

A review on the role of phytase in feed on enhancing fish growth, feed protein content, and aquatic environment

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Abstract. The development of the feed industry in sustainable aquaculture activities largely relies on plant-based proteins, which are widely available and relatively inexpensive, to address the global fishmeal shortage. However, these plant-derived protein sources contain various anti-nutritional factors, such as non-starch polysaccharides, phytates, protease inhibitors, tannins, and saponins, which are less utilizable by fish, thereby limiting nutrient utilization and disrupting mineral bioavailability in aquatic species. Phytate in feed forms complexes by binding to proteins and minerals in the digestive tract of animals. These phytate-protein complexes cause problems in protein digestibility, leading to decreased digestibility, protein utilization, and growth. In addition, phytate cannot be digested by proteolytic enzymes, and the activities of enzymes such as pepsin, amylase, and lipase are inhibited by phytate. Feed supplementation with phytase hydrolyzes phytate, thereby releasing phosphorus from the phytate complex. As a result, phosphorus becomes freely available in the feed, playing an important role in improving the overall performance of fish and increasing the bioavailability of minerals to fish, thereby making it cost-effective and environmentally friendly. Phytase in feed promotes increased fish growth rates due to improved protein digestibility and nutrient absorption as a result of optimal function in the pyloric ceca of the intestine. The addition of phytase to feed can enhance the conversion of trypsinogen to trypsin, which breaks down proteins into amino acids, thereby increasing digestive enzyme activity and improving the digestibility of proteins and amino acids in feed that uses plant-based ingredients as protein sources.

Keywords: digestibility, hydrolysis, minerals, feed, phytase.

Introduction. Aquaculture has become the fastest-growing food production sector, contributing to global food security by meeting the ever-increasing demand for nutrient-rich animal proteins (Subasinghe et al., 2009). In 2022, global aquaculture production reached 185 million tons, with approximately 164.6 million tons allocated for human consumption (FAO, 2024). In addition, the production of cultivated aquaculture species was estimated to reach 63.41 million tons by 2025 and is projected to increase to approximately 75.44 million tons by 2030 (Sharma et al., 2025). This expansion has intensified aquaculture, focusing on maximizing production efficiency and sustainable production approaches to support global food security and economic development (Laktuka et al., 2023).

Economic aquaculture production requires maximum feeding efficiency. The main issues in aquaculture revolve around reducing fishmeal in feeds and substituting fish oil with other ingredients in high-energy diets. By 2030, aquaculture production is expected to account for 62% or 93.6 million tons of global seafood production (FAO, 2024). The use pattern of fishmeal has shifted almost exclusively toward aquaculture feed production from farming operations (Hardy, 2010). Aquaculture consumed 3.72 million tons, or 60.8%, of the total fishmeal produced (Tacon et al., 2011) and 0.78 million tons (73.8%) of global fish oil (FO) in 2008 (FAO, 2012), at the expense of the livestock sector, which continues to reduce its use of these marine commodities. In 2012, fishmeal usage in aquaculture feed increased to 68%, whereas FO usage remained the same (74%) (Tacon

& Metian, 2015). Despite efforts to improve fishmeal availability and quality, global fishmeal production has remained stagnant (5-7 million tons) year after year, owing to fully or overexploited fisheries, whereas grain and oilseed production has tended to increase to 2.9 billion and 574.1 million tons, respectively (USDA, 2015). Therefore, this intensification has simultaneously increased the reliance on nutritionally balanced and cost-effective aquaculture feeds. According to Tacon et al. (2025), global aquaculture feed production is projected to reach 92.73 million tons by 2030.

Artificial feed uses fish meal as an animal protein source in amounts of up to 50%, making fish meal the main and most expensive protein ingredient in aquaculture (Tacon & Metian, 2008). Fish meal serves as a source of animal protein in feed because it provides protein and essential amino acids, essential fatty acids, cholesterol, vitamins, and mineral attractants that are highly required for fish growth (Cheng & Hardy, 2004; NRC, 2011). Fish meal is the primary protein source in aquaculture feed formulations because of its high protein content, better digestibility, balanced amino acid and fatty acid composition, and relatively lower levels of anti-nutritional factors compared with other protein sources (Gabriel et al., 2007; Kumar et al., 2012; Kaiza et al., 2023). However, increasing demand, limited availability from natural sources, rising costs, and ecological concerns related to fish meal production pose challenges to sustainable aquaculture. As fish farming activities continue to increase, the demand for fish meal will continue to rise over time, leading to limited fish meal availability and concerns over the further development of overfishing that disregards the sustainability of natural ecosystems (Liebert & Portz, 2005; Tacon & Metian, 2008). Therefore, replacing fish meal with readily available and cost-efficient alternative protein sources is crucial to ensure the long-term sustainability of aquaculture (Ai et al., 2007; Laktuka et al., 2023).

