signal transduction, and the synthesis of nucleic acids and phospholipids [3]. Despite its importance, phosphorus availability in soil is often low due to its poor mobility and propensity to form insoluble compounds. Improving phosphorus utilization efficiency in plants is critical for sustainable agriculture and environmental protection [4].

Phosphates are inorganic chemical compounds containing the phosphate ion (PO_4^{3-}). They are widely used in the food industry due to their functional properties, which improve the quality and shelf life of food products [5]. Phosphate plays a crucial role in plant growth and development, being a component of nucleic acids, ATP, and membrane lipids [3]. The low solubility and mobility of phosphate in soil make its acquisition a significant challenge for plants [4]. Understanding the mechanisms of phosphate transport is essential for developing strategies to improve phosphate use efficiency in crops, thereby enhancing agricultural sustainability.

2. Phosphate Homeostasis

2.1 Intestinal Absorption

Dietary phosphate is absorbed in the small intestine through both passive and active transport mechanisms. The active transport is mediated by sodium-phosphate co-transporters (NaPi-IIb) located on the apical membrane of enterocytes. Vitamin D enhances the expression of NaPi-IIb, thereby increasing phosphate absorption [6].

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2.2 Bone Storage and Release

Bone serves as the primary reservoir for phosphate. Bone mineralization involves the deposition of phosphate in the form of hydroxyapatite ($Ca_{10}(PO_4)_6(OH)_2$). Osteoblasts facilitate bone formation by secreting matrix vesicles containing alkaline phosphatase, which hydrolyzes phosphate from organic molecules, promoting hydroxyapatite formation. Conversely, osteoclasts resorb bone, releasing phosphate into the bloodstream [7].

2.3 Renal Excretion

The kidneys play a pivotal role in phosphate homeostasis. Phosphate is filtered by the glomerulus and reabsorbed in the proximal tubules via NaPi-IIa and NaPi-IIc co-transporters. Parathyroid hormone (PTH) decreases phosphate reabsorption by downregulating these transporters, leading to increased phosphate excretion. Fibroblast growth factor 23 (FGF23) also promotes phosphate excretion by reducing NaPi-IIa and NaPi-IIc expression and inhibiting vitamin D synthesis [8].

3. Regulatory Mechanisms

3.1 Parathyroid Hormone (PTH)

PTH is secreted by the parathyroid glands in response to low serum calcium levels. It acts on bones, kidneys, and the intestine to increase calcium levels. PTH enhances bone resorption, releasing both calcium and phosphate into the bloodstream. In the kidneys, PTH reduces phosphate reabsorption and stimulates the production of active vitamin D, which increases intestinal absorption of calcium and phosphate [9].

3.2 Vitamin D

Vitamin D, specifically its active form calcitriol (1,25-dihydroxyvitamin D3), is synthesized in the kidneys under the influence of PTH. Calcitriol enhances intestinal absorption of calcium and phosphate and promotes bone mineralization. It also has a feedback inhibitory effect on PTH synthesis [10].

3.3 Fibroblast Growth Factor 23 (FGF23)

FGF23 is produced by osteocytes and osteoblasts in response to elevated serum phosphate levels. It acts on the kidneys to reduce phosphate reabsorption and suppresses calcitriol production. FGF23 thereby lowers serum phosphate levels and inhibits excessive bone mineralization [11].

4. Biological Functions of Phosphate

4.1 Energy Metabolism

Phosphate is a critical component of adenosine triphosphate (ATP), the primary energy carrier in cells. ATP synthesis, storage, and utilization depend on the availability of phosphate [12].

4.2 Nucleic Acids

Phosphate forms the backbone of DNA and RNA, linking nucleotides through phosphodiester bonds. This structural role is fundamental to genetic information storage and transfer [13].

4.3 Bone and Teeth Mineralization

Phosphate, together with calcium, forms hydroxyapatite crystals that provide rigidity and strength to bones and teeth. Proper phosphate levels are essential for maintaining skeletal integrity [14].

