Digestibility of plant-based feeds in omnivorous, carnivorous, and herbivorous fish: A review of Nile tilapia (*Oreochromis niloticus* (Linnaeus, 1758)), North African catfish (*Clarias gariepinus* (Burchell, 1822)), and grass carp (*Ctenopharyngodon idella* (Valenciennes, 1844))

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Abstract. This review examines the digestibility of plant-based feed ingredients across Nile tilapia (Oreochromis niloticus (Linnaeus, 1758)), North African catfish (Clarias gariepinus (Burchell, 1822)), and grass carp (Ctenopharyngodon idella (Valenciennes, 1844)), which represent omnivorous, carnivorous, and herbivorous feeding habits, respectively. Each species exhibits unique digestive adaptations that influence its ability to utilize plant-based ingredients effectively. Nile tilapia, with its balanced enzymatic profile, demonstrates high apparent digestibility coefficients (ADCs) for ingredients such as soybean meal (up to 91.12%) and other plant proteins, facilitating the incorporation of cost-effective plant-based feeds. North African catfish, although adapted for protein-rich animal diets, can efficiently digest plant proteins like soybean meal when supplemented with amino acids or enzymes, achieving ADCs of up to 95%. Grass carp, possessing specialized gut morphology for processing fibrous plant matter, benefit from the high digestibility of ingredients like maize leaves (84.7%) but display variability with more fibrous ingredients like duckweed (50% ADC). This comparative analysis highlights the significance of aligning feed formulations with the digestive capabilities of these fish to enhance feed efficiency, growth, and sustainability in aquaculture. The findings advocate for the strategic selection and processing of plant-based ingredients tailored to the digestive adaptations of each species to optimize nutrition and reduce reliance on fishmeal.

Key Words: digestibility, plant-based feed ingredients, feeding habits.

Introduction. In the pursuit of sustainable and cost-effective aquaculture, the use of plant-based feed ingredients has gained significant attention due to the rising costs and environmental impact of fishmeal and other animal-based proteins (Fantatto et al 2024; Dhar et al 2024; Jamil et al 2023). Effective incorporation of these plant materials into aquaculture diets requires an in-depth understanding of different fish species' digestive capabilities and limitations. Nile tilapia, North African catfish, and grass carp are among the most widely cultured freshwater fish, each exhibiting unique digestive adaptations that influence their utilization of plant-based feeds.

Nile tilapia, an omnivorous species, is renowned for its flexible dietary habits, allowing for the efficient digestion of animal and plant-based proteins (Temesgen et al 2022; Mohamed et al 2019). This versatility is facilitated by a well-developed enzymatic profile that includes proteolytic and amylolytic enzymes, enabling the breakdown of protein and carbohydrates (Fereira et al 2021; El Naby et al 2024). Studies by Koprucu & Ozdemir (2005) and Ribeiro et al (2011) have demonstrated that soybean meal, with high apparent digestibility coefficients (ADCs) of up to 91.12% for protein, serves as an effective plant protein source for Nile tilapia. The species' capacity to utilize a broad spectrum of plant-based feeds supports growth performance and reduces reliance on fishmeal, contributing to more sustainable aquaculture practices (Mehrim et al 2018; Klahan et al 2023; Mohamed et al 2019).

North African catfish, primarily carnivorous have evolved with a digestive system optimized for protein digestion through a high concentration of proteolytic enzymes such as trypsin and pepsin (Jiao et al 2023; Friedman et al 2024; Langi et al 2024). While this enzymatic dominance positions them for the efficient digestion of animal proteins, it also presents challenges when incorporating plant-based feeds, which are often less digestible due to higher fiber content and anti-nutritional factors (Serra et al 2024). However, research highlights that strategic supplementation with amino acids and exogenous enzymes can enhance the digestibility of plant ingredients like soybean meal, yielding protein ADCs up to 95% (Elesho et al 2021; Oyedokun 2024) This adaptability underscores the potential for North African catfish to support more plant-inclusive diets without significant detriments to growth and feed efficiency (Enyidi et al 2017; Fantatto et al 2024; Segaran et al 2023; Barasa et al 2024).