Among the available alternatives, plant-based protein sources such as rapeseed meal, soybean meal, canola meal, sunflower meal, and peanut meal are increasingly drawing the attention of nutritionists (Kumar et al., 2012; Shapawi et al., 2013; Hussain et al., 2020; Rachmawati et al., 2024). The main plant protein sources in aquatic feeds include soybean, corn gluten, sunflower, canola/rapeseed meals, peas, and lupin. The development of the feed industry in sustainable aquaculture activities mostly uses widely available and relatively inexpensive plant proteins to address the global shortage of fish meal (Tacon et al., 2011; Fiorella et al., 2021). Soybean meal can be used as an alternative protein source to replace fish meal because it is inexpensive and beneficial for fish feed (Khan et al., 2011; Hussain et al., 2020). Soybean meal provides the highest proportion of plant protein in fish feed because of its relatively low cost and balanced essential amino acid profile (Tacon & Metian, 2008; NRC, 2011). Nevertheless, these plant-based protein sources contain various anti-nutritional factors, such as non-starch polysaccharides, phytate, protease inhibitors, tannins, and saponins (Baruah et al., 2007; Zhu et al., 2014; Naz et al., 2023), which are less utilizable by fish, limiting nutrient utilization and interfering with mineral bioavailability in aquatic species (Cao et al., 2007). The specific objective of this review is to clarify the current understanding of the role of phytase in feed in enhancing fish growth, feed protein content, and aquatic environment.

Phytate. Phytate is a hexaphosphate ester of meso-inositol cyclic hexahydrate alcohol (Figure 1). Phytic acid, known as inositol hexakisphosphate (IP6) or phytate when in salt form, is the main storage form of phosphorus (P) in many plant tissues, including seeds. Inositol penta- (IP5), tetra- (IP4), and triphosphates (IP3) are also known as phytates. Its molecular formula is $C_6H_{18}O_{24}P_6$ and molecular mass is $660.04 \text{ g mol}^{-1}$ (Selle et al., 2000; Debnath et al., 2005; Bulbul et al., 2015).

Phytate (myo-inositol 1, 2, 3, 4, 5, 6-hexakisphosphate) is the main form of phosphorus storage in plant-based materials, comprising approximately two-thirds (60-80%) of the total phosphorus, which remains unavailable to monogastric and agastric aquatic species (Cao et al., 2007; Hussain et al., 2011; Handa et al., 2020). Phytate forms phytate-protein complexes that cause issues with protein digestibility, thereby reducing the digestibility and utilization of proteins (Cao et al., 2007; Kumar et al., 2012; Hussain et al., 2020). Phytate cannot be digested by proteolytic enzymes (Ravindran et

al., 1994), and the activity of enzymes such as pepsin, amylase, and amylase is inhibited (Baruah et al., 2005; Cao et al., 2007). Spinelli et al. (1983) found that feeding *Salmo gairdneri* with feed containing 0.5% phytate negatively impacted their growth due to a decrease in protein availability in the feed. In addition, phytate forms phytate-mineral complexes that chelate minerals such as phosphorus (P), calcium (Ca), zinc (Zn), iron (Fe), and magnesium (Mg), rendering them insoluble (Papatryphon et al., 1999; Liu et al., 2013), thereby reducing the absorption and bioavailability of macro-and micro-minerals required by fish, which leads to slower fish growth (Akpoilih et al., 2016; Nwanna & Schwarz, 2007).

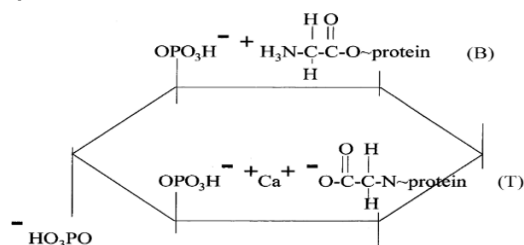


Figure 1. Structure of the phytic acid complex binding binary (B) and ternary (T) proteins (Selle et al., 2000).

