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The Recent Advances to Increase Nutrient Utilization of Dietary Plant Proteins by Enzyme Supplementation and Fermentation in Rainbow Trout (Oncorhynchus mykiss): A Review

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ABSTRACT

Aquaculture is the fastest growing animal production sector globally. However, its sustainability heavily relies on the development of nutritionally balanced cost-effective and environmentally friendly aqua feeds for fish and crustacean species that are already being farmed or future candidate species for intensive farming around the world. Therefore, feeds produced for farmed aquatic species should be highly digestible in terms of nitrogen and phosphorous contents in order to avoid excessive release of these nutrients into the water column through solid and soluble discharge. Excessive nitrogen and phosphorous in the water are the main reason for eutrophication occurring and causing severe depletion of oxygen and creating hypoxia for many aquatic organisms living inside a water column. Strategies like formulating aqua feeds on required DP/DE (Digestible Protein/Digestible non-protein Energy) basis for farmed species and using synthetic enzymes as feed additives in order to make plant phosphorous bioavailable for fish are being utilized by the commercial aqua feed producers around the world. Fermenting plant protein ingredients with microorganisms and using prebiotics and probiotics as feed additives are also considered a viable option to reduce the nutrient load of aquafarms since these have been shown to increase the digestibility of feed ingredients via increased gut health maintaining the optimal composition and environmental conditions for gut microbiome. In this regard, this review is intended to emphasize the importance of the sustainability efforts of aquaculture production from the perspectives of environmentally friendly aqua feed formulations and improvements based on recent knowledge gathered for the effects of dietary external enzyme supplementation and fermentation of plant ingredients on the growth and wellbeing of rainbow trout (*Oncorhynchus mykiss*) throughout the world.

Keywords: Rainbow trout, Plant proteins, Biotechnology, Nutrient utilization, Sustainability

1. Introduction

Fisheries and aquaculture production reached a new record of 214 million tons in 2020. More than 157 million tones (89%) of total aquatic animal production was used for human consumption and aquaculture is the fastest growing food production sector in the world (FAO 2022). Demand for aquatic animal protein has been increasing at a much faster pace than the supply of capture fisheries throughout the world and the gap has been filled by aquaculture for the last two decades (FAO 2022). However, aquaculture activities specifically done in open sea (mariculture) and lakes could have a huge impact on the ecosystems in these areas due to many interactions of aquaculture with the environment. Among those interactions (Figure 1), nutrient pollution stemming from uneaten food, faeces and ammonia excretion is the most complex in nature because the phosphorous, ammonium, nitrate and nitrite severely disrupt the trophic balances, create eutrophic conditions and become toxic to the organisms (Soto & Norambuena 2003; Pandey & Satoh 2008; Wang et al. 2012; Braña et al. 2021). Intensive fish and crustacean farming totally rely on the nutritionally balanced good quality aqua feeds. Feed cost is the biggest expenditure in aqua farms averaging almost 70% of all the farm expenditures. For this reason, the wastage through uneaten pellets and diets that are imbalanced and prepared using unsustainable ingredients like fish meal and oil and poorly digestible ingredients is seen a major obstacle for achieving the cost effectiveness and environmentally friendly status of aqua farms globally (Braña et al. 2021; Kurniawan et al. 2021).

Main considerations in reducing the impact of aquafarms into the aquatic ecosystems have historically been to improve feed production and feeding technology and to optimize the feed composition (Wang et al. 2012). In this respect, feed production based on the knowledge concerning the optimal nutrient requirements of farmed species supplied by highly digestible feed ingredients has gained momentum in parallel to the global developments in methodology of fish nutritional studies over the past twenty years. Therefore, diet formulations based on the optimum DP/DE (Digestible Protein/Digestible non-protein Energy ratio) determined for each farmed species using *in vivo* apparent ingredient nutrient digestibility values have become the standards of

the commercial aqua feed formulations (Engin & Carter 2001; 2006; Glencross et al. 2008). Rainbow trout production in Türkiye reaches approximately 166.000 tones constituting the 35% of the total inland and marine aquaculture production (Yıldırım & Çantaş 2022). In this respect, this review will primarily focus on the strategies available for optimizing dietary nutrient bioavailability in rainbow trout (*Oncorhynchus mykiss*), the most widely cultured freshwater species not only in Türkiye but around the world.





2. Alternative Feed Ingredients to Fish Meal in Rainbow Trout Diets: Efforts to increase plant protein use by increasing the nutrient retention

2.1. Dietary exogenous enzyme use in plant protein based diets

Sustainable and eco-friendly fish farming necessitates the finding of alternative protein and oil feed ingredients to fishmeal and oil that are highly digestible in farmed species (Morales et al. 2018). Fish meal use in commercial salmonid diets has plummeted from almost 65% to as low as 15% over the last three decades thanks to the extensive scientific research conducted in Atlantic salmon (*Salmo salar*) and rainbow trout (*Onchorhynchus mykiss*) (Davies et al. 2021). The biggest fishmeal replacer in commercial salmonid diets has been the full fat or defatted soybean meal and its by-products and, to a lesser, extent rape and sunflower seed meals and wheat and corn gluten meals have been utilized (Gatlin et al. 2007; Kumar et al. 2020; Davies et al. 2021). Although terrestrial plant proteins are increasingly being used in commercial aqua feeds for salmonids, this was mainly achieved by industrial and technical measures applied to these ingredients to alleviate the Anti Nutritional Factors (ANFs) that they contain. Many plant proteins including soy products contain ANFs such as lectins, saponins, oligosaccharides and trypsin inhibitors that could severely disrupt the absorption process of dietary nutrients in fish (Stone et al. 2005; Gatlin et al. 2007; Yiğit & Ölmez 2011; Glencross et al. 2012; Barrows & Frost 2014). In addition, phosphorus, an indispensable micronutrient that