4.4 Cell Membranes

Phospholipids, which constitute cell membranes, contain phosphate groups. These molecules are crucial for membrane structure, fluidity, and function, including signal transduction and cellular communication [15].

5. Clinical Implications of Phosphate Imbalance

5.1 Hypophosphatemia

Hypophosphatemia, characterized by low serum phosphate levels, can result from inadequate dietary intake, malabsorption, excessive renal excretion, or shifts from extracellular to intracellular compartments. Clinical manifestations include muscle weakness, hemolytic anemia, bone pain, and osteomalacia. Severe hypophosphatemia can lead to respiratory failure and cardiac dysfunction [16].

5.2 Hyperphosphatemia

Hyperphosphatemia, or elevated serum phosphate levels, is commonly associated with chronic kidney disease (CKD), where impaired renal function reduces phosphate excretion. Other causes include excessive dietary intake, tissue breakdown, and certain medications. Hyperphosphatemia can lead to vascular calcification, secondary hyperparathyroidism, and bone disease [17].

6. Phosphate Cycle and Availability of Phosphorus to Plants

6.1 The Phosphate Cycle

The phosphate cycle encompasses the movement of phosphorus through different environmental compartments, including rocks, soil, water, and living organisms. The primary stages of the phosphate cycle include weathering, absorption by plants, movement through the food web, decomposition, and sedimentation.

6.2 Weathering

Phosphorus enters the cycle through the weathering of phosphate-rich rocks, such as apatite. Weathering releases phosphate ions (PO_4^{3-}) into the soil, making them available for plant uptake [18]. This process is generally slow and often limits the amount of bioavailable phosphorus in soils.

6.2 Absorption by Plants

Plants absorb phosphate from the soil solution primarily through their root systems. The absorbed phosphate is utilized in various metabolic processes and is incorporated into organic molecules such as ATP, nucleic acids, and phospholipids [3]. The efficiency of phosphate absorption is influenced by the plant's root architecture, mycorrhizal associations, and the presence of phosphate transporters.

6.3 Movement Through the Food Web

Phosphorus moves through the food web as plants are consumed by herbivores, which in turn are consumed by carnivores. The phosphorus is used in numerous biological processes within these organisms and is eventually returned to the soil through excretion and decomposition [19].

6.5 Decomposition and Sedimentation

When plants and animals die, decomposers such as bacteria and fungi break down their organic matter, releasing phosphorus back into the soil or water. In aquatic environments, phosphorus can settle as sediment and, over geological timescales, form new phosphate-containing rocks, thus completing the cycle [20].

7. Factors Affecting Phosphorus Availability to Plants

7.1 Soil Characteristics

Soil properties such as pH, texture, and organic matter content significantly influence phosphorus availability. Phosphorus is most available to plants in soils with a pH range of 6 to 7. In acidic soils, phosphorus can become bound to iron and aluminum compounds, while in alkaline soils, it can precipitate with calcium [21]. Soil texture affects the retention and movement of phosphorus, with clay soils typically holding more phosphorus than sandy soils. Organic matter can enhance phosphorus availability by forming soluble organic phosphorus compounds and by promoting microbial activity.

7.2 Microbial Activity

Soil microorganisms, including bacteria and fungi, play a crucial role in phosphorus cycling. Mycorrhizal fungi form symbiotic relationships with plant roots, extending the root system and enhancing phosphorus uptake [22]. Phosphate-solubilizing bacteria (PSB) can convert insoluble phosphorus compounds into forms that are accessible to plants through the production of organic acids and enzymes [23].

7.3 Agricultural Practices

Fertilization practices, crop rotation, and soil management techniques influence phosphorus availability. The application of phosphate fertilizers can temporarily increase the concentration of available phosphorus in the soil, but overuse can lead to environmental issues such as eutrophication [24]. Crop rotation and the use of cover crops can improve soil structure and reduce phosphorus loss through erosion. Conservation tillage practices help maintain soil organic matter and enhance microbial activity, promoting phosphorus availability [25].