Mineral phosphorus (P) is an essential component for fish in various aspects, including being a major constituent of nucleic acids, cell membranes, and bones (Baeverfjord et al., 1998; Tang et al., 2012; Fraser et al., 2019). Furthermore, phosphorus is involved in various metabolic functions in the body, such as fish reproduction, genetic coding, ATP synthesis, and skeletal development (Papatryphon et al., 1999; Kumar et al., 2012). Phytate binds with phosphorus and chelates proteins, amino acids, digestive enzymes, and essential minerals such as magnesium, zinc, iron, and calcium, forming insoluble complexes (Debnath et al., 2005; Rachmawati et al., 2023a). These complexes limit digestibility and interfere with overall nutrient digestion and absorption, thereby negatively affecting fish growth (Liebert & Portz, 2005; Shahzad et al., 2021; Rachmawati et al., 2023b). In addition, undigested phytate-bound phosphorus is excreted through feces into the aquatic environment, stimulating algal blooms and resulting in eutrophication and hypoxic conditions in aquatic ecosystems (Xu et al., 2021).

Phytase. Phytase is known as myo-inositol (1,2,3,4,5,6)-hexaphosphate phosphohydrolase, which hydrolyzes phytate-P compounds, making P available for intestinal absorption (Baruah et al., 2004; Debnath et al., 2005). This enzyme removes the orthophosphate group from the inositol ring of phytate to yield free inorganic P along with lower phosphate ester chains (from inositol pentaphosphate to inositol monophosphate) as intermediates (Figure 2) (Song et al., 2019).

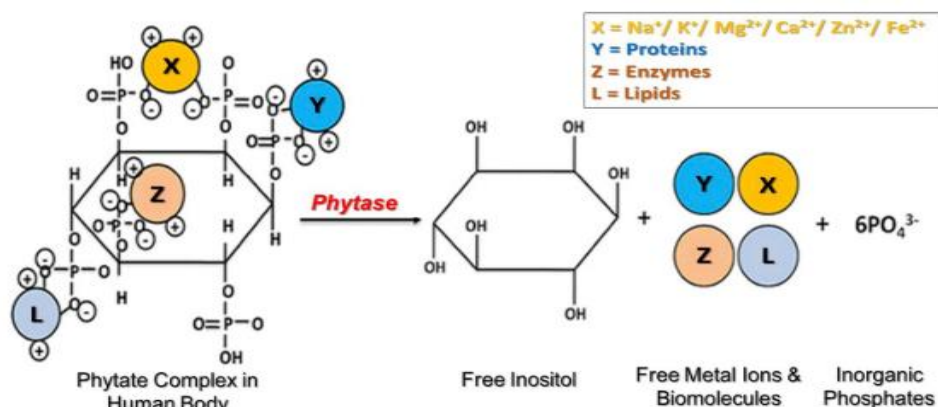


Figure 2. Hydrolysis reaction of phytate catalyzed by phytase (Song et al., 2019).

Phytase is widespread in nature and is found in animals, plants, and microorganisms. In general, phytase activity in animals is negligible compared to that in plants and microbes (Weremko et al., 1997; Cao et al., 2007). Phytase originates from plants and microorganisms such as yeasts, bacteria, and fungi (Adeola & Sands, 2003; Rizwanuddin et al., 2023). Plant phytase is more stable at temperatures ranging from 38 to 55°C and pH values between 4.5 and 6.0, compared to microbial phytase (Adeola & Sands, 2003). Phytase-producing bacteria include *Pseudomonas* sp., *Bacillus* sp., *Prevotella* sp., *Mitsuokella multiacidus*, *Aerobacter aerogenes*, *Citrobacter braakii*, and *Enterobacter* spp. (Cao et al., 2007; Handa et al., 2020). Bacterial phytase exhibits various characteristics such as resistance to proteolysis, broad substrate specificity, high catalytic efficiency, and extreme heat stability (Kumar et al., 2012). Phytase produced from filamentous fungi includes those from *Trichoderma*, *Penicillium*, *Myceliophthora*, *Rhizopus*, *Mucor*, and *Aspergillus* (Handa et al., 2020; Rizwanuddin et al., 2023). Fungal phytase is more desirable because of its greater thermostability and chitin effect, activity from acidic to alkaline pH, protease limits in the intestine, and high substrate specificity (Song et al., 2019). The effect of chitin on fungal phytase is related to the structural characteristics and enzyme stability that make it superior and more resistant to certain environmental conditions compared to phytase from other sources (Handa et al., 2020). Monogastric and agastric fish lack endogenous phytase and are therefore unable to utilize 50-80% of phosphorus (Kumar et al., 2012; Sarfraz et al., 2020).