is required for energy generating cellular metabolic pathways in all living organisms, is found as phytates in plants and classified as non-bioavailable inositol phosphate salts (Morales et al. 2018). Therefore, effective use of alternative terrestrial plant protein sources to fishmeal in aqua feeds necessitates the total removal or reduction of above mentioned ANFs in plant ingredients using numerous methods varying from mechanical to microbiological ones. In this respect, the majority of the latest investigations in rainbow trout appears to be related to the improvement in the retention efficiency of nutrients of dietary plant protein ingredients through fermentation and other processing techniques or dietary addition of external enzymes (Tanemura et al. 2016; Morales et al. 2018; Greiling et al. 2019; Lee S A et al. 2020). Decades earlier scientists were able to demonstrate that the high level of fish meal phosphate (tri-calcium phosphate in the form of bone P source) significantly lowered N and P retention efficiencies in rainbow trout compared to that of fish fed low-P plant ingredients (defatted soybean meal and corn gluten meal) indicating dietary total P surpassing the optimal requirement could actually prevent its bioavailability to the trout (Satoh et al. 2003). Recent study by Morales et al. (2018) demonstrated that dietary 4 g.kg⁻¹ inclusion of external P sources as monosodium phosphate, monocalcium phosphate and monoammonium phosphate to the plant protein based diets making the total dietary P content up to 10 g.kg⁻¹ significantly increased the growth rate and feed conversion in rainbow trout. The authors also concluded that the bioavailability of P, measured as P digestibility was significantly higher in fish fed monosodium and monoammonium phosphates compared to that of fish fed monocalcium phosphate indicating the higher solubility of P salt and absorption and lower particulate P discharge to water through faeces for monosodium and monoammonium phosphate sources in trout when used as dietary additives (Sugiura et al. 2001; Kals et al. 2012; Morales et al. 2018).

Besides finding the best possible dietary P source, research objectives have also focused on the increase of bioavailability of myo-inositol-hexakis dihydrogen phosphate to farmed fish, classified as phytic acid, a commonly found P source in all dietary plant protein ingredients used in aqua feeds as the amount used increased greatly over the years (Hua & Bureau 2010; Greiling et al. 2019). The forefront of the methodological approach to make phytic acid more bioavailable to farmed fish has been specifically through the dietary enzyme addition to diets or the fermentation of the plant proteins with several strains of microorganisms. Phytic acid salts are the primary form of Phosphorus (InsP₆) in plant seeds and raw feed ingredients originating from plant seeds (Cheng & Hardy 2003; Okungoya et al. 2006; Singh 2008; Rodehutscord et al. 2016; Greiling et al. 2019; Lee S A et al. 2020). The hydrolysis of InsP₆ is needed for the InsP₆ bound P to be released and absorbed in digestive tract of fish (Greiling et al. 2019). Enzymes such as phytases and phosphatases catalyse the hydrolytic cleavage of InsP₆ and its salts to myoinositol via several phosphorylated intermediary products enabling P to be released from the ring and become available for absorption (Greiner & Konietzny 2010; Greiling et al. 2019). Because fish in general lack these enzymes in their digestive track, the bioavailability of myo-inositol bound P as P source is limited in fish. However, it was reported that tilapia was able to digest the InsP₆-P on a certain extent compared to species that belong to *cyprinidae* and *Salmonidae* families (Hua & Bureau 2010). Rodehutscord & Pfeffer (1995) demonstrated that trout fed diets containing 60% of dietary P as phytate P supplied by plant protein ingredients mostly from soybeans considerably increased P digestibility and utilization from 25 to 57% and 19 to 49% respectively at 15 °C water temperature when microbial phytase included in diets compared to those fish fed the control diet not supplemented with phytase. The authors also found that the P utilization at 10 °C increased from 6 to 25% but feed intake and growth rate of trout were very low regardless of phytase supplementation to the experimental diets. Similarly, Cheng & Hardy (2003) reported that total dietary P and phytate P digestibility significantly increased in trout fed diets containing extruded full fat and expelled soybeans supplemented with microbial phytase (0 to 1000 FTU/kg diet increased by 200 FTU/kg diet). The authors also concluded that the optimal dosage to include diets for trout appeared to be around 400 FTU/kg diet in order to release the P and other minerals effectively when extruded full fat soybean is used in diets (Cheng & Hardy 2003). However, the apparent digestibility coefficients for total phosphorus and phytate phosphorus appeared to be significantly lower in trout fed the diet containing expelled soybean meal and supplemented with the phytase at 200 FTU/kg level compared to that of fish fed diets containing extruded full fat soybean meals supplemented with increasing amount of microbial phytase (Cheng & Hardy 2003). Diets containing two types of pre-dephytinized soy proteins with very low amount of fishmeal have also been demonstrated to significantly improve the growth, feed utilization, P and Zn retention in the juvenile rainbow trout indicating the effective reduction of phytic acid contents in microbial phytase pre-treated soy products compared to non-treated counterparts (Vielma et al. 2004). A recent study by Greiling et al. (2019) hypothesized that dietary supplementation with mineral phosphorus as monoammonium phosphate (MAP, 1 g/kg DM Diet) and/or Aspergillus oryzae 6-phytase (2800 FTU kg/ DM Diet) might increase the clearance of dietary phytic acid thereby retaining the P in Atlantic Salmon and trout. The results showed that trout were better able to hydrolyse phytic acid (InsP₆) and its salts (phytate-P) therefore absorbing P in the presence of dietary phytase and/or MAP than Atlantic salmon were owing to having a much lower stomach pH, living in freshwater and higher optimal ambient temperature (Greiling et al. 2019). A study by Lee S A et al. (2020) also found that trout fed completely plant protein based diets not supplemented with inorganic P source but containing advanced Escherichia coli phytase at 500 and 2500 FTU/kg at two different ambient temperatures (11 vs 15 °C) retained P around 19 to 29% and 23 to 25% higher compared to that of fish fed diets supplemented with inorganic P source (positive control) and negative control without phytase supplementation respectively. Authors also concluded that significantly higher N (nitrogen) and P retention efficiencies with phytase supplementation in trout at both temperatures indicated the efficacy of the microbial phytase, which may differ widely according to the source and biotechnological methods used in the production (Griener & Konietzny 2010; Morales et al. 2011), in this experiment, even at 11 °C (Lee S A et al. 2020) contradicting the findings of similar investigations earlier (Yiğit et al. 2018). Furthermore, a study by Demir & Yılayaz (2020) demonstrated that dietary phytase supplementation at 1000 FTU/kg diet effectively reduced the particulate P discharge whilst increasing the dissolved P and N discharge in trout fed diets containing hazel nut and soybean meal as main plant protein sources in diets. Besides temperature and animal related factors such as species,