Grass carp, as true herbivores, have specialized adaptations for plant digestion, including an elongated intestine and a microbial community proficient in fermenting fibrous material, enabling them to process complex carbohydrates and derive energy from high-fiber feeds (Wildhaber et al 2023; Cai et al 2018; Yang et al 2019; Hao et al 2017). For instance, maize leaves exhibit good protein digestibility, with digestibility coefficients reaching 84.7% in grass carp (Dongmeza et al 2010). However, the digestibility of different plant-based feeds varies, as seen in the lower protein digestibility coefficients (50%) for duckweed, highlighting the need to carefully select and process feed materials to match their digestive physiology (Gan et al 2012). Lower digestibility in certain feeds can be attributed to their higher fiber content and the presence of anti-nutritional factors that hinder nutrient absorption (Köprücü 2012). Understanding the dietary requirements and digestive capabilities of grass carp is crucial for optimizing growth performance and feed efficiency. The inclusion of exogenous enzymes in their diet has been shown to improve digestibility by breaking down complex carbohydrates, enhancing the overall digestibility of plant-based feeds. The diversity and activity of cellulolytic bacteria in the gut of grass carp are positively correlated with the consumption of high-fiber diets, further supporting their ability to digest fibrous plant materials (Li et al 2014b). Moreover, supplementation with essential amino acids, such as lysine and methionine, has been found to improve the digestibility of plant protein sources and support the growth of grass carp on diets with less reliance on fishmeal (Abdullah et al 2020; Wang et al 2014).

Understanding the comparative digestibility of plant-based feeds across these three fish species is critical for optimizing feed formulations that meet their nutritional needs and support sustainable aquaculture practices. This review synthesizes current knowledge on the utilization of plant-based ingredients by Nile tilapia, North African catfish, and grass carp, examining the interplay of enzymatic activity, gut morphology, and microbial support in determining feed efficiency and growth outcomes.

Digestive enzyme activities in fish. Digestive enzyme activities in fish play a crucial role in determining their ability to process various types of food, particularly plant ingredients. The enzymatic composition differs significantly among carnivorous, herbivorous, and omnivorous fish due to their distinct dietary habits (Jiao et al 2023; (Ren et al 2011; Savona 2011). These variations in enzyme activities have profound implications for aquaculture, particularly in the formulation of diets that meet the nutritional needs of different fish species.

Carnivorous fish. Carnivorous fish, such as North African catfish, have evolved a digestive system highly specialized for protein digestion. This specialization is characterized by the dominance of proteolytic enzymes, including trypsin, pepsin, and chymotrypsin, which efficiently break down proteins into absorbable amino acids (Riaz & Naeem 2020; Cipriano et al 2016). These enzymes play a vital role in nutrient absorption and support the protein-rich diets required by carnivorous fish. Compared to herbivorous and omnivorous species, North African catfish exhibits significantly higher protease activity, reflecting a dietary dependence on protein levels ranging from 40% to 55% for optimal growth and metabolism (Rosenau et al 2022). The efficiency of protein digestion in North African catfish is further enhanced by high lipase activity, which aids in digesting animal protein-based feed ingredients essential for their nutrition (Cipriano et al 2016). However, this adaptation is accompanied by a significant limitation in carbohydrate digestion, as evidenced by the lower activity of amylase, the enzyme responsible for breaking down starches and carbohydrates (Gioda et al 2017). This enzymatic limitation poses challenges in aquaculture, where plant-based ingredients are increasingly included to enhance sustainability. The limited ability of North African catfish to utilize carbohydrates affects growth performance and feed conversion efficiency when fed diets high in plant materials (Gioda et al 2017). Understanding the enzymatic profile of North African catfish is critical for developing feeds that balance appropriate protein sources with the species' limited carbohydrate digestion capabilities. Optimized feed formulations can enhance growth and health while promoting sustainable aquaculture practices (Jiao et al 2023).