Phytase can hydrolyze phytate, allowing the release and absorption of essential minerals bound in the phytate complex in feed ingredients by fish (Li & Robinson, 1997; Adeshina et al., 2023). Phytase can prevent the antinutritional effects of phytate by hydrolyzing phytate into inositol and phosphoric acid and breaking the bonds between phytic acid and proteins and minerals, thereby increasing the bioavailability of nutrients (Song et al., 2019). According to Adeola & Sands (2003), phytase does not hydrolyze proteins but only releases protein bonds from phytic acid so that digestive enzymes can function properly and effectively and be optimally absorbed by the body. There are two types of phytases, namely [3-phytase (EC 3.1.3.8) and 6-phytase (EC 3.1.3.26)], based on their preferential attack on the carbon atoms present in phytic acid, as classified by the Nomenclature Committee of the International Union of Biochemistry and Molecular Biology (NC-IUBMB) (Singh & Satyanarayana, 2015).

The first commercial phytase product based on *Aspergillus niger* was introduced in 1991, successfully reducing phosphorus (P) excretion by breaking the P bond in phytate (Selle & Ravindran, 2007; Salem et al., 2022). Since then, phytase activity has been defined as phytase units (FTU or U), where one FTU is defined as the amount of enzyme that liberates 1 μmol of inorganic P per minute from 0.0015 mol L⁻¹ sodium phytate at pH 5.5 and 37°C (Simons et al., 1990). This definition provides a useful quantitative measure of phytase activity and a simple benchmark. Several microbial phytase products are currently available (Table 1). Phytase can be incorporated into fish feed in powder, granulated, or liquid form through post-pelleting processes or pre-treatment to avoid thermo-stability issues at high pelleting temperatures (> 80°C). Commercially produced phytases are derived from mutated fungal strains or recombinant DNA technology. Three commonly used feed phytase enzymes are derived from *A. niger*, which is a 3-phytase, and *Peniophora lycii* and *Escherichia coli*, which are 6-phytases. Fungal phytases have higher thermo-stability and lower optimum temperatures, whereas different phytase sources possess varying characteristics that must be considered before application in fish diets (Ravindran et al., 1994; Adeshina et al., 2023).

Table 1 summarizes the properties of the published phytases and commercial information from various authorized phytase companies. Phytase activity was determined based on the amount of inorganic P released from phytate. Owing to the clear differences related to the cultivation conditions and slight differences related to the assay conditions, a comprehensive comparison and evaluation of the production strains is difficult. According to a market research report (Liang et al., 2022), phytases from Europe and North America are more competitive than those produced by Asian companies. This is because phytases from Europe and North America have higher activity per unit weight. Typically, the activity of powder-form phytases from Europe and North America ranges

from 40.000 to 4.000.000 U g⁻¹. Their liquid phytase activity exceeds 40.000.000 U mL⁻¹. In addition, these phytases have a broader pH range and temperature tolerance than those of products from Asian companies (Lemos & Tacon, 2017). For example, the Natupohs enzyme produced by BASF Company can retain 75% of its activity at 75°C for 15 min (Bavaresco et al., 2020). The phytase produced by Alltech Company can retain more than 60% of its activity when the pH is above 6.5 or below 2.5. The market price of phytases from these companies (approximately \$12.5-15 per kg) is also more stable than that of subsequent companies (Lemos & Tacon, 2017). Conversely, phytases from several Asian companies, such as those in China, Japan, and South Korea, are still being developed. However, their formulation methods are still being developed. Phytase activity usually ranges from 500 to 5,000 U g⁻¹ or from 5,000 to 50,000 U mL⁻¹. The price of these phytases fluctuates in the range of \$3-10 per kg (Bavaresco et al., 2020).

Table 1

Commercial production information of microbial phytase

<i>Company</i>	<i>Country</i>	<i>Phytase source</i>	<i>Production strain</i>	<i>Trademark</i>
AB Enzymes	Germany	<i>Aspergillus awamori</i>	<i>Trichoderma reesei</i>	Finase ^{a)}
Alko Biotechnology	Finland	<i>A. oryzae</i>	<i>A. oryzae</i>	SP, TP, SF ^{a)}
Alltech	USA	<i>A. niger</i>	<i>A. niger</i>	Allzyme phytase ^{a)}
BASF	Germany	<i>A. niger</i>	<i>A. niger</i>	Natuphos ^{a)}
BioZyme	USA	<i>A. oryzae</i>	<i>A. oryzae</i>	AMAFERM ^{a)}
DSM	USA	<i>P. lycii</i>	<i>A. oryzae</i>	Bio-Feed Phytase ^{a)}
Fermic	Mexico	<i>A. oryzae</i>	<i>A. oryzae</i>	Phyzyme ^{b)}
Finnfeeds International	Finland	<i>A. awamori</i>	<i>T. reesei</i>	Avizyme ^{b)}
Genencor International	USA	<i>P. simplicissimum</i>	<i>Penicillium funiculosum</i>	ROVABIO
Roal	Finland	<i>Aspergillus awamori</i>	<i>T. reesei</i>	Finase
Novozymes	Denmark	<i>A. oryzae</i>	<i>A. oryzae</i>	Ronozyme® ^{b)} Roxazyme® ^{b)}

Note: ^{a)}Haefner et al. (2005); ^{b)}Liang et al. (2022).