age and gastric retention time, it is understood that the efficacy of the exogenous phytases may also appear to be closely linked to the dietary source of protein that high fishmeal diets actually provide reasonable amount of protein and available P to meet the requirements limiting the response to phytase by the fish (Morales et al. 2013; Dersjant-Li et al. 2015; Yiğit et al. 2018; Lee S A et al. 2020).

Although its use in fish diets is new, dietary exogenous supplementation of proteases has been widely documented in poultry (Mahagna et al. 1995; Simbaya et al. 1996; Kaczmarek et al. 2014; Mahmood et al. 2017; Walk et al. 2018). Proteases are expected to have an effect on ANF's specifically the protease inhibitors that exist in most of the raw and mechanically processed plant protein sources used in aqua feeds by breaking down macromolecular proteins. They may also compensate the endogenous enzyme deficiency in young animals. A recent study by Lee S. et al. (2020) investigated the effects of dietary supplementation of 175 mg protease complex/kg diet on ingredient apparent nutrient digestibility coefficients (ADC) in rainbow trout. The ingredients used in the study consisted of two different fish, animal, animal by-products and an insect meal (feather meals, two poultry by-product meals, two meat and bone meals, sardine meal, menhaden meal, black soldier fly larvae meal), single cell protein meal (Methanococcus maripaludis), plant protein meals (soybean meal, canola meal, distiller's dried grains with soluble (DDGS), cotton seed meal, peanut meal, sunflower meal) and an algae meal (Lee S et al. 2020). The results indicated that dietary supplementation of protease complex significantly increased ingredient-specific ADC's for dry matter, energy, most of the essential amino acids and aspartic and glutamic acids in rainbow trout with most ingredients having improved digestibility of at least one amino acid (Lee S et al. 2020). Ingredient wise, soybean meal was found to have the most profound improvement for nutrient ADC's in rainbow trout by dietary supplementation of protease complex (Lee S et al. 2020). Several commercial carbohydrate enzyme complexes specifically targeting the fibrous components of plant protein meals used in aqua feeds were also investigated for nutrient absorption and retention efficiencies in rainbow trout (Ogunkoya et al. 2006; Denstadli et al. 2011; Collins et al. 2018; Kumar et al. 2020). Carbohydrases are also reported to increase gut and overall health of animals promoting the growth of beneficial bacteria among the microbiome community of the intestine (Adeola & Cowieson 2011; Zhou et al. 2013; Castillo & Gatlin 2015). A commercial enzyme cocktail reported to have xylanase, amylase, cellulase, protease and β -glucanase activity was tested at two different doses in a study designed to improve the nutrient retention efficiencies in trout fed 0, 100 and 200 g/kg diet soybean meal (Ogunkoya et al. 2006). The authors found that enzyme cocktail coated diets (at 1 and 2.5 g/kg diet) containing soybean meal did not improve trout growth rate at 15 °C water temperature but solid P and N wastes were significantly lower in fish fed diets specifically coated with 2.5 g/kg enzyme cocktail (Ogunkoya et al. 2006). They also postulated that the very little effect of enzyme supplementation on growth and nutrient digestibility in trout might be related to the pellet making through extrusion or ingredients used are being highly digestible for trout. The effectiveness of exogenous supplementation of enzymes on the hydrolysis of the bonds between biomolecules in dietary plant ingredients is thought to be closely related to the degree of previous mechanical treatment that the ingredients are exposed to probably during protein and oil extraction procedures or expansion and gelatinization as a result of dietary production (Stone et al. 2003; 2005; Castillo & Gatlin 2015). The effects of soybean meal, rapeseed meal, pea meal and sun flower cake treated with or without a commercial enzyme cocktail (β -glucanase, hemicellulase and pectinase) in semi-moist (45% water) and wet conditions (85% water) at different ambient temperature and durations on the hydrolysis of NSP (Non-Starch Polysaccharides) were also investigated in vitro and in vivo growth experiments in rainbow trout (Denstadli et al. 2011). The *in vitro* experiment indicated that the degradation of NSP's in these plant ingredients appeared not to be limited by time, temperature and the amount of water in pretreatments but rather the complex nature of NSPs showing the most prominent changes occurred with the uronic acid, xylose and arabinose in all pretreatment conditions tested in the investigation (Denstadli et al. 2011). The trout growth was unaffected by the ingredient pretreatment and the enzyme supplementation probably due to released substrates of small carbohydrate polymers during enzyme pretreatment of diets either being excreted or bound to other nutrients thus lowering the absorption specifically at water temperature of 12 °C (Glencross et al. 2003; Denstadli et al. 2011).

