



IMPLICATIONS OF FERMENTED PLANT PROTEIN INGREDIENTS: A CRITICAL REVIEW OF NUTRITION, PHYSIOLOGY AND GROWTH RELATED ASPECTS

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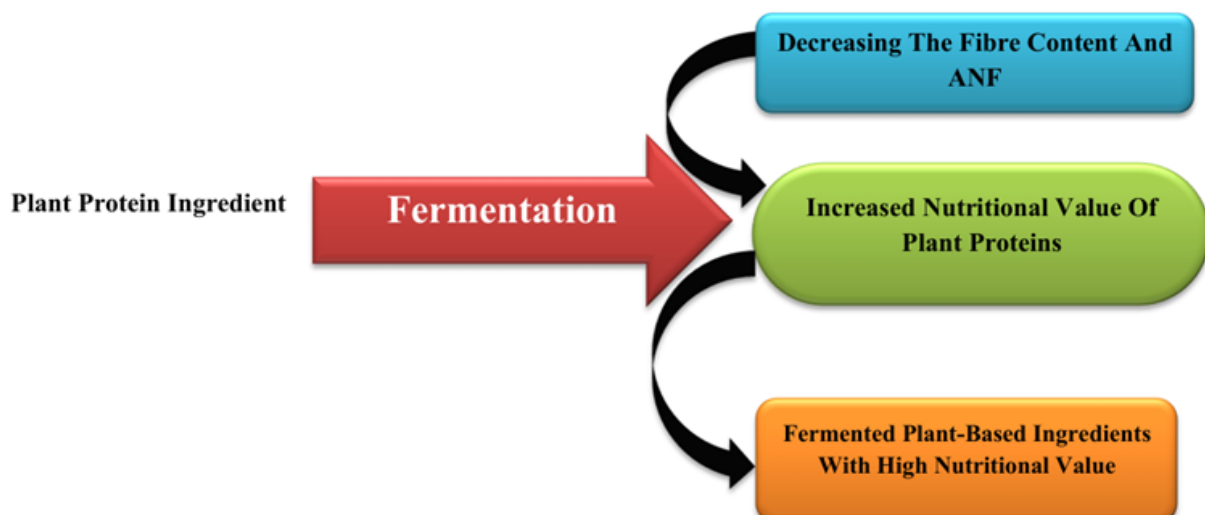
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Abstract

Recently, aquaculture has experienced some limitations, such as the limited availability of land, water, feed ingredients, and biosecurity concerns. Managing economic activity has become mandatory to confront global climate change. In the last few decades, fish meal has been recognized as the best source of protein for aquafeeds; however, the shortage of fish meal supply and its high demand have encouraged its replacement with different plant ingredients, which have been increasingly used in aquafeeds in comparison to fish meal, making them the most viable choice as an alternative. However, plant protein ingredients are recognized for their high content of antinutritional factors (ANFs), which limits their use in feed. Recently, the application of fermentation to overcome these problems has gained significant attention because it provides the health and growth-promoting benefits, palatability, enhances nutrients assimilation, availability, and breaks down ANFs in plant protein ingredients that consequently affect growth, immune system response, disease outbreaks and control pathogen infections that aim to achieve aquaculture sustainability. The present review discusses the use of advanced processing and fermentation technology techniques to reduce or eliminate ANFs and increase nutritional value in plant protein sources and effects on fish.

Key words: alternative sources, plant protein ingredients, solid state fermentation, submerged fermentation, antinutritional factors

Graphical abstract



Nowadays aquaculture signifies the rapid-growing food production sector around the world, which contributes half of the fish supply, and this sector has great potential to expand in order to fulfill the growing protein demand around the world, which is expected to reach 9.7 billion people by 2050 (Filipe et al., 2023; Ragab et al., 2024; Awad et al., 2024; Eide et al., 2025), while the capture fisheries have remained almost static, which led to a decrease in fish meal (FM) inclusion levels in aquafeeds. With increasing demand and a rising price of FM, the use of FM is gradually becoming unsustainable due to competition, cost, and ecological challenges (Davies et al., 2019, 2020; Heshmatfar et al., 2023; Rehemujiang et al., 2023; Mugwanya et al., 2023; Manna et al., 2024; Chen et al., 2025; Qu et al., 2025). Fish meal serves as the main source of protein in aquafeeds which is obtained from wild forage fish, owing to its high digestible protein and balanced EAAs (Novriadi et al., 2023). During the past 20 years, the increasing price of FM, competition with other animal livestock production and the shortage of FM supply forced researchers, nutritionists and feed manufacturers to search for alternative, less expensive protein sources for FM in aquafeeds without affecting their performance (Macusi et al., 2023; Awad et al., 2024; Qu et al., 2025). The important factors concerning the possibility of alternative ingredients to substitute FM in fish and shrimp diets are: i) the protein content of the feedstuffs; ii) access to affordable feedstuffs; and iii) the quality and nutritive value of the novel ingredient (Filipe et al., 2023). Consequently, adopted and implemented novel methods to enhance the quality of plant proteins for partially or totally replacing FM are required to minimize the costs and achieve sustainability of fish production (Heshmatfar et al., 2023).

In recent years, the sustainability of aquaculture growth has depended on the ability to find alternatives to fishmeal, as demand has exceeded supply (Mohamady et al., 2023; Feng et al., 2024). In addition, feed contributes the largest amount to production costs in aquaculture which represent 60–70% (Rehemujiang et al., 2023; Macusi et al., 2023); by 2025, an extra 37.4 million tons will be required from fish diets (Abd El-Naby et al., 2024). Therefore, it has become necessary to conduct more research to find alternative protein sources for common ingredients used as FM and SBM, which is urgent to limit their incorporation into aquafeeds (Heshmatfar et al., 2023; Wang et al., 2024). Recently, numerous trials have been conducted to investigate the quality of various plant proteins as a potential ingredients to replace FM (Goda et al., 2019; Ragab et al., 2024; Novriadi et al., 2023; Chen et al., 2025; Qu et al., 2025), due to its availability and competitive prices compared to fishmeal, making it the most viable candidate as an alternative (Xu et al., 2020). However, increasing the incorporation levels of plant protein is restricted because of its un-palatability, lack of one or more of EAAs, and the presence of ANF (Mugwanya et

al., 2023; Manna et al., 2024; Eide et al., 2025). In this context, adopting and implementing novel technology is the importance task in feed production sector to enhance the quality of fish feed (Abd El-Naby et al., 2024; Awad et al., 2024). Nowadays, production of high quality ingredients in aquafeeds requires promising technique such as either solid state fermentation (SSF) or submerged fermentation (SmF) (Xu et al., 2020; Duan et al., 2022), where large amounts of antinutritional factors are hydrolyzed, thus improving the availability and palatability of nutrients in feeds (Zhang et al., 2023 a, b; Rehemujiang et al., 2023; Eide et al., 2025), which give the possibility for high incorporation of plant protein ingredients in aquafeeds (Soltan et al., 2023; Elhalis et al., 2023; Awad et al., 2024; Qu et al., 2025). These studies highlight the benefits of fermentation which not only decreases the ANFs, but also increases the growth and immunity of the fish which is controlled by some external and internal biological factors.