The effects of phytase on growth, nutrient utilization, mineral bioavailability, and phosphorus bioavailability have been demonstrated in livestock and fish studies, most of which were based on corn-soybean meal diets (Cheng & Hardy, 2003; Cao et al., 2007). However, prior to the 1990s, phytase supplementation was mainly considered a way to enhance phytate-P utilization in poultry and swine feeds, whereas it was less commonly used in fish feeds because of limited research information and production constraints (Baruah et al., 2004). Since the mid-1990s, a growing body of research has focused on the effects of phytase supplementation on nutrient utilization. Therefore, studies on growth performance based on diets supplemented with phytase have been conducted in several aquaculture species (Cheng & Hardy, 2004; Vielma et al., 2004).

Phytase has been used by spraying onto fish feed (Cain & Garling, 1995), pretreatment, or dephytinizing feed ingredients before pelleting (Storebakken et al., 1998; Vielma et al., 2000). Phytase supplementation is required in feed to hydrolyze the complex phytate molecule (Shahzad et al., 2021; Salem et al., 2022; Adeshina et al., 2023; Rachmawati et al., 2023b). Research conducted has primarily focused on the effects of phytase on the digestive system during various phases of fish growth, studies on dose-response relationships, phytase types specific to certain fish species, as well as the most efficient supplementation methods (Cheng & Hardy, 2003; Shapawi et al., 2013; Song et al., 2019). It has been well documented that the use of microbial phytase in fish feed can increase the bioavailability of phytate-bound P and nitrogen, thereby reducing P discharge into the aquatic environment (Simons et al., 1990; Rodehutsord & Pfeffer, 1995; Sugiura et al., 2001; Xu et al., 2021). Therefore, phytase is increasingly regarded as an indispensable additive for cost-effective and environmentally friendly fish feeds. Currently, research is focused mainly on the effects of phytase in dose response

studies, the most efficient supplementation methods, the digestive system at various fish developmental stages, and sources and phytase variants for fish (Debnath et al., 2005; Wang et al., 2009).

Studies on the effects of phytase supplementation in feed have shown to improve protein digestibility, feed utilization efficiency, mineral digestibility, and growth in several fish species, such as *Oncorhynchus mykiss* (Forster et al., 1999), *Ictalurus punctatus* (Li & Robinson, 1997), *Clarias gariepinus* (Van Weerd et al., 1999), *Salmo salar* (Storebakken et al., 1998), *Morone saxatilis* (Papatryphon et al., 1999), *Oreochromis niloticus* (Liebert & Portz, 2005; Rachmawati et al., 2024), *Marsupenaeus japonicus* (Bulbul et al., 2015), *Sparus aurata* (Salem et al., 2022), *Psetta maxima* (von Danwitz et al., 2016), *Labeo rohita* (Hussain et al., 2017), *Cirrhinus mrigala* (Naz et al., 2023), *Cyprinus carpio* (Shahzad et al., 2021; Rachmawati et al., 2023a), *Pangasius pangasius* (Debnath et al., 2005), *Epinephelus fuscoguttatus* (Shapawi et al., 2013), and *Carassius auratus* (Nie et al., 2017).

The impact of phytase supplementation in feed on fish growth performance.

Previous studies have investigated the effects of various phytases on the growth performance of different fish species. In general, increased growth has been observed in studies using diets that are entirely or almost entirely based on plant protein sources. Many studies have reported that the addition of phytase to feed has been proven to enhance growth performance. Phytase supplementation in feed can neutralize the negative effects of phytates and promote fish growth. The positive impact of phytase on fish growth has been reported by a number of researchers, including Jackson et al. (1996) on *I. punctatus*, Van Weerd et al. (1999) on *C. gariepinus*, Papatryphon & Soares (2001) on *M. saxatilis*, Shahzad et al. (2021) on *C. carpio*, Naz et al. (2023) on *C. mrigala*, Salem et al. (2022) on *S. aurata*, and Hussain et al. (2017) on *L. rohita*. These researchers demonstrated phytase hydrolysis in plant-based feeds that improved fish growth.