Recent application of enzyme bioprocessing technology developed by Ohio Soybean Council was applied to soybean meal and demonstrated to be effective on substantially lowering many ANFs present in unprocessed soybean meal such as TI, lectins, oligosaccharides and phytic acid (Hulefeld et al. 2018; Kumar et al. 2019; 2020). This EnzoMeal was also investigated for its effect on trout growth performance and growth related gene expressions by Kumar et al. (2020). Authors specifically tested the low and high dietary inclusion levels of EnzoMeal (8 and 16%) or the equal combination of SBM and EnzoMeal replacing up to 18% of fishmeal in the highest inclusion level. Control diet included 25% of fishmeal and contained neither the unprocessed soybean meal nor the EnzoMeal. EnzoMeal significantly improved trout growth performance and nutrient retention compared to fish fed diets containing same amount of traditional SBM (Soybean meal) but the effect was even greater at high dietary inclusion levels indicating improved nutrient quality index as a result of reduction of major ANFs in EnzoMeal. Camelina sativa, an oil seed, is a rich source of linolenic (18:3n3) acid and its pressed cakes after oil extraction and the oil itself are increasingly being considered as fishmeal and oil replacer in aqua feeds for many farmed fish species including rainbow trout (Hixson et al. 2014; 2015; Ofori-Mensah et al. 2020). A study by Collins et al. (2018) investigated the effects of the water, carbohydrases and Rhizopus oligosporus treated high oil residue camelina meal (HORM) on the growth performance and gut health of the juvenile rainbow trout. They were able to demonstrate that 80 g/kg inclusion of all the treated HORM products resulted in similar growth and nutrient retention rates and villus structure was not compromised compared to that of fish fed the fishmeal control diet but rainbow trout fed untreated HORM and Rhizopus oligosporus treated HORM diet attained lower growth and SGR respectively (Collins et al. 2018). Regardless of mechanical, enzymatic or microbiological treatments, previous studies pointed out that rainbow trout were able to utilize both the solvent extracted and the high oil residue camelina meal better than Atlantic salmon

depending on primarily the size of the fish and the water salinity levels (Hixson et al. 2014; 2015; Brown et al. 2016; Ye et al. 2016).

The results of studies regarding to dietary exogenous enzyme inclusions on the growth performance of rainbow trout summarized in the text are short-listed in Table 1.

Table 1- The effects of dietary exogenous enzyme supplementation on growth parameters of rainbow trout (Oncorhynchus mykiss) fed plant protein based diets

Enzymes and Treatment Conditions	Dietary Plant Protein	Effects	Reference
Aspergillus niger Phytase at 10 and 15 °C water temperatures	Soybean Meal	Considerably higher P digesti- bility and retention at 15 °C	Rodehutscord & Pfeffer (1995)
Microbial phytase (Natuphos 5000 l) Included at increasing dosage to evaluate nutrient digestibility Activity 5.537 FTU/g	Raw, Extruded and Expelled Full Fat Soybean Meals	Significantly higher ADCs of Total P Phytate-P, Mg, Mn, Zn for Extruded SBM, Optimal dosage 400 FTU/kg	Cheng & Hardy (2003)
Pre-treatment of dietary plant-proteins with microbial phytase (Natuphos)	Two different commercial soy protein	60 and 40 % increase in weight gain and P retention for both Soy proteins	Vielma et al. (2004)
Top coating the diets with a commercial enzyme mix showing xylanase, amilase, cellulose, protease and β -glucanase activity at 1 and 2.5 g.kg-1 levels	0, 10 and 20 % dietary inclusion of Soybean Meal	Marginal effects of soybean meal and external enzyme on growth and nutrient retention but reduced faecal cohesiveness and sinking speed	Ogunkoya et al. (2006)
Semi-moist (45% water at 45 °C) pre- treatment of dietary plant proteins with enzyme RONOZYME®	Soybean Meal Rape Seed Meal Sun Flower Cake	No effects on pellet quality and nutrient digestibility but decreased growth and feed utilization were observed	Denstadli et al. (2011)
Interactive effect of dietary Aspergillus oryzae-6-Phytase (2800 FTU/kg DM diet) and MAP (Monoammonium Phosphate 1 g P/kg DM diet) on disappearance of Phytic acid in plant protein only diets	Soy Protein Concentrate Wheat Gluten Whole Fava Beans Corn Gluten	Increased InsP6-P hydrolysis with Phytase supplementation and additive effect of MAP and Phytase on digested P	Greiling et al. (2019)
Dietary commercial enzyme treated soybean meal and (EnzoMeal TM) and normal soybean meal replacing fishmeal at 8 and 16% levels	Soybean Meal Enzyme treated SBM Soy Protein Concentrate	Increased growth and protein retention with EnzoMeal [™] at both replacement level compared to SBM	Kumar et al. (2020)
Measurement of nutrient ADCs using commercial Protease complex at 175 g.kg-1 dietary inclusion level	Soybean Meal Peanut Meal Cottonseed Meal Canola Meal Sunflower Meal DDGS	Ingredient specific improvements on nutrient digestion with SBM showing the most profound increments specifically on dry matter and most of the EAA ADCs with protease supplementation	Lee S. et al. (2020)
Post pellet liquid application of <i>Escherichia coli</i> phytase at 0, 500 and 2500 FTU/kg to plant protein only based diets with low P levels at 11 and 15 °C	Soy Protein Concentrate Pea Protein Concentrate	Increased growth and enhanced N and P utilization even at lower temperatures by enzyme supplementation	Lee S.A. et al. (2020)