Fermentation strategies

Adopting and implementing novel technology is the important task in feed production sector to enhance the quality of fish feed (Awad et al., 2024). Recently, research has focused on the biological processes of bioprocessing and detoxification of plant proteins to eliminate or reduce ANFs by fermentation processes (Kari et al., 2020). Fermentation, a cost-effective biological treatment method, improves plant-based protein quality in fish diets (Siddik et al., 2024; Awad et al., 2024; Rehemujiang et al., 2023; Chen et al., 2025; Qu et al., 2025), increasing protein content, and providing exogenous enzymes such as carbohydrates, amylase and protease (Elhalis et al., 2023; Feng et al., 2024), thus enhancing fish digestibility and growth performance by degradation of ANFs (Filipe et al., 2023), by using a combination of microorganisms (Feng et al., 2024).

Moreover, fermented ingredients can substitute FM and reduce the cost of production, and be environmentally friendly (Dawood and Koshio, 2020; Rehemujiang et al., 2023; Abd El-Naby et al., 2024). Figure 1 shows a summary of the positive effects of fermentation in aquatic feeds. Thus the fermentation improves the quality of feed ingredients as follows: i) it promotes protein digestibility through converting complex compounds into easily digestible components (Choi et al., 2020; Pratiwy and Triyani, 2022); ii) it reduces ANFs compounds (Manna et al., 2024); iii) it changes the aroma and taste to be easily liked; iv) the shelf life of the feed becomes longer (Pratiwy and Triyani, 2022). Fermentation benefits could be summarized as follows: i) a procedure to convert low-quality feed ingredients into high-quality; ii) produces some functional compounds and bioactive compounds (Shi et al., 2021); and iii) eliminates ANFs in plant protein ingredients (Shi et al., 2021). Fermentation processes vary depending on the type of substrate and microorganisms used (Filipe et al., 2023; Feng et al., 2024; Phinyo et al., 2024).



Figure 1. Effects of using fermentation to increase the nutritional value of different plant protein sources

The role of fermentation relies on several factors such as: i) the nature of organism used in the process as bacteria and/or fungi; ii) the fermentation methods (Awad et al., 2024); iii) the quality of the fermentation process environment; iv) addition of materials; (v) mixing (between different environments); (vi) time of fermentation (Sugiharto and Ranjitkar, 2019). Recently, fermented plant protein has been used in different fish species, such as sea basses (Davies et al., 2020; Rahimnejad et al., 2021; Filipe et al., 2023), mud grouper (Shiu et al., 2015), rainbow trout (Choi et al., 2020), star pomfret (Nguyen et al., 2020), tilapia (Hassaan et al., 2018), and turbot (Li et al., 2019). Table 1 states the optimum substitutions levels of soybean meal and fish meal with various fermented plant proteins sources.

Increasing the nutritional value of plant proteins through fermentation

Fermentation processes are playing an important role in aquafeed industry (Awad et al., 2024; Chen et al., 2025; Qu et al., 2025). The positive role of fermentation process comes from its capacity to: i) decrease crude fiber content; ii) increase protein content; iii) enhance digestive enzymes activity through optimizing the pH of gastrointestinal tract to boost the efficiency of digestive enzymes activity; iv) eliminate ANFs, and v) enhance the digestion of amino acids and minerals, which leads to higher AAs, microbial protein production, other cellular components, and decreased fiber degradation through enzyme secretion (Mohammady et al., 2023; Abd El-Naby et al., 2024), leading to increased nutritional value of plant proteins (Siddik et al., 2024). However, several factors affect the efficiency of the fermentation process such as type of microorganisms and fermentation conditions during the processing technique. The advantages of using fermentation process include: i) increases protein content coming from total or partial breakdown of either sugar or dry matter (Olukomaiya et al., 2020; Weng et al., 2023), or the microorganisms such as bacteria and yeast used during the fermentation process considered as an exter-

nal source of microbial proteins and microbial enzymes (Nkhata et al., 2018; Qu et al., 2025); ii) increases the contents of essential amino acids, except methionine and cysteine (D'Este et al., 2018); iii) breaks down the ANFs (Hassaan et al., 2015; Shiu et al., 2015; Chen et al., 2025); iv) increases protein digestion through microbial enzymes.

Previous research confirmed the benefits of fermentation and Awad et al. (2024) stated that using a combination of fermented cottonseed meal and jojoba meal (CSJM) by *S. cerevisiae* resulted in superior levels of EAA content and inferior level of fiber content versus conventional plant ingredients. Following the same patterns, Hassaan et al. (2015) and Dawood et al. (2019) stated that fermented plant proteins resulted in high levels of digestible crude protein, low levels of crude fiber and a significant degradation of ANFs. In addition, Ramachandran et al. (2005) found that using of microorganisms in fermented plant protein significantly reduced ANFs.

Furthermore, FSBM with *Bacillus subtilis* increased crude protein by 6.57% compared to unfermented SBM (Dai et al., 2017). In contrast, Hassaan et al. (2015) showed that after fermentation of SBM, crude protein increased by 13.6%. Therefore, the difference in the relative increase of crude protein despite the similarity of the type of plant protein is due to the difference in the type of substrate and microorganisms used during the fermentation process (Zahir et al., 2020; Filipe et al., 2023). The use of a mixture of microorganisms during the fermentation process increases the crude protein content of various plant proteins. For example, using a mixture of *A. ibericus*, *A. uvarum*, or *A. niger* during brewer's spent grain (BSG) fermentation increased the crude protein content by 38.5% (Sousa et al., 2018). Many factors such as fermentation conditions, microorganism species, and substrate utilized have effects on the crude protein content of the fermented substrate (Filipe et al., 2023).