Proteolytic enzymes are the cornerstone of protein digestion in North African catfish. These enzymes, secreted in inactive forms known as zymogens, become active in the digestive tract to hydrolyze peptide bonds, releasing absorbable amino acids (Riaz & Naeem, 2020). High trypsin activity is particularly crucial, reflecting an evolutionary adaptation to protein-rich, animal-based diets where proteins serve as the primary energy source. Carnivorous fish, including North African catfish exhibit significantly higher proteolytic activity than herbivorous or omnivorous species, which rely more on carbohydrates and have a more balanced enzymatic profile (Jiao et al 2023). This enzymatic adaptation allows North African catfish to thrive on animal protein-rich diets, supporting growth and efficient nutrient utilization (Cipriano et al 2016). However, the limited amylase activity presents a clear disadvantage for dietary flexibility, particularly when plant-based ingredients are used as feed alternatives (Jiao et al 2023).

The digestive system of North African catfish is optimized for protein digestion, dominated by proteases and lipases, while exhibiting minimal carbohydrase activity (Abro et al 2014; Solovyev et al 2014). This enzymatic limitation poses challenges in aquaculture, where the rising costs of animal protein necessitate the use of plant-based feed alternatives. Research consistently shows that North African catfish experience poor growth performance and reduced feed conversion efficiency when fed diets rich in plant ingredients (Orire & Sadiku 2014; Djauhari & Simamora 2021). This is due to their low amylase activity, which hampers carbohydrate digestion. For instance, herbivorous fish exhibit significantly higher amylase activity, enabling efficient hydrolysis of starches and other carbohydrates (Abro et al 2014; Rani et al 2023). In contrast, the low carbohydrase activity of North African catfish underscores its reliance on animal protein sources for optimal growth and health. The digestive inefficiency with plant-based ingredients presents a major obstacle to reducing reliance on animal proteins while maintaining sustainable and economically viable aquaculture practices (Hlophe-Ginindza & Moyo 2018; Djauhari & Simamora 2021).

In aquaculture, achieving optimal protein digestion is critical for maximizing growth and feed utilization. Studies reveal that higher dietary protein levels stimulate proteolytic enzyme activity, enhancing nutrient absorption and growth performance in carnivorous fish like North African catfish (Melo et al 2012). Animal protein-based diets consistently yield superior growth and feed conversion ratios compared to plant-based feeds, further underscoring the species' dependency on protein-rich diets (Hlophe-Ginindza & Moyo

2018). Nevertheless, the rising cost of animal protein necessitates the inclusion of plant-based ingredients in aquafeeds. While this shift aligns with sustainability goals, it also highlights the digestive limitations of North African catfish. Low amylase activity results in suboptimal carbohydrate digestion, leading to reduced growth rates and less efficient feed utilization (Abdel-Warith et al 2020). This enzymatic profile underscores the need for innovative feed formulations that cater to the species' digestive capabilities while integrating sustainable practices (Alotaibi et al 2019). Efforts to improve the nutritional quality of plant-based feeds, such as the use of enzyme supplements or protein concentrates, are essential for enhancing digestibility and supporting growth in North African catfish. Understanding the digestive physiology and limitations of this species is key to balancing its nutritional requirements with sustainable aquaculture practices.

***Herbivorous fish**.* Herbivorous fish, such as grass carp, possess unique digestive adaptations that enable them to thrive on plant-based diets. These adaptations make herbivorous fish crucial to sustainable aquaculture systems focused on reducing reliance on animal-based feed ingredients. A defining characteristic of herbivorous fish is their significantly higher levels of amylase activity, an enzyme that is vital for breaking down complex carbohydrates like starch into simpler sugars. Studies have demonstrated that grass carp exhibit much greater amylase activity than carnivorous fish, reflecting its dietary specialization in carbohydrate-rich plant materials (Jiao et al 2023; Gioda et al 2017). This enzymatic advantage allows grass carp to effectively metabolize starches, meeting energy and growth requirements (Ngugi et al 2017).