Liebert & Portz (2005) stated that optimal growth of *O. niloticus* is achieved with phytase supplementation at a dose of 750-1250 FTU kg⁻¹ in plant-based feeds. In a study by Li & Robinson (1997), *I. punctatus* fed diets containing phytase at a dose of 250 FTU kg⁻¹ feed consumed more feed, experienced greater weight gain, and had a lower feed conversion ratio than fish fed basal diets without phytase. Hussain et al., (2016) on reported that *L. rohita* fed a diet supplemented with 1000 FTU kg⁻¹ phytase had an average weight gain of 25%. Similar results were reported by Rachmawati et al. (2023b) for *C. gariepinus*, Debnath et al (2005) for *P. pangasius*, Salem et al. (2022) for *S. aurata*, Shapawi et al (2013) for *E. fuscoguttatus*, and von Danwitz et al (2016) for *P. maxima*.

Phytase supplementation at a level of 750 FTU kg⁻¹ in canola meal-based feeds is sufficient to improve the nutrient digestibility and growth performance of *L. rohita* fingerlings (Hussain et al., 2017). The addition of phytase to feed promotes increased growth rate and performance, which can be attributed to various factors, either individually or in combination, namely improved phosphorus bioavailability (Rodehutsord & Pfeffer, 1995; Vielma et al., 2000; Baruah et al., 2007; Rachmawati et al., 2023a) and minerals (Vielma et al 2004; Debnath et al 2005), increased protein digestibility (Vielma et al 2004; Debnath et al 2005; Liebert & Portz 2005; Baruah et al 2005; Salem et al 2022), and enhanced nutrient absorption due to the proper functioning of the pyloric ceca region of the intestine (NRC, 1993; Adeshina et al., 2023). However, several studies have reported no significant differences in growth performance, for example, Vielma et al. (2000) reported no significant effect of phytase supplementation on the performance of *O. mykiss* fed diets supplemented with 1000 FTU kg⁻¹ of phytase. Oliva-Teles et al. (1998) stated that the addition of phytase to seabass (*Lates calcarifer*) feed had no effect on growth performance, protein digestibility, or energy retention in seabass. Sajjadi & Carter (2004) reported no improvement in the growth of *S. salar* fed canola protein concentrate diets mixed with phytase. Similarly, Masumoto et al. (2001) reported no effect of phytase in feed on the weight gain of *Paralichthys olivaceus*. These differences may be related to differences in feed composition and rearing conditions (Baruah et al., 2007). In addition, Baruah et al. (2004) suggested that variations in results among

researchers may be caused by differences in phytate content in various feedstuffs, the species used, various characteristics of feed materials, or possibly the presence or absence of a stomach in certain fish species, as phytase activity is pH-specific.

The impact of phytase in feed on protein availability. Phytase supplementation in feed can increase the availability of protein and amino acids by breaking down phytin-protein complexes and neutralizing the negative effects of phytate on protein and other nutrients in the feed (Orisasona et al., 2017; Baruah et al., 2007; Hussain et al., 2017). This is because the phytic acid present in the feed was hydrolyzed by the phytase enzyme, thereby releasing protein from the phytate complex and improving the digestibility of feed protein. Xu et al. (2021) stated that the addition of phytase can enhance the conversion of trypsinogen to trypsin, which breaks down proteins into amino acids, thereby increasing digestive enzyme activity and improving protein digestibility. Phytase supplementation in plant-based feeds has been reported to improve protein digestibility in several studies. The addition of phytase to feed has resulted in improved protein utilization in *S. salar* (Storebakken et al., 1998), *L. calcarifer* (Oliva-Teles et al., 1998), *P. pangasius* (Debnath et al., 2005), *C. gariepinus* (Rachmawati et al., 2023b), *S. aurata* (Salem et al., 2022), *C. carpio* (Shahzad et al., 2021), *C. mrigala* (Naz et al., 2023), by breaking down previously formed phytate-protein complexes.