Table 1. Previous studies on how fermentation of plant proteins affects growth and physiological processes in various fish and crustacean species

Fermented plant protein	Fish species	Optimum substitution levels	Results	Reference
1	2	3	4	5
FSFM	Atlantic salmon <i>Salmo salar</i>	Up to 10%	↑growth performance; ↑intestinal histology; ↑goblet cell; ↑intestinal macrobiotic; ↑immune gene expression	Eide et al., 2025
	Nile tilapia <i>Oreochromis niloticus</i>	Up to 40% SBM	↑↓growth performance ; ↑anti-inflammatory genes (tgf-β1); ↑intestinal histology; ↑pro-inflammatory gene expression (tnf-α, il-1β, il-6, il-8).	Huang et al., 2024
FCSM	White shrimp <i>Litopenaeus vannamei</i>	Up to 75% SBM	↑growth performance; ↑antioxidant capacity; ↑essential amino acid;	Han et al., 2022
	White shrimp <i>Litopenaeus vannamei</i>	Up to 50% FM	↑↓growth; ↑↓feed utilization	Sun et al., 2016
	Black sea bream <i>Acanthopagrus schlegelii</i>	Up to 16% FM	↑↓growth; ↑↓feed utilization	Sun et al., 2015
	Golden pompano <i>Trachinotus ovatus</i>	Up to 25% FM	↑growth performance; ↑feed utilization; ↑gene expression; ↑blood physiological; ↑hepatic antioxidant	Wang et al., 2024
FSM	White shrimp <i>Litopenaeus vannamei</i>	Up to 30% FM	↑growth; ↑↓gut micro- biota	Shao et al., 2019 a
	White shrimp <i>Litopenaeus vannamei</i>	Up to 20% FM	↑↓growth; ↑↓feed utilization; ↑↓immune performance	Shao et al., 2019 b
	Seabass <i>Lateolabrax japonicus</i>	Up to 20% FM	↑↓growth performance; ↑↓feed utilization ; ↑↓flesh quality	Liang et al., 2017
	Prawn shrimp <i>Farmeropenaeus indicus</i>	Up to 50% FM	↑↓growth; ↑↓production, ↓cost effectiveness	Sharawy et al., 2016
	Nile tilapia <i>Oreochromis niloticus</i>	Up to 37% FM	↑↓growth; ↑↓nutrient digestibility; ↑↓physiological condition	Hassaan et al., 2015
	<i>Oncorhynchus mykiss</i>	Up to 20% 40% FM	↑↓growth; ↑↓feed utilization	Choi et al., 2020
	Largemouth bass <i>Micropterus salmoides</i>	30%	↑growth performance; ↑↓intestinal histology; ↑proximate composition of muscle; ↑intestinal microbiota	He et al., 2020
	Largemouth bass <i>Micropterus salmoides</i>	Up to 30% FM	↑↓growth; ↑↓feed utilization; ↑↓antioxidant gene expression	Weng et al., 2023
	Coho salmon <i>Oncorhynchus kisutch</i>	10% FM	↑↓growth; ↑↓protein deposition; ↑↓digestive enzyme activity; ↑↓immune-related genes	Zhang et al., 2023 a
	Nile tilapia <i>Oreochromis niloticus</i>	Up to 25% FM	↑growth performance; ↑disease resistance	Phinyo et al., 2024
	Nile tilapia <i>Oreochromis niloticus</i>	FSBM an excellent candidate to replace FM	↑nutritional value; ↑↓growth performance; ↑↓feed utilization	Boonmee et al., 2024
	White shrimp <i>Litopenaeus vannamei</i>	Up to 40% FM	↑↓growth performance; ↑↓feed digestibility; ↑↓antioxidant enzymes	Abd El-Naby et al., 2024
FSCB	Coho salmon <i>Oncorhynchus kisutch</i>	10% FM	↑growth performance; ↑serum biochemical indexes; ↑antioxidant capacity	Zhang et al., 2024
CFP	White shrimp <i>Litopenaeus vannamei</i>	Up to 30% FM	↑growth; feed utilization; ↑immune response; ↑disease resistance	Hamidoghli et al., 2020
	White shrimp <i>Litopenaeus vannamei</i>	Up to 18% FM and SBM	↑↓growth; ↑↓health condition	Novriadi et al., 2022
FDF	Pacific white shrimp <i>Litopenaeus vannamei</i>	Up to 35% FM	↑survival; ↑↓growth performance	Flores-Miranda et al., 2015
FRM	Red sea bream <i>Pagrus major</i>	Up to 50% FM replaced by FRM	↑immune defence mechanisms; ↑exerted anti-oxidative effects; ↑growth performance; ↑feed utilization	Dossou et al., 2018 a
	Juvenile red sea bream <i>Pagrus major</i>	Up to 56% FM	↑↓growth; ↑↓nutrient utilization; ↑innate immune response or oxidative stress	Dossou et al., 2018 b
	White shrimp <i>Litopenaeus vannamei</i>	25%	↑↓growth performance; ↑↓gut microbiota; ↑immune response	Qu et al., 2025

Table 1 – contd.

1	2	3	4	5
FSP	African catfish <i>Clarias gariepinus</i>	Up to 50% FM	↑growth; ↑health status	Abdul Kari et al., 2022
SSF	Nile tilapia <i>Oreochromis niloticus</i> Common carp <i>Cyprinus carpio</i>	UK lupin meal Up to 25% SBM	↑growth; ↑feed performance; gut integrity ↑growth performance; ↑nutrient utilization	Bowyer et al., 2020 Anwar et al., 2020
FPPC	Olive flounder <i>Paralichthys olivaceus</i>	Up to 28% FM	↑↓growth performance; ↑organosomatic indices, ↑↓wholebody proximate composition; ↑hematological parameters; ↑non-specific immune responses	Seong et al., 2018
FPCs	Rainbow trout <i>Oncorhynchus mykiss</i>	Up to 30% FM	↑↓growth; ↑↓health status	Montruzzaman et al., 2018
FWPC	Nile tilapia <i>Oreochromis niloticus</i>	Up to 30% FM	↑↓growth performance; ↑↓feed utilization	Omar et al., 2022
FFMLs	Gibel carp <i>Carassius auratus gibelio</i>	Up to 40% FM	↑growth; ↑feed utilization	Zhang et al., 2020
SFPY	Common carp <i>Cyprinus carpio</i>	Up to 50%	↑growth; ↑feed performance; ↑gut integrity; ↓lower costs; disease	Wang et al., 2024

↑: increase; ↓: deficiency; ↑↓: no effect; FSEM = fermented sunflower meal; FCSM = fermented cottonseed meal; FSM = fermented soybean meal and corn gluten meal; CFP = corn fermented protein; FDF = fermented duckweed flour; FRM = fermented rapeseed meal; FSP = fermented soy pulp; SSF = commercial solid-state fermentation; FPPC = fermented plant-based protein concentrate; FWPC = fermented wheat protein concentrate; FMLs = fermented moringa leaves; SFPY = solid-state fermentation of yeast.