The enhanced amylase activity is supported by other plant-specific digestive enzymes in herbivorous fish, which facilitate the breakdown of fibrous plant components and the absorption of essential nutrients (Jiao et al. 2023). Together, these enzymes enable herbivorous fish to utilize diets rich in plant ingredients, making them suitable for plant-based aquaculture feeds (Li et al 2014b). Herbivorous fish play a critical role in advancing sustainable aquaculture, particularly as the industry shifts toward plant-based feeds. The ability of species like grass carp to efficiently digest carbohydrate-rich diets enables the reduction of fishmeal and other animal proteins in aquaculture feeds, thereby lowering environmental and economic costs (Ngugi et al 2017).

The shift toward plant-based feeds also presents significant economic and environmental benefits. Feed costs, which make up over 70% of total production expenses in aquaculture, can be lowered by using cost-effective plant ingredients (Omeje et al 2023). Moreover, cultivating plant-based feeds produces fewer greenhouse gas emissions than fishmeal production, thereby reducing the overall carbon footprint of aquaculture operations (Alleway et al 2023). These economic and environmental advantages are especially pertinent as global demand for sustainable seafood continues to increase. Herbivorous fish, with their digestive efficiency and adaptability to plant-based diets, are well-positioned to meet these demands while supporting the long-term viability of aquaculture as a food source (Froehlich et al 2017). By decreasing reliance on fishmeal and incorporating plant-based ingredients, aquaculture systems can achieve lower environmental impacts and greater economic viability efficiency.

***Omnivorous fish**.* Omnivorous fish, such as Nile tilapia, demonstrate an exceptional ability to digest both animal and plant-based materials. This capability provides them with a more balanced enzymatic profile compared to strictly carnivorous or herbivorous species. This trait is especially advantageous in aquaculture, where utilizing diverse food sources and developing cost-effective feed formulations are critical for sustainability. The digestive enzyme activity in omnivorous fish like Nile tilapia plays a key role in their adaptability and feed efficiency. Research indicates that Nile tilapia exhibit higher amylase activity, an enzyme essential for carbohydrate digestion, than carnivorous fish, which have lower amylase levels due to their animal-based diets (Jiao et al 2023). This elevated amylase activity allows Nile tilapia to efficiently utilize a variety of carbohydrate sources, making them suitable for plant-based diets (Rodrigues et al 2011). For instance, Nile tilapia achieve optimal growth when fed diets containing substantial amounts of plant materials, such as alternative flours (Herdiyanti et al 2018).

This adaptability not only improves growth rates but also reduces reliance on fishmeal and other animal protein sources, contributing to the sustainability of aquaculture systems (Martínez et al 2019). The ability to digest plant materials enables diversified feed formulations, which are essential for addressing rising fishmeal costs and ensuring food security in aquaculture. By incorporating alternative protein sources such as insect meals or plant-based ingredients, aquaculture operations can maintain profitability while minimizing environmental impacts (Florien et al 2022). Furthermore, this dietary flexibility allows for the optimization of feed formulations tailored to specific growth stages and environmental conditions, enhancing feed efficiency and fish health (Huang et al 2015).

Nile tilapia also possess physiological and morphological traits that support their omnivorous diet. Compared to carnivorous fish, they have relatively longer intestines, which facilitate the digestion and absorption of a broader range of nutrients, including carbohydrates and fibers from plant sources (Adamek-Urbańska et al 2023). This anatomical adaptation, combined with their enzymatic profile, underscores their importance in sustainable aquaculture practices. They can thrive on diverse feed inputs while contributing to nutrient recycling within aquaculture systems (May et al 2022).