2.2. Fermentation of dietary plant meals with microorganisms

Fermentation of fibrous plant feed ingredients with one type or the mixture of different types of microorganisms and their effects on growth and intestinal health is an active research area in ruminants and poultry (Villas-Bôas et al. 2002; Nigam & Pandey 2009; Hooge et al. 2010; Picoli et al. 2022). However, research in farmed finfish gathered pace only after the partial replacement of dietary fishmeal with oil extracted or full fat oil seeds and legumes was demonstrated as a possibility without compromising the growth and intestinal health of fish (Yamamoto et al. 2010; Barnes et al. 2015; Tanemura et al. 2016; Wang et al. 2016; 2019). Fermentation is reported to increase the nutritional value of unconventional plant feed ingredients by increasing protein and lipid contents mainly because of reduction in the fibre and ANF content (Dawood & Koshio 2020). It is generally defined as useful bioconversion or metabolic decomposition through which complex substrates are transformed into simple compounds by the microorganisms (Balakrishnan & Pandey 1996). During the fermentation process, there may also be increase in the population of probiotic microorganisms and secondary metabolites with prebiotic activity that could result in the increment of overall absorption and therefore the ADCs of dietary nutrients in fish (Picoli et al. 2022). Furthermore, fermentation using mixture of different types of microorganisms composed of bacteria and yeast are reported to further increase the useful metabolic

decomposition of dietary plant ingredients because better use of substrates is possible as a result of the production of different enzymes by these organisms capable of attacking wide variety of compounds (Fossi et al. 2014; Dawood & Koshio 2020; Picoli et al. 2022). It appears that research targeting nutritional improvement of dietary plant ingredients using several fermentation techniques in salmonid species including rainbow trout is lagging behind compared to those conducted for other farmed carnivorous and omnivorous fish and crustacean species in the literature (Wang et al. 2016; Dawood & Koshio 2019).

Recent investigations on the use of fermented plant dietary ingredients in rainbow trout targeted the possibility of the inclusion of traditional plant ingredients used in aqua feeds such as soybean and lupin meals in higher amounts by way of using special fermentation conditions and methods like Solid State Fermentation (Sealey et al. 2009; Yamamoto et al. 2010; Barnes et al. 2015; Tanemure et al. 2016; Davies et al. 2021). A study by Sealey et al. (2009) hypothesized that juvenile rainbow trout fed probiotic supplemented soybean meal containing starter diets (up to 20% dietary inclusion on DM basis) could develop immune mediated soybean tolerance making it possible to include higher levels of dietary soybean meal in their feeds during the growout period. The authors were able to demonstrate that trout exposed to soybean in starter diets supplemented with probiotics (combination of naturally occurring Saccharomyces cerevisiae, Enterococcus faecium and Lactobacillus sp.) showed less severe pathological changes and increased protein digestion and absorption when encountering much higher (43% DM basis) dietary soybean meal during the grow-out period probably indicating intestinal colonization by putative probiotics that could principally help the host in adjusting to dietary changes (Heikkinen et al. 2006; Sealey et al. 2009). Although it is much debated, the probiotic mechanism appears to occur in several multifaceted processes including in the production of anti-bacterial inhibitory compounds and competition for chemicals and adhesion sites leading to an improved microbial balance as well as host immune modulation and the modification of dietary components to increase utilization by the host organisms (Verschuere et al. 2000; Heikkinen et al. 2006; Sealey 2009). This hypothesis was put to the test in a recent investigation conducted by Özil et al. (2023) in rainbow trout. The study demonstrated that a dietary inclusion of 1.1% probiotic mixture (Table 2) in combination with 1% either sage (Salvia officinalis) or myrtle berry (Myrtus communis) powder as medicinal plants showed a positive effect on the growth performance, intestinal microflora and histology, antioxidant enzyme activities and disease resistance in juvenile rainbow trout fed 30% soybean meal as the main dietary plant protein source (Özil et al. 2023). Previously different medicinal plants from different geographical locations not only in Turkey but around the world have been studied for their effects on digestive enzyme activities, intestinal health, immunomodulatory response and antioxidant capacities in trout extensively and it remains an active research topic in aqua feed additives (Awad et al. 2012; Sönmez et al. 2022; Filogh et al. 2023)