8. Strategies for Enhancing Phosphorus Availability

8.1 Improved Fertilization Practices

Precision agriculture techniques, such as soil testing and targeted fertilizer application, can optimize phosphorus use and minimize environmental impacts. The development and use of slow-release and controlled-release fertilizers can also enhance phosphorus use efficiency [26].

8.2 Mycorrhizal Inoculation

The use of mycorrhizal inoculants can improve phosphorus uptake by enhancing the root surface area available for absorption. This symbiotic relationship can be particularly beneficial in low-phosphorus soils [22].

8.3 Phosphate-Solubilizing Microorganisms

Inoculating soils with phosphate-solubilizing microorganisms (PSM) can increase the availability of phosphorus by converting it from insoluble to soluble forms. Research and development of effective PSM inoculants can provide a sustainable approach to improving phosphorus availability [23].

9. Mechanisms for Improving Phosphorus Utilization Efficiency in Plants

9.1 Physiological Mechanisms

9.1.1 Root Architecture

Root architecture plays a significant role in phosphorus acquisition. Plants adapt their root systems to explore a larger soil volume and enhance phosphorus uptake [27]. For instance, root hairs increase the root surface area, aiding in the absorption of phosphorus from the soil [28]. Additionally, modifications such as increased root length, lateral root proliferation, and cluster root formation are beneficial for phosphorus acquisition [56].

9.1.2 Mycorrhizal Associations

Arbuscular mycorrhizal (AM) fungi form symbiotic relationships with plant roots, significantly improving phosphorus uptake 22. These fungi extend the root's absorptive surface area through their hyphal networks, facilitating access to phosphorus beyond the root depletion zone. The AM symbiosis enhances PUE by enabling plants to utilize both inorganic and organic phosphorus sources more effectively [29].

9.1.3 Organic Acid Exudation

Plants exude organic acids such as citric acid and malic acid into the rhizosphere, which chelate soil-bound phosphorus, making it more available for plant uptake [30]. This mechanism is particularly evident in cluster root-forming species such as white lupin (*Lupinus albus*), which exudes large amounts of organic acids under phosphorus-deficient conditions [31].

9.2 Genetic Mechanisms

9.2.1 Phosphate Transporters

Phosphate transporters are integral membrane proteins that facilitate phosphorus uptake and translocation within the plant. Overexpression of high-affinity phosphate transporters can enhance phosphorus uptake, especially under low-phosphorus conditions 32. For example, the Arabidopsis PHT1 family of phosphate transporters has been shown to play crucial roles in phosphorus uptake and homeostasis [33].

9.2.2 Genetic Engineering

Genetic engineering offers promising avenues for improving PUE in crops. Transgenic approaches include overexpressing genes involved in phosphorus uptake, transport, and metabolism. For instance, transgenic rice plants overexpressing OsPT6, a phosphate transporter gene, exhibited enhanced phosphorus uptake and growth under low-phosphorus conditions [34].

9.3 Biotechnological Interventions

9.3.1 Microbial Inoculants

Microbial inoculants, such as phosphate-solubilizing bacteria (PSB) and mycorrhizal fungi, can enhance phosphorus availability in the soil. PSB solubilize insoluble phosphorus compounds through the production of organic acids and enzymes [23]. The combined application of PSB and AM fungi has been shown to synergistically improve phosphorus uptake and plant growth [35].

9.3.2 Biofortification

Biofortification aims to increase the nutrient content of crops through conventional breeding and biotechnological methods. Enhancing the phosphorus content in edible plant parts can contribute to better nutrition and health. For example, biofortified crops with higher phosphorus content in seeds have been developed through selective breeding and genetic engineering [36].

9.4 Phosphate Transport in Plants

9.4.1 Phosphate Transporters

Phosphate transport in plants is mediated by specific phosphate transporters, which are divided into several families based on their sequence similarity and functional characteristics.

9.4.1.1 PHT1 Family

The PHT1 family consists of high-affinity phosphate transporters primarily responsible for phosphate uptake from the soil. These transporters are predominantly expressed in roots and are regulated by phosphate availability [37]. Members of the PHT1 family, such as PHT1;1 and PHT1;4, play crucial roles in phosphate acquisition under low-phosphate conditions [32].