Although Nile tilapia have lower proteolytic enzyme activity than carnivorous fish, they still produce sufficient levels of key enzymes, such as trypsin, necessary for protein digestion. These enzymes break down proteins into absorbable nutrients critical for growth and health. Studies have highlighted that Nile tilapia possess a balanced enzymatic profile, enabling them to efficiently digest protein sources from both animal- and plant-based feeds. For instance, the activities of alkaline digestive proteases like trypsin and chymotrypsin can serve as indicators of the fish's nutritional status. A high trypsin-to-chymotrypsin ratio suggests adequate protein intake, while a lower ratio may indicate insufficient feeding (Uscanga et al 2010). This enzymatic adaptability allows Nile tilapia to perform well on diets that include fishmeal or plant proteins like corn gluten and wheat gluten, maintaining growth rates even with reduced reliance on expensive animal-based proteins (Al-Thobaiti et al 2017). Additionally, the proteolytic enzymes in Nile tilapia help break down proteins into amino acids essential for physiological functions like growth, reproduction, and immune response (Uscanga et al 2010). Their ability to digest diverse protein sources aligns with efforts to formulate cost-effective feeds while addressing environmental concerns. For example, replacing fishmeal with plant-based proteins has been shown to maintain or even enhance growth performance in Nile tilapia, demonstrating their adaptability to various feed compositions (Shi et al 2016). The balanced enzymatic profile of omnivorous fish, particularly Nile tilapia, offers significant advantages for aquaculture. Their ability to digest both animal- and plant-based materials reduces dependency on fishmeal, a costly and environmentally taxing ingredient. This shift toward plant-based feeds not only lowers costs but also alleviates pressure on marine resources, promoting sustainability as global fish demand rises and fishmeal availability becomes increasingly limited (Merino et al 2012).

Omnivorous feeding habits also allow Nile tilapia to exploit a wide range of local feed ingredients, supporting food security and reducing aquaculture's environmental footprint (Jennings et al 2016). Incorporating plant-based feeds can significantly reduce feed costs, as these ingredients are often more affordable and sustainable compared to traditional animal proteins. Moreover, the ability to utilize carbohydrate-rich feeds provides energy for critical physiological functions, such as metabolism, reproduction, and immunity (Ayoola & Ishola 2020).

The enzymatic efficiency of Nile tilapia supports optimal feed conversion ratios (FCRs), a critical factor in the economic viability of aquaculture. Enzymes like amylase and proteases enable the effective digestion of carbohydrates and proteins, facilitating nutrient absorption and growth. This digestive efficiency is particularly beneficial in aquaculture systems aiming to optimize feed utilization while minimizing waste.

Studies have shown that Nile tilapia achieve high growth rates when fed mixed diets that combine plant and animal proteins, emphasizing their adaptability to diverse nutritional formulations (Yu et al 2023). Additionally, their resilience in varied environmental conditions makes them suitable for aquaculture systems in diverse geographic settings. This adaptability is especially advantageous for operations aiming to utilize locally available feed ingredients, further enhancing sustainability and economic feasibility (Torres et al 2015). The enzymatic and physiological adaptations of Nile tilapia make them an ideal species for sustainable aquaculture. Their ability to digest both animal and plant materials reduces reliance on environmentally unsustainable ingredients like fishmeal, while their flexible dietary requirements allow for cost-effective feed formulations. By utilizing a balanced enzymatic profile, Nile tilapia achieve efficient nutrient absorption, growth, and health. Their adaptability to diverse feed inputs not only enhances aquaculture profitability but also supports efforts to address the growing challenges of food security and environmental conservation. As the global demand for aquaculture products continues to rise, Nile tilapia's role as a versatile and sustainable species will remain pivotal.