The addition of phytase to feed can hydrolyze complex phytate-protein compounds into amino acids that are easily digested to support fish growth (Cao et al 2007; von Danwitz et al., 2016; Hussain et al 2020). Akpoilili et al. (2016) reported that phytase supplementation aids in the hydrolysis of phytate, resulting in increased nutrient digestibility in fish. Furthermore, Wang et al. (2009) reported that breaking the phytate-protein complex bonds enhances the activity of trypsinogen and trypsin, which are involved in breaking down proteins into amino acids. Improved protein digestibility means higher amino acid absorption, thus improving overall protein digestion. In addition, Cheng & Hardy (2003) stated that phytase supplementation in soybean significantly increased the crude protein digestibility of *O. mykiss* feed compared with that of soybean without supplementation. Debnath et al. (2005) reported that feed protein digestibility significantly increased as result of phytase supplementation, whereas feed without supplementation showed low digestibility in *P. pangasius*, confirming the known property of phytate to form phytate-protein complexes that are resistant to proteolytic digestion. In their study, protein digestibility increased with phytase supplementation at a dose of 500 FTU kg⁻¹ feed. Similar results have also been found in fish species, such as *C. gariepinus* (Orisasona et al., 2017) and *O. mykiss* (Forster et al., 1999; Sugiura et al., 2001). Phytase supplementation in feed at a dose of 1000 FTU kg⁻¹ feed can increase protein digestibility and feed efficiency, as reported by Hussain et al. (2020), Adeshina et al. (2023), and Rachmawati et al. (2023a, b).

Effect of phytase in feed on P bioavailability. The positive effect of phytase supplementation on the total availability of P in fish feed ingredients is presented in Table 2, which shows the bioavailability of P when phytase is added to the feed ingredients for various types of fish feed components. Table 2 also shows that phytase supplementation is substantially efficient in increasing the bioavailability of P and thus reducing the amount of P in feces. Phytase supplementation in fish feed decreases the phosphate load in water and ultimately prevents contamination caused by excessive algal growth. Any reduction in P excreted by fish and other animals benefits the environment and the sustainable production of aquaculture. P is an essential constituent of nucleic acids and cell membranes, a major component of skeletal tissue structure, and is directly involved in all cellular energy-producing reactions (NRC, 2011) and fish reproduction (Hardy & Shearer, 1985; Schäfer et al., 1995; Sarfraz et al., 2020). However, phosphate absorption from water by fish is minimal, and dietary sources are more important than water for meeting P requirements in fish. P is a critical aquatic pollutant. Excessive P concentrations are the most common cause of eutrophication in rivers, lakes, and reservoirs (Correll, 1999; Shahzad et al., 2021). The addition of microbial phytase to fish

feed is driven by the need to reduce P excretion and loss to the environment, where P pollution poses a risk to water quality.

Table 2

Total P and phytate-P in common plant-based ingredients

<i>Ingredients</i>	<i>Total P (g kg⁻¹)</i>	<i>Phytate-P (g kg⁻¹)</i>	<i>Proportion of phytate-P in total P (%)</i>
Maize	2.40	2.05	85.4
Corn	2.50	1.70	73.0
Rice (rice grain)	1.20	0.80	65.0
Rice bran (rice waste)	17.51	15.83	90.2
Soybean (soybeans)	5.55	3.08	55.5
Soybean meal (soy flour)	6.66	4.53	68.3
Cassava	1.60	0.40	25.0

Note: ^{a)}Kumar et al (2012); ^{b)}Ravindran et al (1994).

The variation in phytase dosage in feed depends on the ingredients, composition of the feed formulation, and the species studied. Accordingly, studies on the mechanism of phytic acid degradation in various fish species need to be conducted, considering that the process depends on differences in feed formulation, specific characteristics of the digestive tract, and the diversity of activity across various phytase sources (Cao et al., 2007; Rizwanuddin et al., 2023). Numerous studies have shown that phytase supplementation makes phytate-P chelates available to fish (Rodehutscord & Pfeffer, 1995; Baruah et al., 2004). Schäfer et al. (1995) reported that 20% and 40% of phytate-P could be released with the addition of 500 and 1000 FTU kg⁻¹ feed of phytase, respectively, in common carp fed soybean meal-based diets. Hussain et al. (2016) found that in soybean meal-based diets for *L. rohita*, 60% and 80% of phytate-P could be released with the addition of 500 and 1000 U kg⁻¹ phytase, respectively. Rodehutscord & Pfeffer (1995) and Rachmawati et al. (2023a) stated that phytase supplementation in plant-based diets reduced phosphorus excretion into the aquatic environment through feces to a lower level in fish fed diets with phytase supplementation than in fish fed unsupplemented diets. These studies show that increased phosphorus digestibility reduces phosphorus release in *C. carpio* fed a diet with phytase enzyme supplementation compared to fish that did not receive supplementation.