Types of fermentation

There are two main types of fermentation, depending on the presence or absence of an aqueous medium: solid-state fermentation (SSF) and submerged fermentation (SmF) or liquid fermentation (LF) (Dawood and Koshio, 2020; Elhalis et al., 2023; Wang et al., 2024; Abd El-Naby et al., 2024; Chen et al., 2025; Qu et al., 2025). Figure 2 compares between the submerged and solid-state fermentations.

Solid-state fermentation (SSF)

The SSF method is defined as a fermentation process occurring in the absence of water and used for the production of enzymes and organic acids (Dharmakar et al., 2023) and is an optimum medium for the growth of fungus since the moisture content ranged between 12 and 70% in SSF; this is an optimum environment for the growth of fungi (Mora-Uzeta et al., 2020), which is considered as an indirect source of microbial enzymes and microbial protein that boost the nutritive value of plant protein ingredients (Enyidi and Etim, 2020; Bowyer et al., 2020). In the SSF method the microorganism grows on solid substrates, as plant protein sources, and produces hydrolyzing enzymes which break down complex carbohydrates into simple sugar as glucose, in addition to reducing the content of fiber and increasing nutrient bioavailability and digestibility (Filipe et al., 2023). Figure 3 shows a schematic representation of the steps involved in solid-state fermentation.

SSF is crucial for high-value feed production due to its advantages, such as: i) reduced waste generation; ii) lower costs; iii) high-volume productivity; iv) short process time (Seong et al., 2018; Olukomaiya et al., 2019; Wang et al., 2024). The mode of action of SSF includes but is not limited to: i) releasing microbial enzymes and source of microbial protein that enhance the quality of raw materials and the nutrients consumption and assimilation; ii) breaking down the ANFs; iii) elevating the amounts of trace elements, protein and AAs; and iv) enhancing physical characteristics of the pellets (Yafetto, 2022).

The quality of the output product of SSF mechanisms is controlled by the structure and forms of feed, processing technique conditions, storage conditions and type of microorganisms. However, the disadvantages of SSF include but are not limited to: i) complications on upgrade; ii) release of heat; iii) struggle to control the process conditions; and iv) higher pollution end product (Olukomaiya et al., 2019; Elhalis et al., 2023). Previous research has shown the benefits of SSF as a promising technique to enhance the nutritive values of plant proteins without any record of negative impacts.

Submerged fermentation (SmF) or liquid fermentation (LF)

The SmF method can be used for probiotic preparations, and is founded on the development of bacteria and/or fungi in fluid medium (Shim et al., 2010). Therefore, it is more appropriate for bacteria growth due to high

water activity (Liu and Kokare, 2017). The benefits of SmF could be summarized in the following points: i) optimum controller of the conditions of the fermentation processing through its role to homogenize the liquid media (Domínguez-Espinosa and Webb, 2003); ii) reduction of the dehydration of the fungal filament (Mitchell et al., 2006); iii) less limitations in the growth of different bacteria and/or fungi able to grow in the medium (Garrido-Galand et al., 2021). The financial and ecological compensations of SSF over SmF: i) the limitation of the presence of inhibitors in SSF versus SmF increases the possibility of the amounts of end products since SSF could convert ~ 20–30% while SmF is able to convert only 5% (Liu and Kokare, 2017); ii) SSF is safe for water consumption and reduces the leftover of water; iii) minimizes the water activity and is prone to less contaminations; iv) SSF procedure includes using compacted bioreactor and a low amount of moisture resulting in high volumetric activity; and lastly v) cheap and simpler downstream procedures in case of extraction needs (Garrido-Galand et al., 2021).

Factors affecting microbial growth in the fermentation process

Fermentation quality is dependent on various factors, including temperature, pH, water activity (A_w), type of substrate, microorganisms, and fermentation process duration (Dawood and Koshio, 2020), as shown in Figure. 4. Dozens of research studies were conducted to identify the factors' effect on SSF as mentioned by Zhang et al. (2020) and Siddik et al. (2024) who stated that the optimal conditions of fermented SBM using SSF are T of 44°C, pH of 7.5, and the thickness of SBM layer of 2.0 cm.

Water activity (A_w)

Water activity (A_w) refers to the water requirements of microorganisms involved in fermentation process (Chen et al., 2025). In addition, A_w is affected by several factors, such as the chemical capacity of water, the condensation phase of the absorbed water, relative humidity (RH). A lower A_w affects the growth of microorganisms and leads to decreased production (Tapia et al., 2020), while increased water content hinders fungal expansion. Furthermore, water content affects water retention, permeability, thermal conductivity, and fulfills microbe's physiological requirements (Chilakamaray et al., 2022).

pH

The pH value is critical in fermentation processes as it affects the microbial population, but controlling pH levels during fermentation throughout the system is challenging. In addition, measuring pH within SSF is difficult using traditional methods, due to the low water content of the substrate. The optimum pH of microorganisms ranges between pH 5 and 7, with neutrophils growing best at pH 4.5–8, acidophiles at pH below 5.5, and alkaliphiles at pH above 8.5. Figure 5 shows the different pH ranges at which microorganisms can grow (Behera et al., 2020). pH changes in fermentation processes due to organic acid production can be addressed by using buffer formulations such as urea as a nitrogen source (Picone et al., 2021). According to Siddik et al. (2024), adjustment of the initial pH of the fermentation relied on the microorganisms, substrate, and production technique to achieve high-quality fermented products.