Intestinal morphology and its role in digestibility. The structure of the digestive system, particularly the intestines, plays a vital role in determining how effectively fish species can digest different types of food (Jiao et al 2023; Kalhoro et al 2017). Intestinal morphology varies significantly among carnivorous, herbivorous, and omnivorous fish, reflecting their dietary preferences and digestive needs (Moreira et al 2020; Gioda et al 2017). These structural differences are key to understanding how each group of fish processes and absorbs nutrients, particularly plant-based materials, which pose unique challenges for digestion (Jiao et al 2023; Moreira et al 2020; Sa 2023; Burns 2021).

Carnivorous fish. Carnivorous fish exhibit distinct adaptations in their intestinal morphology, reflecting their animal-based diets. Unlike herbivores, carnivorous species have evolved digestive systems optimized for protein absorption, as their diet predominantly consists of easily digestible animal proteins (Jiao et al 2023). Their relatively short intestines correlate with the simplicity and speed of protein digestion, contrasting with the longer intestinal tracts required to break down fibrous plant material (Kalhoro et al 2017).

The intestines of carnivorous fish are lined with microvilli—finger-like projections that enhance nutrient absorption by increasing surface area. Species like North African catfish benefit greatly from this adaptation, which enables efficient absorption of nutrients from protein-rich diets (Kalhoro et al 2017). This structural specialization supports rapid and efficient nutrient uptake, critical for their growth and metabolic needs (Hernandez & Lazo 2010). For North African catfish, diets rich in animal-based proteins result in superior growth performance and nutrient utilization, highlighting the importance of these adaptations (Ojewole et al 2022). Microvilli play a pivotal role in maximizing protein absorption, ensuring the fish meet their nutritional requirements (Jiao et al 2023).

Despite their proficiency in digesting proteins, carnivorous fish face challenges when consuming plant-based materials. Their short intestines and lack of specialized structures for processing cellulose and complex carbohydrates hinder the digestion of fibrous plant matter (Jiao et al 2023; Ojewole et al 2022). North African catfish, in particular, exhibits reduced growth and nutrient absorption when fed diets high in plant ingredients (Ofek et al 2021; Agboola et al 2019). These limitations are significant in aquaculture, where balancing cost-effective, sustainable feeds with species-specific nutritional needs is critical.

The dietary needs of carnivorous fish like North African catfish underscore the necessity of formulating feeds that align with their natural feeding habits. While economic considerations may necessitate some plant inclusion, excessive reliance on plant-based ingredients often leads to poor growth and feed conversion ratios (Jiao et al 2023; Ojewole et al 2022). Studies confirm that while North African catfish can consume plant materials, their digestive systems are ill-suited for breaking down fibrous components, resulting in lower absorption rates from such feeds (Langi et al 2024; Shaw et al 2024).

Recent research in aquaculture highlights the importance of high-quality animal protein sources in promoting optimal growth and health in carnivorous fish. Fishmeal and fish oil remain essential as they provide vital amino acids and fatty acids absent in plant-based feeds (Agboola et al 2020). However, the sustainability of aquaculture demands innovative alternatives. Insect-based feeds have emerged as a promising substitute, meeting the nutritional requirements of carnivorous species while reducing reliance on traditional fishmeal sources (Musingi et al 2023).

Dietary supplementation and feeding strategies also play a crucial role in enhancing digestive efficiency and overall performance. Enzyme supplementation has shown promise in improving nutrient absorption and growth outcomes, particularly when plant-based feeds are used (Najafi 2024). Enzymes that aid in breaking down complex carbohydrates and proteins can mitigate some challenges associated with less digestible plant ingredients (Hossain et al 2016). Furthermore, optimizing feeding frequency and rates has been demonstrated to improve feed conversion ratios (FCR) and growth performance. Adjusting feeding practices not only enhances resource utilization but also supports the efficiency of aquaculture operations (Huang et al 2015; Hamed et al 2021).