9.4.1.2 PHT2 and PHT3 Families

The PHT2 and PHT3 families are involved in phosphate transport within the plant. PHT2;1 is a low-affinity phosphate transporter located in the chloroplast envelope, facilitating phosphate uptake into chloroplasts for photosynthesis and other metabolic processes [38]. The PHT3 family members are mitochondrial phosphate transporters, essential for mitochondrial function and energy metabolism [39].

9.4.1.3 PHT4 Family

The PHT4 family comprises transporters localized to various intracellular compartments, including the Golgi apparatus, plastids, and vacuoles. These transporters are involved in maintaining phosphate homeostasis and redistribution within the cell [40]. For instance, PHT4;1 is localized to the Golgi and is implicated in phosphate recycling during cellular processes [41].

9.5 Regulation of Phosphate Transport

The expression and activity of phosphate transporters are tightly regulated by internal and external phosphate levels. Several regulatory mechanisms ensure phosphate homeostasis and efficient utilization.

9.5.1 Phosphate Starvation Response

Under phosphate deficiency, plants activate a series of adaptive responses collectively known as the phosphate starvation response (PSR). PSR involves upregulation of high-affinity phosphate transporters, enhanced root growth, and secretion of organic acids and phosphatases to mobilize phosphate from the soil [3].

9.5.2 SPX Domain Proteins

SPX domain-containing proteins play crucial roles in phosphate sensing and signaling. These proteins interact with phosphate transporters and transcription factors to modulate their activity based on phosphate availability [42]. For example, AtSPX1 and AtSPX2 inhibit PHR1, a key transcription factor in the PSR, under phosphate-sufficient conditions [43].

9.5.3 MicroRNA Regulation

MicroRNAs (miRNAs) also contribute to the regulation of phosphate transporters. miR399 is induced under phosphate deficiency and targets PHO2, a ubiquitin-conjugating enzyme that negatively regulates phosphate transporters [44]. This regulation enhances the stability and activity of phosphate transporters, improving phosphate uptake under low-phosphate conditions.

10. Applications of Phosphates in Food Technology

10.1 Leavening Agents

Phosphates are commonly used as leavening agents in bakery products. They react with baking soda to release carbon dioxide, which helps dough and batter rise, resulting in light and fluffy baked goods [45]. Sodium acid pyrophosphate and monocalcium phosphate are typical examples of phosphates used for this purpose [5].

10.2 pH Stabilizers

Phosphates act as pH stabilizers, maintaining the desired pH levels in various food products. This is crucial in preventing microbial growth and ensuring the stability of food during processing and storage [46]. For instance, phosphoric acid is often used in soft drinks to provide a tangy flavor and maintain acidity.

10.3 Emulsifiers

In food emulsions, such as salad dressings and processed cheese, phosphates function as emulsifiers. They help to stabilize mixtures of oil and water, preventing separation and improving texture and consistency [47]. Sodium tripolyphosphate is a common emulsifying agent used in meat and seafood products to enhance water retention and improve texture [48].

10.4 Preservatives

Phosphates are used as preservatives to extend the shelf life of various food products. They inhibit the growth of bacteria and other microorganisms, thereby enhancing food safety 49. For example, sodium phosphate is used in processed meats to prevent spoilage and maintain freshness.

10.5 Nutritional Supplements

Phosphates are added to certain foods as nutritional supplements to fortify them with essential minerals. Calcium phosphate, for instance, is used to enrich cereals and dairy products with calcium, contributing to bone health [50].

11. Regulatory Aspects

The use of phosphates in food products is regulated by various food safety authorities, including the U.S. Food and Drug Administration (FDA) and the European Food Safety Authority (EFSA). These agencies set limits on the permissible levels of phosphate additives in different food categories to ensure consumer safety [49, 51].

11.1 FDA Regulations

In the United States, phosphates are classified as Generally Recognized As Safe (GRAS) when used in accordance with good manufacturing practices. The FDA specifies maximum allowable concentrations for different types of phosphates in various food products [49].