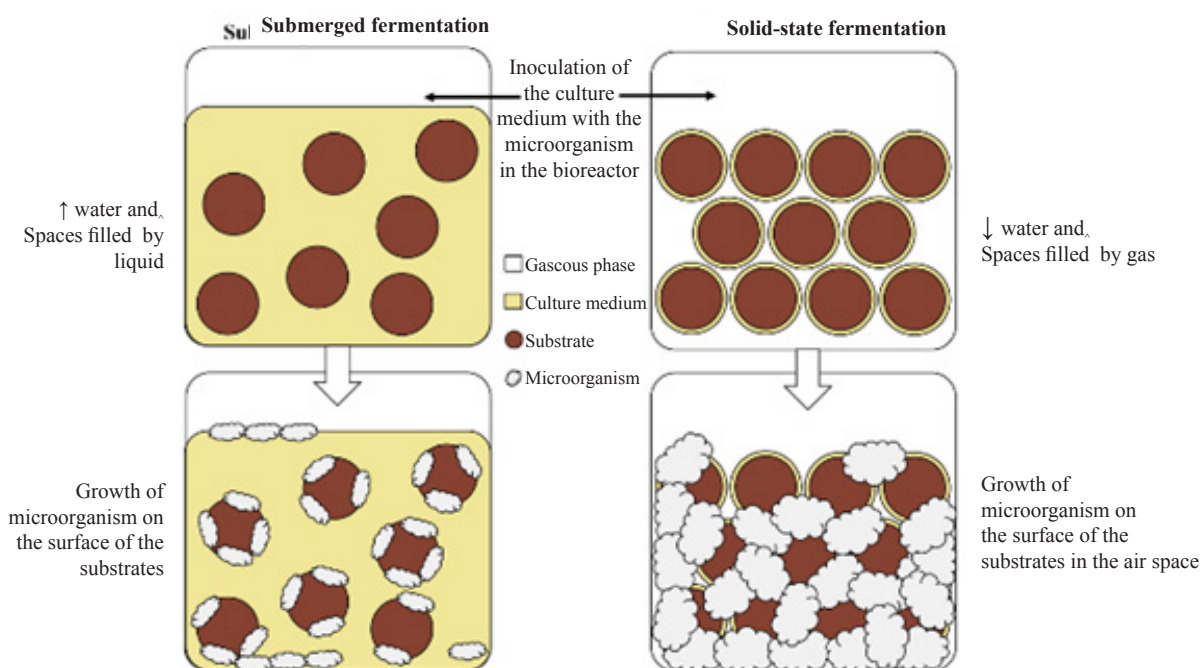


Figure 2. Comparison between submerged and solid-state fermentations (Garrido-Galand et al., 2021)

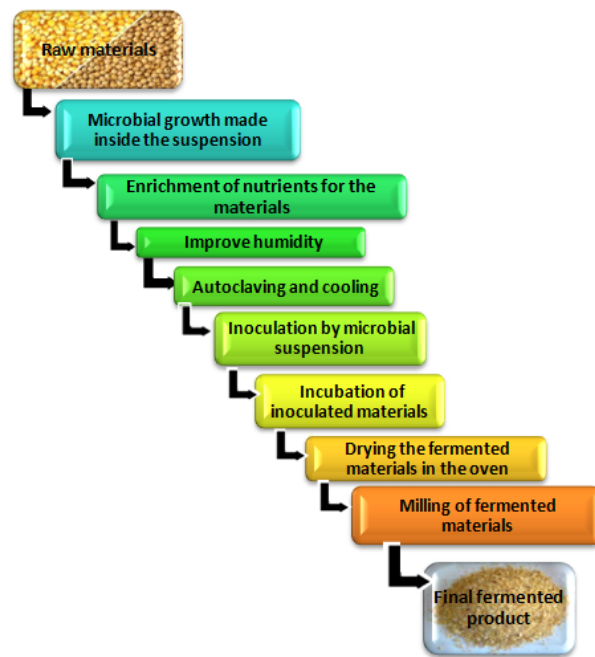


Figure 3. Schematic representation of steps involved in solid-state fermentation of substrates (Olukomaiya et al., 2019)

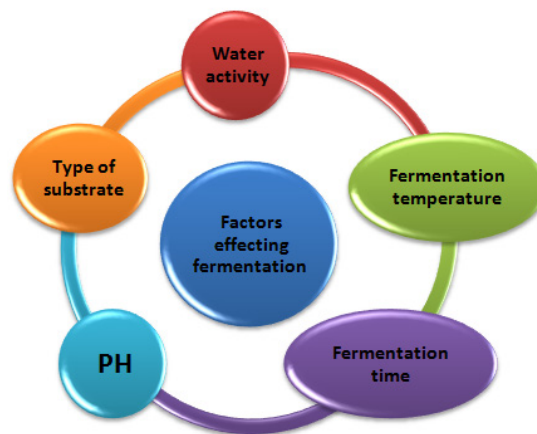


Figure 4. Factors affecting fermentation

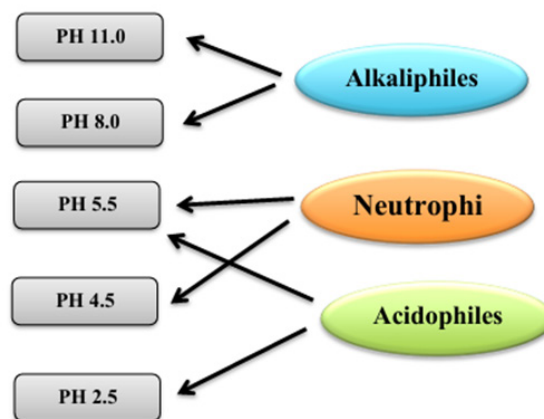


Figure 5. The different pH ranges at which microorganisms can grow (Behera et al., 2020)

Substrate

The fermentation process requires substrates which are recognized as agricultural products or other products derived from agro-industry by-products. Two common solid substrates are used in fermentation: 1) cereals, and 2) animal and plant by-products. The importance of substrates in fermentation process includes controlling the growth of microorganisms and the amount of final product (Subramaniyam and Vimala, 2012; Siddik et al., 2024). The preparation and pretreatment of substrate is important to act as active adsorption substrate for carbon and energy. The pretreatment includes size reduction using chemical and physical reactions to improve substrate supply. However, choosing the substrate depends on the price and obtainability (Raman et al., 2021).

Temperature and process duration

Fermentation temperatures and time play an important role in fermentation process. The best temperature for the growth of microorganisms ranges between 45 and 70°C, and below this temperature, growth slows down, reducing cellular production (Jiang et al., 2017; Afifah et al., 2023). Therefore, evaporative cooling is an important method of temperature control in fermentation processes, as it is able to remove 60–80% of the calories in the substrate (Behera et al., 2020). Type of the strain used in the fermentation process has an effect on the fermentation time. The study by Croat et al. (2016) revealed that the duration of fermentation significantly affects the types of microorganisms produced.

Engin and Koyuncu (2023) reported that increasing soybean fermentation time to approximately 7 and 10 h, respectively, increased crude protein in the diet of trout (*Oncorhynchus mykiss*) compared to unfermented soybean. Likewise, Shiu et al. (2015), Engin and Koyuncu (2023), and Picoli et al. (2022) reported that fermentation conditions such as temperature and duration have a beneficial effect on increasing the nutritional value of FSBM products in the diets of turbot, Nile tilapia, and spotted grouper.