Phytase supplementation in feed has proven highly beneficial in developing environmentally friendly grow-out feed for *C. carpio* by increasing mineral digestibility and reducing mineral excretion into the aquatic environment, which is expected to help reduce water pollution (Gabriel et al., 2007; Goda, 2007; Hussain et al., 2017). Furthermore, Rachmawati et al. (2023a) reported that a phytase enzyme dose of 1000 FTU kg⁻¹ feed is optimal, resulting in maximal mineral utilization within the fish body and minimizing mineral excretion into the aquatic environment via feces. Hussain et al. (2011) linked the reduction in mineral excretion in fish feces to the hydrolysis of phytate content due to phytase enzyme supplementation, which allows for more optimal mineral utilization. In this study, the positive effects of phytase supplementation were attributed to the ability of the phytase enzyme to hydrolyze phytate-mineral complexes, thus releasing chelated minerals and increasing the digestibility of these minerals (Hussain et al., 2017). Similar results were reported by Nwanna et al. (2007), who found that most of the activity of phytase centers on phytate degradation, resulting in the release of more minerals and ultimately enhancing the digestibility of minerals. A phytase supplementation of 1000 FTU kg⁻¹ was the best dosage for mineral digestibility in *C. carpio* during the grow-out phase. This differs from the findings of other studies, which showed that the optimal phytase enzyme dose was 500 FTU kg⁻¹ for several fish species, including *P. pangasius* (Debnath et al., 2005), *L. rohita* (Baruah et al., 2007), and *C. carpio* (Sardar et al., 2007). Hussain et al. (2020) reported that phytase has great

potential for the research and development of environmentally friendly technologies for biological wastewater treatment and bioremediation. Phytase supplementation in feed has proven highly beneficial in developing environmentally friendly grow-out feed for common carp by increasing mineral digestibility and reducing mineral excretion into the aquatic environment, which is expected to help reduce water pollution (Goda, 2007; Hussain et al., 2017).

The effect of phytase in feed on the bioavailability of other nutrients. Phytase can also chelate with other minerals, thereby reducing their bioavailability in fish. Phytase supplementation can hydrolyze phytate and increase the concentrations of minerals such as magnesium, calcium, manganese, and zinc in the plasma, bone, and whole body (Vielma et al., 2004; Kumar et al., 2012; Sarfraz et al., 2020; Rachmawati et al., 2023a). Sanz-Penella et al. (2012) and Shahzad et al. (2021) reported that fish fed diets supplemented with phytase showed increased digestibility of minerals (Ca, Mg, Na, K, Fe, Cu, Zn, and Mn). Yan et al. (2002) stated that *I. punctatus* fed diets with phytase supplementation had higher concentrations of ash, calcium, phosphorus, and manganese in their bones than those fed non-supplemented diets. Similar results have been reported, showing that the addition of phytase to diets can enhance mineral availability, and this enzyme has been used to improve feed mineral retention in *O. mykiss* (Vielma et al., 2004), *L. rohita* (Baruah et al., 2007), and *S. aurata* (Salem et al., 2022).

According to Baruah et al. (2005), phytase supplementation (500 U kg⁻¹) in the diet of juvenile *L. rohita* significantly increased bone Na, Ca, K, Mn, and Fe content by 15, 12.1, 17.4, 20.4, and 40.7%, respectively. Furthermore, the increase due to phytase supplementation was more pronounced in groups containing 3% citric acid, resulting in a significant interaction between citric acid and microbial phytase. Rachmawati et al. (2023a) reported the highest digestibility values for Ca, P, Na, K, Mg, Fe, Cu, Mn, and Zn in *C. carpio* fed a diet supplemented with phytase at a dose of 1000 FTU kg⁻¹ feed, whereas the lowest values were found in feed with a dose of 0 FTU kg⁻¹ feed. These results indicate that phytase increases the bioavailability of several minerals by breaking the bond between minerals and phytate and that mineral absorption is increased at acidic pH, thereby increasing bone mineral retention. However, the absorption and utilization of certain minerals may be species-specific and depend on the feed ingredients used, thus requiring further investigation.

Conclusions. Phytase supplementation in feed hydrolyzes phytate into inositol and phosphoric acid, resulting in the release of phosphorus from the phytate complex. Thus, phosphorus becomes freely available in the feed and plays an important role in enhancing overall fish performance. In addition, it increases the bioavailability of minerals in fish, making it cost effective and environment friendly. Furthermore, it promotes increased fish growth rates due to improved protein digestibility and nutrient absorption as a result of better pyloric ceca function, boosting digestive enzyme activity and improving protein digestibility, thereby increasing the availability of protein and amino acids in feeds that use plant based ingredients as a source of plant protein.

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Conflict of Interest. The authors declare that there is no conflict of interest.

Data Availability. The data supporting the findings of this study are available from the corresponding author upon reasonable request.

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