The effects of two different fermentation conditions of defatted and heat-treated soybean meal on growth and nutrient digestibility and physiological conditions of juvenile rainbow trout were investigated by Yamamoto et al. (2010). In the study, the soybean meal was fermented using 30 and 45% (w.w⁻¹) water for about 7 and 10 h respectively until the material temperature reach 80 °C in both fermentation conditions and almost 48% (on wet weight basis) non-fermented and fermented soybean meals constituted the experimental diets except the fishmeal control diet. The results showed that increased water and duration in fermentation process appeared to influence the growth performance and dietary carbohydrate and lipid digestibility values positively as well as making the morphological abnormalities in distal intestine and liver tissues associated with soybean consumption less visible in trout (Yamamoto et al. 2010). The beneficial effects of the fermentation conditions (temperature and duration) of soybean products using Lactobacillus plantarum and a mixture of several yeast and bacterial species on growth performance, intestinal histopathological changes and other related physiological mechanisms including antioxidant capacities of Turbot, Nile tilapia and orange spotted grouper were also reported by several authors (Shiu et al. 2015; Wang et al. 2016; Picoli et al. 2022). The most recent investigation by Davies et al. (2021) tested the effectiveness of biotechnologically developed dietary additive (Synergen[™]) manufactured based on Solid State Fermentation with Aspergillus niger technology on the growth performance, nutrient digestibility and intestinal morphology using nutritionally balanced diets containing yellow lupin and soybean meals at 300 and 181 g.kg⁻¹ of the diets respectively in the juvenile rainbow trout. The product was added into nutritionally balanced diets at two different concentrations (1 vs 5 g.kg⁻¹ of diets DM basis). It appeared that 0.5% dietary inclusion of SynergenTM significantly improved growth, crude protein and fibre digestibility and serum glucose levels in trout compared to that of fish fed the same diets with 0.1% supplementation or without supplementation indicating the effective hydrolysis of cellulosic and hemicellulosic oligosaccharides in plant proteins thereby absorbing the glucose more freely into the blood (Davies et al. 2021). This was also supported with the significantly lower number of goblet cells found in fish fed the diet supplemented with 0.5% synergenTM in this study because the goblet cell numbers and their proliferation rate are closely associated with high dietary fibre content in mono gastric animals. However, this reduction of goblet cells could also be influenced by the microbiome characteristics indicating a reduced investment in mitigating the effect of stressors within the lumen (Davies et al. 2021).

Apart from investigating the effects of fermentation process itself on the nutritional value of fermented plant ingredients on fish performance, research specifically in trout recently concentrated on the identifying the comparative response to same fermented soybean meal by different strains (Barnes et al. 2015). In the investigation, dietary fishmeal was replaced by 35 and 50% of commercially produced fermented soybean meal and fed by hand to satiation once per day to rainbow trout from Shasta and McConaughy strains at 23.4 and 15.9 g initial average weight respectively for a 94-d grow-out period. The results showed that both strains of rainbow trout gained significantly lower weight when fed 50% dietary fermented soybean compared to fish fed fishmeal control and 35% fermented soybean meal diets. However, the much lower weight gain and higher HSI (Hepatosomatic index) values achieved by the McConaughy strain than that of those achieved by the Shasta strain at each dietary

fermented soybean meal replacement levels probably indicated that increased fat deposition due to the slow growth and decreased feed efficiency in the McConaughy strain of rainbow trout (Barnes et al. 2015). They also reported that distal intestine morphology scores of fish fed diet containing 35% fermented soybean meal in both strains of rainbow trout were similar to that of fish fed fishmeal control diet but at 50% replacement level the Shasta strain had significantly higher lengths of lamina propria of simple folds and connective tissue at base of folds indicating this strain, compared with the McConaughy strain, might be more susceptible to saponins that is a compound associated with soybean meal induced enteritis (Krogdahl et al. 2003; Knudsen et al. 2008) in fish (Barnes et al. 2015). Recently dietary 30 and 50% of fish meal replaced by several treated or not treated plant protein concentrates before fermentation process and supplemented with shrimp soluble extract were also investigated for their effects on rainbow trout growth and nutrient retention, intestinal histology, non-specific immune response and haematological analysis by Moniruzzaman et al. (2018). An equal mixture of soybean and corn gluten meal fermented with Bacillus subtilis according to the solid-state fermentation technique and the same ingredients pre-treated through acid hydrolysis to increase the solubility of substrate and their substitution with 2% shrimp soluble extract constituted the isonitrogenous and isolipidic main four dietary treatments in this investigation (Moniruzzaman et al. 2018). The total number of experimental diets increased to ten with four replicates at each replacement level and the LT-FM and Vietnam FM diets as positive controls (Monurizzaman et al. 2018). Trout whole body nutrient composition and blood biochemistry parameters did not significantly change with regards to pre-treatment of plant protein concentrates replacing dietary fish meal at 30 and 50% replacement levels but final body weight and percentage weight gain of trout fed fermented soybean and corn gluten meal diets with supplemented shrimp soluble extract at both replacement levels were significantly higher than that of fish fed not-supplemented diets indicating the positive effect of some of the essential amino acids that are missing in plant proteins but sufficiently existed in shrimp protein (Tulli et al. 2010; Kader et al. 2012; Jo et al. 2017; Moniruzzaman et al. 2018). It appears that higher than 35% dietary inclusion of fermented plant protein sources in trout diets lowers the growth rates simply by changing the morphology of villus preventing the effective nutrient absorption giving way to decreased non-specific immune response measured as SOD (superoxide dismutase), lysozyme and MPO (myeloperoxidase) enzyme activities as similarly reported in other salmonids and farmed bream species (Knudsen et al. 2008; Krogdahl et al. 2010; Kader et al. 2012; Kokou et al. 2012; Khosravi et al. 2015; Moniruzzaman et al. 2018).