Microorganisms

The selection of microorganisms is an important factor affecting the outputs of fermentation process (Behera and Ray, 2020), through acceleration of the fermentation process. The common microorganisms involved in fermentation process are *Bacillus* sp., *Saccharomyces* and *Aspergillus* sp. (Yang et al., 2023; Awad et al., 2024). In addition, the output produced during the fermentation process varied depending on the type of microorganism; for example, *Lactobacillus* produces lactic acid bacteria (LAB), citric acid, and fungi produce CH₄ and CO₂ (Subramaniyam and Vimala, 2012); in addition, it produces microbial enzymes that degrade ANFs and complex compounds (Dawood and Koshio, 2020). The main factor of success of the SSF technique is using appropriate microorganisms grown on large scale of substances and producing enough quantities of a vari-

ety of compounds. Thus a proper microorganism should meet the following criteria (Makiš et al., 2024): i) act on a large scale of substances and break it down into suitable particles for nutrient utilization; ii) production of the required amounts of hydrolytic enzymes and desired bioactive compounds; iii) satisfactory growth at reduced water activity; iv) not producing any toxic compounds; and v) the ability to eliminate the ANFs in the substrate.

Previous findings concluded that using combination of multi-strain and fermentation methodology was more efficient in ANF elimination versus using single strain and fermentation (El-Haroun et al., 2009, El-Haroun and Bureau 2007). According to Dawood and Koshio (2020) and Siddik et al. (2024), lactic acid bacteria (LAB) ferment a wide range of substrates and reduce the pH and carbohydrate content of fermented products, which prevents the colonization of harmful microbes. Similarly, yeast produces CH₄ and CO₂ during fermentation, which results in a reduction of pH levels in fermented feedstuffs (Stanbury et al., 2012) and promotes the growth of lactic acid bacteria, which break down sugar and produce ATP. This process increases digestibility, improves the palatability of feed and texture, and can be used alone or combined (Wing et al., 2019; Zapašnik et al., 2022). Picoli et al. (2022) and Engin and Koyuncu (2023) showed that the use of *Lactobacillus plantarum* or a mixture of several bacterial species in soybean meal fermentation results in increased crude protein, feed utilization, and growth performance of turbot, Nile tilapia, and spotted grouper. Dawood and Koshio (2020) and Picoli et al. (2022) showed that fermentation using a mixture of different types of microorganisms increases the nutrients in plant protein because the production of different enzymes by these organisms leads to a significant increase in crude protein and improved growth performance.

Effects of fermentation of feed ingredients on the biological functions of fish

Many biological processes of fish species are positively impacted by diet such as growth performance, immune system enhancement, and antioxidant activity. Table 1 shows some studies investigating the effects of feed ingredients fermentation on growth and physiological functions in fish and crustaceans.

Body composition

Body chemical composition is affected by either endogenous or exogenous factors, however, feed composition is considered as a main factor effect on fish body chemical composition (Taufek et al., 2019). Anwar et al. (2020) found that different sources of fermented plant proteins could replace up to 25% of fish meal in Nile tilapia diets without influencing moisture, protein, or lipid content. Furthermore, Wang et al. (2018) and Xu et al. (2016) reported that fermented plant proteins do not have significant impacts on the body chemical composition. Following the same patterns, Moniruzzaman et al. (2018) found that replacing 20 and 50% of fish meal by

FSBM in rainbow trout has no significant impacts on chemical body composition. Zhang et al. (2023 a), Choi et al. (2020) and Abd El-Naby et al. (2024) stated that replacing FSBM with FM significantly increased muscle protein content in juvenile coho salmon, rainbow trout and white shrimp but did not affect crude lipid and ash levels due to the fermentation increasing the content of bioactive peptide, protease activity, and free amino acids, which enhances the assimilation of AAs in the feed, easing protein deposition in fish muscles. Differences between these results can be attributed to feed types, fish species and age, feed mixture, type of fermentation, type of microorganisms used, plant protein cultivation conditions, fermentation time, and plant protein replacement ratio.

Growth response and feed utilization

The importance of fermentation process in aquaculture is related to its role of enhancing growth, feed utilization efficiency and immune system response via increasing protein content, its digestibility, availability, breaking down ANFs and enriching the raw ingredients with bioactive compounds (Yang et al., 2020; Zhao et al., 2022). Nowadays dozens of research studies proved the possibility of totally or partially substituting FM or SBM in different fish species with fermented plant protein ingredients without a negative effect on growth and FCR of Nile tilapia and channel catfish (Omar et al., 2022). In addition, Davies et al. (2021), Choi et al. (2020), Shao et al. (2019 a, b), Han et al. (2022), Novriadi et al. (2022), Abd El-Naby et al. (2024), Dossou et al. (2018), Bowyer et al. (2020), Awad et al. (2024), Boonmee et al. (2024), Phinyo et al. (2024), Anwar et al. (2020), Wang et al. (2024), Chen et al. (2025) and Qu et al. (2025) stated that the inclusion of fermented products using SSF in diets for rainbow trout, white shrimp, *Litopenaeus vannamei*, Asian seabass (*Lates calcarifer*), red sea bream, Nile tilapia, and common carp improved growth performance and feed utilization efficiency. Furthermore, Sharawy et al. (2016) and Bowyer et al. (2020) observed that fermented soybean meal could replace up to 50% of fish meal in Indian white shrimp, while Liang et al. (2017) found that replacing up to 25% of FM by FSBM in Japanese seabass resulted in performance and morphometric parameters matching the control groups. Finally, the potential to use different fermentation products is highly dependent on the types of fermentative bacteria, types of fermentation processes, FM levels, and fish species. Moreover, Phinyo et al. (2024), Choi et al. (2019) and Boonmee et al. (2024) found that inclusion of fermented soybean meal (FSBM) in the diet of Nile tilapia is possible without having adverse effects on growth performance or feed utilization in fish. Also, Lee et al. (2016) reported that 40% of fish meal could be replaced by FSBM in trout and grouper diets, while replacing up to 70% in shrimp diet (Lin and Chen, 2022) and up to 30% in largemouth bass diet (Weng et al., 2023) is possible without affecting growth performance or feed utilization. Likewise, Zhang et al.

(2023 a) reported that incorporation of FSBM in coho salmon instead of fish meal enhanced the growth in comparison with using non-fermented SBM. The improvements in growth performance of previous trials are the following: i) improvement in nutritional quality (Jiang et al., 2017) ; ii) enhancement of nutrient digestibility; iii) increase in digestive enzymes activity; and iv) degradation of the ANFs (Zhuo et al., 2016).