11.2 EFSA Regulations

The EFSA provides guidelines on the acceptable daily intake (ADI) of phosphates and monitors their use in the European Union. The ADI for phosphates is set to prevent potential health risks associated with excessive phosphate intake [51].

12. Health Implications

While phosphates are generally safe when consumed within regulatory limits, excessive intake may pose health risks. High phosphate levels in the diet have been linked to adverse effects on bone health and kidney function [52]. Therefore, it is essential to monitor phosphate consumption and adhere to recommended dietary guidelines.

12.1 Bone Health

Excessive phosphate intake can disrupt the balance of calcium and phosphate in the body, potentially leading to bone demineralization and an increased risk of osteoporosis [53]. This is particularly concerning for individuals with chronic kidney disease, who may have difficulty excreting excess phosphate [54].

12.2 Kidney Function

In individuals with impaired kidney function, elevated phosphate levels can contribute to vascular calcification and cardiovascular disease. Managing phosphate intake is crucial for these individuals to prevent complications [55].

Phosphate is indispensable for numerous physiological functions, including energy metabolism, nucleic acid synthesis, and skeletal health. The tight regulation of phosphate homeostasis is achieved through the coordinated actions of the intestine, bones, and kidneys, influenced by PTH, vitamin D, and FGF23. Imbalances in phosphate levels can have significant clinical consequences, highlighting the importance of understanding phosphate physiology for the management of related disorders. Future research should focus on elucidating the molecular mechanisms underlying phosphate regulation and developing targeted therapies for phosphate-related conditions.

13. Conclusion

Phosphate is indispensable for numerous physiological functions, including energy metabolism, nucleic acid synthesis, and skeletal health. The tight regulation of phosphate homeostasis is achieved through the coordinated actions of the intestine, bones, and kidneys, influenced by PTH, vitamin D, and FGF23. Imbalances in phosphate levels can have significant clinical consequences, highlighting the importance of understanding phosphate physiology for the management of related disorders. Future research should focus on elucidating the molecular mechanisms underlying phosphate regulation and developing targeted therapies for phosphate-related conditions. The phosphate cycle is a complex process that significantly influences the availability of phosphorus to plants. Understanding the factors that affect phosphorus availability, such as soil characteristics, microbial activity, and agricultural practices, is crucial for optimizing phosphorus use in agriculture. Implementing strategies to enhance phosphorus availability, such as improved fertilization practices, mycorrhizal inoculation, and the use of phosphate-solubilizing microorganisms, can contribute to sustainable crop production and environmental conservation. Improving phosphorus utilization efficiency in plants is essential for sustainable agriculture and environmental protection. Various physiological, genetic, and biotechnological mechanisms can enhance PUE, including modifications in root architecture, symbiotic relationships with mycorrhizal fungi, organic acid exudation, genetic manipulation of phosphate transporters, and the use of microbial inoculants. Future research should focus on integrating these approaches to develop crops with superior PUE, ensuring food security while minimizing environmental impacts. Phosphate transport in plants involves a complex interplay of transporters, regulatory networks, and adaptive strategies. High-affinity phosphate transporters from the PHT1 family play a central role in phosphate uptake from the soil, while other transporter families facilitate phosphate distribution within the plant. The regulation of phosphate transport is tightly controlled by phosphate availability, involving mechanisms such as the phosphate starvation response, SPX domain proteins, and miRNA regulation. Understanding these processes is crucial for developing strategies to improve phosphate use efficiency in crops, contributing to sustainable agricultural practices. Phosphates are versatile additives that play a significant role in enhancing the quality, safety, and nutritional value of food products. Their applications as leavening agents, pH stabilizers, emulsifiers, and preservatives make them indispensable in the food industry. However, it is essential to regulate their use to prevent potential health risks associated with excessive phosphate intake. Adhering to regulatory guidelines and recommended dietary allowances will ensure the safe and beneficial use of phosphates in food technology.

14. Conflict of interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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