In vivo and in vitro nutrient digestibility measurements are an inseparable part of the nutritional evaluation of novel dietary ingredients before these ingredients are widely included in commercial feed formulations manufactured for many farmed animals including fish. The fermentation of plant protein ingredients specifically with Lactobacillus spp. is reported to increase nutrient digestibility most likely through the alteration of the composition of microbiota in the gastrointestinal tract or the digestive enzyme activities or the chelation of minerals and the increased solubility of nutrients due to increased acidification caused by lactic acid production in the process (Ringé 1991; Yanbo & Zirong 2006; Pandey & Satoh 2008; Lim et al. 2015; Latorre et al. 2016; Zhou et al. 2016; Lin & Chen 2022). In addition, Bacillus spp. has previously been associated with the detoxification of potentially harmful dietary components and producing vitamin B complexes specifically vitamin B12 and biotin which are in return known to improve overall feed utilization and digestibility of feed ingredients (El-Haroun et al. 2006; Han et al. 2015; Dawood & Koshio 2020). The mechanism behind the beneficial effects of naturally occurring organic acids during fermentation with microorganisms on nutrient absorption and utilization was hypothesized in rainbow trout fed low fishmeal diets by Pandey & Satoh (2008) using dietary supplementation of Lactic acid (LA) and Citric acid (CA), Methionine Hydroxy Analog (MHA) and Liquid Trace Elements (LTE) at 1% inclusion levels. The authors also included the diet supplemented with calcium phosphate at 0.5% and non-supplemented with any P-source as positive and negative controls in the investigation. The better growth performance achieved by trout fed diets supplemented with CA and LTE compared to that of fish fed the other dietary treatments was implicated as the positive effects of increased P and N retention efficiencies found in fish fed these diets (Pandey & Satoh 2008). It was also postulated that CA and LTE in acid solutions effectively improved the de-phosphorylation of phytate P in plant ingredients increasing the bioavailability of P to trout compared to inorganic P thereby reducing the amount excreted into the environment (Pandey & Satoh 2008). In a recent study the effects of fermentation of several conventional (*i.e.* soybean meal and rapeseed meal) and non-conventional (algal and macrophyte meals) dietary plant ingredients with three species of white-rot fungi on in vitro and in vivo nutrient digestibility was investigated in rainbow trout (Tanemura et al. 2016). The species of white-rot fungi used in the study were Tramates coccinea, Lentinula edodes and Pleurotus sajor-caju and the meals were fermented semi-anaerobically at 38 °C (for T. coccinea) and 28 °C (for L. edodes and P. sajor-caju) in an incubator maintained under 90-100% humidity. In vitro degradability rates of NDFs (Neutral Detergent Fiber) in all the fermented dietary ingredients decreased significantly except the macrophyte meal probably indicating the fungi utilized non-NDF carbohydrates such as starch for their growth (Tanemura et al. 2016). It is also speculated that certain ingredients like macrophyte meal rich in minerals, specifically Mn and Fe, might prevent fungi breaking down the cellulose during fermentation (Dillon et al. 1988; Manubens et al. 2007; Tanemura et al. 2016). Authors were also able to demonstrate that CP (crude protein) contents of all the fermented ingredients increased compared to corresponding non-fermented control groups because of decreased yield rates increasing the relative amount of CP in fermented ingredients. However, decreased CP digestibility measurements in juvenile rainbow trout fed diets containing fermented ingredients indicated that CP contributed by the fungal mycelium growth during fermentation was not utilized as efficiently as intact proteins in the ingredients itself (Tanemura et al. 2016). It is documented that mycelium may contain N-containing chitin for up to 5% of its dry weight and is not digested well by all mono-gastric animals including fish (Lindsay et al. 1984; Yoshida et al. 1987). Furthermore, a study by Tanemura et al. (2016) re-iterated that the P bioavailability in trout fed diets containing fermented rapeseed and soybean meals significantly increased compared to that of fish fed diets containing non-fermented counterparts indicating the ability of fungi breaking down the Phytate-P and making it bioavailable to the fish regardless of the species of fungi.

The results of the investigations concerning the dietary inclusion of fermented plant proteins on the growth performance and several physiological mechanisms in rainbow trout summarized in the text are short-listed in Table 2.