Nutrients digestibility

Awad et al. (2024) reported that nutrients digestibility coefficient of fermented mixed plant proteins increased compared to unfermented treatments. The improvement of nutrients digestibility could be attributed to different scenarios such as: i) breakdown of the ANFs (Hassaan et al., 2021); ii) the microorganism involved in fermentation technique considered as a source of microbial enzymes that improve nutrients digestibility (Vieira et al., 2023); iii) the fermentation improves the nutritional values of plant proteins (Vieira et al., 2023); and iv) the fermentation enhances the histology and topography of gastrointestinal tract, increases the length and width of villi (Hassaan et al., 2021). Vieira et al. (2023) confirmed these theories by finding that *D. labrax* fed a diet containing a mixture of fermented plant feeds improved the nutrient digestibility versus basal diet without fermentation. In addition, Hassaan et al. (2020) found that Nile tilapia fed a diet containing up to 50% of FM replaced by FSBM recorded the highest ADC of nutrients. Moreover, El-Haroun et al. (2006) reported that inclusion of Biogen® in tilapia diets improved growth and feed utilization. Furthermore, Zhang et al. (2023 a) stated that partial replacement of fish meal by FSBM enhanced the activity of digestive enzymes and nutrients digestibility by hydrolysis of ANFs. Likewise, Engin and Koyuncu (2023) and Abd El-Naby et al. (2024) found that fermented mixture of plant protein ingredients by *Lactobacillus* spp. enhances the nutrients digestibility by modifying and adjusting the gut microflora, digestive enzyme activities, or chelation of minerals, and increasing the solubility of nutrients due to increased acidification by the production of lactic acid in the digestive tract. Similarly, fermentation of plant protein components by *Bacillus* spp. helps detoxify harmful dietary components and produce vitamin B complexes, specifically vitamin B₁₂ and biotin, which enhance feed utilization and digestibility of feed ingredients (El-Haroun et al., 2006; Dawood and Koshio, 2020). In contrast, Hassaan et al. (2018) found that the replacement of more than 50% of fish meal with yeast-fermented SM significantly reduced the apparent digestibility of dry matter, energy, crude protein, and crude lipids. The differences in those results may be related to differences in the fermentation process of the raw material.

Serum biochemical indices

Measurements of blood parameters are good indicators of stress management (Anwar et al., 2020). Dozens of trials have been conducted to investigate the roles of

different fermentation products in Nile tilapia, common carp, prawn shrimp, *Fenneropenaeus indicus* and white shrimp growth, health and immune response, respectively (Vong and Liu, 2016; Bowyer et al., 2020; Anwar et al., 2020; Sharawy et al., 2016; Abd El-Naby et al., 2024). Jiang et al. (2023) stated that inclusion of FSBM up to 40% in largemouth bass enhances plasma biochemical indices. In addition, Zhang et al. (2023 a, b) and Abd El-Naby et al. (2024) found that partially replacing FM with FPPs increased blood protein level, metabolic capacity, and immune activity of fish. Likewise, Wagner and Congleton (2004) reported that blood parameters were increased by partially replacing FM by FSBM in serum of rainbow trout and turbot. The results can be attributed to the fact that after fermentation by microorganisms, ANF is partially or completely decomposed into plant protein, which enhances the physiological functions of fish liver and intestines and promotes nutrients assimilation (Shiu et al., 2015).

Histology of gastrointestinal tract

The intestinal morphology is considered as an indicator of nutrients digestion and assimilation and reflects and assesses the potential impacts of diets (Eide et al., 2025; Chen et al., 2025). Plant proteins contain ANFs that have negative impacts on intestinal morphology and topography of fish (Anwar et al., 2020). However, Shiu et al. (2015) found that fermented plant proteins increased the absorption site size in gastrointestinal tract, which enhanced nutrient assimilation and consequently fish growth. Confirming the previous results, Eide et al. (2025) found improvements in gut health in fish fed diets with 10% fermented sunflower meal, improvement in the length and width of villi, increased number of goblet cells and reduction of tissue damage and cell division, and increased colonization of positive intestinal microbiota. Bowyer et al. (2020) reported lupin meal treated with SSF commercial products Synergen™ to have a positive impact on gut integrity in tilapia. Following the same patterns, Wang et al. (2019) found that substituting up to 45% of FM by FSBM has a remarkable impact on the morphology of intestine versus 60% replacement in juvenile turbot and largemouth bass, respectively. On the contrary, Shiu et al. (2015) found that replacement of FM by FSBM up to 30% has harmful pathological impacts in orange-spotted grouper. The positive contribution of using SSF to improve absorption site of fish could be attributed to the presence of functional compounds produced during the fermentation process (Shi et al., 2021). Moreover, De Villa et al. (2023), Wang et al. (2024) and Chen et al. (2025) reported that the addition of SFPY reduced inflammatory factors in the intestine, thus improving intestinal health of carp. The previous study interpreted that the improvements in the histology of gastrointestinal tract were due to the impacts of fermentation process: (i) modification of gut microbiota that aided nutrients assimilation (De Villa et al., 2023; Wang et al., 2024); (ii) increasing positive bacteria as LAB community and

inhibiting the growth of pathogenic bacteria (Wang et al., 2024); (iii) degradation of complex compounds (De Villa et al., 2023); and (iv) breakdown of ANFs (De Villa et al., 2023; Wang et al., 2024). In conclusion, several factors affect the impacts of fermentation in gastrointestinal morphology such as fish species, substrate concentrations, type of fermentation process and laboratory conditions.

Intestinal microbiota

Intrusion and colonization of intestinal microbiota in aquatic animals reflect diets composition and are controlled with different factors such as fish species, fish size, age and physiological conditions (Huang et al., 2024; Zhou et al., 2023). Diet chemical composition is considered as a main factor affecting the gut microflora community, immunity, and disease resistance (Wei et al., 2020). Liu et al. (2021), Wang et al. (2023), Li et al. (2023), Yang et al. (2023) and Chen et al. (2025) reported that improving the nutritive value of feed ingredients resulting from the fermentation process could be attributed to enhanced nutritive value, nutrients digestion, assimilation and destruction of ANFs that consequently improve feed utilization in fish and maintain the stability of gut microflora balance (Qu et al., 2025).