Table 2- The results of dietary inclusion of fermented plant proteins on the growth performance and several physiological mechanisms in rainbow trout (Oncorhynchus mykiss)

Fermentation method and conditions	Plant Protein	Effects	Reference
Induction of soy tolerant juveniles by dietary supplementation of commercial probiotics containing live <i>Saccharomyces cerevisiae</i> and several <i>Lactobacillus</i> spp. in the starter diets followed by exposition to 43% of the same plant ingredient in grow-out period	Soybean Meal	Improved soybean meal utilization and less severe pathological changes in fish exposed to SBM with probiotic supplementation in the starter period	Sealey et al. (2009)
Pre-fermentation of the plant ingredient with <i>Bacillus</i> spp. at 80 °C using two different water levels and time duration	Defatted and heat treated Soybean Meal	Increased water and time during fermentation improved growth with no visible distal intestine abnormalities and regardless of fermentation method both carbohydrate and lipid digestibility increased	Yamamoto et al. (2010)
Dietary fishmeal replacement by commercially available fermented, soybean meal at 0, 35 and 50 % for Shasta and McConoughy strains of rainbow trout	Fermented Soybean Meal	Up to 35 % inclusion appeared to be feasible considering similar growth feed utilization and distal intestine morphology indices to fishmeal control in both strains	Barnes et al. (2015)
Fermentation of several plant meals by three species of white-rot fungi at 38 or 28 °C for 6 weeks to evaluate <i>in</i> <i>vitro</i> and <i>in vivo</i> nutrient ADCs	Soybean Meal Rapeseed Meal Algal Meal (<i>Gelidiaceae</i> spp.)	Trametes coccinea and Lentinula edodes were more effective in lowering NDFs but increased ash as a result of reduction in yield rates after fermentation decreased organic and dry matter and crude protein but significantly increased P digestibility	Tanemura et al. (2016)
Replacement of dietary fish meal by fermented plant protein source (soybean and corn gluten mixing ratio 1:1) using <i>Bacillus subtilis</i> with solid state fermentation technique at 30 and 50 % levels	Soybean Meal Corn gluten	Supplementation of diets with shrimp soluble extract significantly improved growth at both replacement levels but villus morphological structure compromised at 50% replacement level	Moniruzzaman et al.(2018)
Commercial Solid State Fermentation product used as feed additive at 1 and 5 g.kg-1 levels in diets containing 53 % plant protein sources	Yellow Lupin Meal Soybean Meal	Improved growth, crude protein and fibre digestibility and decrease in goblet cell numbers were observed at 5 g.kg-1 dietary inclusion level	Davies et al. (2021)
1.1 % dietary supplementation of Probiotic mixture in combination with 1 % of either sage or myrtle powder; Probiotic mixture include: Lactobacillus spp, Lactococcus spp Lactobacillus acidophilus, Bifidobacterium spp. Kluyveromyces marxianus (isolated from kefir) and Lactobacillus sakei (isolated from trout intestines)	Soybean Meal Wheat Gluten	Improved growth and significantly increased villi length and width and goblet cell numbers and total bacteria count	Özil et al. (2023)

3. Conclusions

The need to reduce the impact of aqua feeds into the aquatic environment whilst maintaining the general health and wellbeing of farmed fish and crustacean species is a priority research area in fish nutrition studies. The widespread use of plant protein sources as an alternative to fishmeal is only made possible with increased nutrient digestibility and decreased ANFs in these dietary ingredients for fish. Dietary external supplementation of enzymes that are specific to certain nutrient compounds in plant protein sources and known to be not inherited to exist in digestive tract of fish is an active research topic in nutritional studies for fish since the replacement of certain amounts of dietary fishmeal by these plant protein sources has been demonstrated previously (Romarheim et al. 2006; Gatlin et al. 2007). The fermentation of plant protein sources with numerous microorganisms

such as Lactobacillus spp., Aspergillus niger and Saccharomyces cerevisiae and Rhizopus oligosporus has also been used as a strategy to increase the amounts to be used in fish diets without compromising growth and overall health and other related physiological mechanisms. Although not studied as extensively as in terrestrial farm animals, research targeting the possibility of dietary inclusion of biotechnologically produced enzymes and fermented plant ingredients in farmed fish has been growing over the past twenty years. Research has so far demonstrated that up to 50% of dietary fishmeal could be replaced by plant proteins in rainbow trout following dietary external supplementation of proteases, carbohydrases and phytases and fermentation of these protein sources with several species of yeast and bacteria including *Saccharomyces* spp. and *Lactobacillus* spp. without compromising growth and the gastrointestinal integrity of the fish (Sealey et al. 2009; Barnes et al. 2015; Collins et al. 2018; Moniruzzaman et al. 2018; Kumar et al. 2020). Increased P digestibility and retention was also observed in these investigations indicating specifically the ability of external supplementation of phytases on the de-phosphorylation of phytate-P (Greiling et al. 2019; Demir & Yılayaz 2010). However, the standardization of these biotechnological innovations for aqua feeds is far from being realized since the effectiveness of enzymes and fermentation methods immensely depends on the species differences and their farming conditions specifically the environmental temperature and pH as well as the technology and the fermentation conditions and the type of microorganisms to produce these novel ingredients. In order to understand the true potential of these biotechnologically developed ingredients for fish feed, research addressing the effects of these differences on the degradation of NDFs and some of the ANFs (Non-Starch Polysaccharides, phytic acid and trypsin inhibitors) in plant proteins in a wide variety of farmed fish species is required. Future research specifically targeting the bio compounds that generates following the fermentation processes by different microorganisms and their interaction with other nutrients therefore the nutrient absorption and other physiological mechanisms in fish is also much needed.

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