Recent research highlighted the role of fermentation process on improving the diversity of gut bacteria (Dai et al., 2019; Pan et al., 2021), thereby improving its immunity and controlling pathogen infection (Weng et al., 2023). Moreover, Tang et al. (2021), Li et al. (2020), Wang et al. (2019), Yang et al., (2020), Eide et al. (2025), Qu et al. (2025) and Chen et al. (2025) stated that fermentation process significantly promoted the diversity of intestinal flora in fish. Furthermore, Huang et al. (2024) found that the 40% substitution with SM or FSM significantly enhanced the variety and fertility of the intestinal flora of tilapia. This improvement could be attributed to the presence of bioactive compounds in fermented ingredients including small peptides, probiotics, organic acids, and flavonoids in FSBM, which provide optimum media for the growth and reproduction of different microflora. Eide et al. (2025) found that including fermented sunflower meal adjusted and modified gut microflora community in Atlantic salmon by enhancing the growth of gut lactic acid bacteria *Lactiplantibacillus* and *Lactobacillaceae*. Likewise, Catalán et al. (2018) found that feeding 30% FSBM to juvenile salmon led to an increase of gut lactic acid bacteria. They suggest that FSBM had a prebiotic-like effect with positive impacts on intestinal health with increased mucin production and intestinal trans-cellular uptake of water. Following the same patterns, inclusion of FSBM resulted in higher numbers of gut *Lactobacillus* and *B. subtilis* versus basal diets. On the opposite side, Cao et al. (2021) found inclusion of FSBM instead of conventional SBM had no significant effect on the intestinal flora of grass carp. Moreover, previous research on European sea bass, Asian seabass and white shrimp showed no significant changes of gut microflora when

replacing fish meal with a mixture of vegetable meals (Torrecillas et al., 2017; Apper et al., 2016; Shao et al., 2019 a, b). This discrepancy may be related to the lab conditions, fish species, size and age, feed composition, and fish intestinal morphology. Therefore, more research on the effect of fermented ingredients on gut microbiota is needed.

Gene expression

Expression of growth genes

Metabolomics, growth, immune, inflammatory gene expression are controlled by diet chemical composition (Sun et al., 2024; Zhao et al., 2024). Awad et al. (2024) found that tilapia fed fermented mixture plant protein showed up-regulation of GH versus basal diet without fermented plant protein. Moreover, Anbazahan et al. (2014) and Hassaan et al. (2015, 2021) found enhanced levels of C3, IGF-I, and GH in Nile tilapia fed diets with FM replaced by different fermented products.

Expression of immune-related genes

Inflammatory genes expression of fish fed diets containing fermented plant proteins boost immunity- and inflammation-related gene expression such as TNF- α , IL-10, IL-1 β , and IL-8 (Hosseini et al., 2016; Hou et al., 2019). Recently, Weng et al. (2023) reported that largemouth bass fed diets containing fermented plant proteins boost genes expression related to inflammation and immunity, suppressing the expression of lipogenesis-related genes and promoting fatty acid oxidation (Sun et al., 2023). In addition, Wang et al. (2023) found that incorporation of fermented cotton seed meal (FCSM) boosted antioxidant and inflammatory gene expression such as TNF- α , IL-1 β , IL-8, and NF- κ B, indicating that high level inclusion of fermented ingredients induced inflammatory responses that consequently reduced the chance of fish infection with pathogens. Likewise, Yu et al. (2021) and Chen et al. (2024) reported that inclusion of FSBM enhanced the mRNA expression of shrimp. In addition, Zhang et al. (2024) and Wang et al. (2024) found that oxidative and inflammatory gene expression was upregulated in fermented feed group versus basal diet. Furthermore, Huang et al. (2024) reported that replacing conventional SBM with FSBM upregulated gene expression of zo-1 and claudin that highlight the role of fermentation process to enhance the expression of genes related to growth, immunity and antioxidant. On the other hand, FSBM exhibited better intestinal inflammation alleviation effects and significantly downregulated the expression of intestinal tnf- α , il-1 β , and il-8 mRNA levels. In addition, Yan et al. (2016) reported that replacing FM with fermented ingredients significantly upregulated antimicrobial peptides related genes. Moreover, Zhang et al. (2023 a) found that partial replacement of FM with FSBM upregulated immune genes expression such as lyz, tnf-1, il-1, and il-6 genes of coho salmon. Similarly, Li et al. (2019) found that replacing FM by FSBM downregulated the pro-inflammatory and tumor necrosis fac-

tors gene expression. These results can be attributed to the following scenario: i) fermentation breaks down the ANFs; ii) acts as immunostimulant; iii) boosts the intestinal health promotion; and iv) fermented plant proteins upregulate the growth and immune gene expression.

Antioxidant activity

Antioxidant enzymes are recognized as effective tools for the deterrence of diseases caused by oxidative damage (Zhang et al., 2024; Nassar et al., 2024; Weng et al., 2023).

The presence of ANFs in unfermented plant proteins results in inhibition of antioxidant enzymes activity and their genes expression such as GPx, SOD and CAT (Zhang et al., 2023 a). On the other hand, the fermentation process either by SSF or SMF results in enhanced mechanisms of antioxidant enzymes activity via increasing the availability of cofactors involved in the antioxidant mechanisms such as vitamins and polysaccharides, as well increasing the release of the bioactive compounds acting as immunostimulants in plant proteins (Verni et al., 2019). Furthermore, microorganisms involved in the fermentation process containing bioactive compounds stimulate and boost immune and inflammatory genes expression (Zhang et al., 2023 a). In addition, Zhang et al. (2023 a) found that inclusion of FSBM promoted the activity of SOD, GPx and CAT and decreased the MDA level. Moreover, Zhang et al. (2024), Ashrafizadeh et al. (2022), Bu et al. (2021) and Nassar et al. (2024) stated that replacing FM with FSBM significantly increased the antioxidant capacity of fish. Likewise, Lee et al. (2016) found inclusion of FSBM in fish diet to increase the activities of oxidative enzymes in the liver. Moreover, Weng et al. (2023) and Dan et al. (2022) reported that the levels of oxidative enzymes improved in the liver of largemouth and turbot fed FSBM groups compared to those fed basal diet. Also, Zhang et al. (2023 a) reported that the partial replacement of FM with fermented plant protein significantly increased the antioxidant capacity of fish. The previous results could be attributed to: i) the role of fermented plant proteins to enhance the activity of Nrf2 pathway that consequently enhance antioxidant capacity; ii) the presence of peptides and phenols of fermented plant proteins could up-regulate Nrf2 gene expression and improve the antioxidant ability of the body; iii) during the fermentation low-molecular-weight peptides and AAs are produced which increase dietary antioxidant activities, and the nonspecific immune responses.

Conclusions and future perspective

Recently, the use of fermentation strategies has played an important role to enhance the nutritional quality of plant proteins and become promising novel ingredients to substitute fish meal and soybean meal, the most common ingredients used in aquafeeds and addressing sustainability in aquaculture. Thus, the growth and update of the fermentation protocols resulting in increasing the production of fermented ingredients and aspects of sus-

tainable production of these ingredients and use should be addressed. Therefore, further research is needed to improve fermentation strategies and its technical aspects for successful implementation.

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