The cultivation of North African catfish and other carnivorous fish requires strategic feeding practices and diet formulations tailored to their unique digestive capabilities. Incorporating high-quality animal proteins, adopting sustainable feed alternatives, and employing dietary supplements and optimized feeding strategies can promote growth, health, and aquaculture sustainability.

Herbivorous fish. In contrast, herbivorous fish, such as grass carp have evolved specialized digestive adaptations to efficiently process plant-based diets, which are critical for their survival in environments dominated by fibrous plant materials (Burns 2021; Jiao et al 2023). One of the most notable adaptations is their significantly elongated intestines, which increase retention time, enabling thorough digestion and nutrient absorption from complex plant matter (Burns 2021; Gioda et al. 2017). This characteristic stands in stark contrast to the shorter intestines of carnivorous fish, which are optimized for rapid digestion of protein-rich diets.

The extended intestinal tract of herbivorous fish is essential for breaking down cellulose and other complex carbohydrates abundant in plant materials. These fibrous compounds are difficult to digest without prolonged retention and the activity of specialized enzymes (Jiao et al 2023). Grass carp have also evolved specialized digestive regions harboring diverse gut microbiota that facilitate the fermentation of fibrous plant components. These microbial communities, including cellulolytic bacteria such as Aeromonas, produce enzymes that degrade cellulose into simpler compounds, enhancing nutrient absorption and overall digestive efficiency (Liu et al 2021).

Additionally, the digestive enzyme profile of grass carp is well-adapted to its herbivorous diet. Studies reveal significantly higher activities of amylase and maltase compared to carnivorous fish, reflecting the species' capacity to efficiently process starches and polysaccharides found in plant materials (Jiao et al 2023; Gioda et al 2017). This enzymatic capability underscores the grass carp's effectiveness in utilizing plant-based feeds, supporting its survival and growth in herbivorous environments (Jones et al 2018; Liu et al 2021).

These herbivorous adaptations are particularly valuable in aquaculture, where grass carp has emerged as an ideal candidate for systems aiming to reduce reliance on fishmeal and other animal-based feeds. Grass carp's ability to digest fibrous plant materials efficiently makes it a cornerstone species in integrated aquaculture systems, contributing to nutrient recycling and enhancing sustainability (Wang et al 2020). By leveraging the grass carp's natural adaptations, aquaculture operations can minimize environmental impact while promoting economic efficiency.

Research highlights that incorporating more plant-based ingredients into aquafeeds for grass carp can significantly reduce dependence on fishmeal, a resource often associated with overfishing and unsustainable practices (Gunnarsson et al 2020). For instance, the inclusion of fermented plant proteins has been shown to enhance the nutritional profile of aquafeeds, improving digestibility and growth performance in herbivorous species like grass carp (Mugwanya et al 2022). Fermentation processes can also reduce anti-nutritional factors in plant ingredients, further supporting the fish's health and nutrient absorption. Moreover, integrating diverse plant protein sources into aquafeeds can provide balanced nutrient profiles that optimize growth and health outcomes. Studies have demonstrated that well-formulated plant-based diets can meet the specific nutritional needs of grass carp while promoting sustainable aquaculture practices (Wang et al 2020). The ability of grass carp to thrive on such diets underscores its role as a model species for advancing eco-friendly aquaculture approaches.

The longer intestinal tract and specialized microbial communities of grass carp not only facilitate the efficient digestion of fibrous materials but also highlight the importance of tailoring feed formulations to the digestive capacities of herbivorous fish. For example, diets enriched with plant-based proteins and supplemented with essential nutrients can improve feed conversion ratios and growth rates, ensuring optimal performance in aquaculture settings (Jiao et al 2023; Sparagon et al 2022). Furthermore, understanding the digestive limitations and enzymatic needs of grass carp can guide innovations in feed technology, such as the development of enzyme-supplemented diets that further enhance the fish's ability to utilize plant materials (Liu et al 2021).

The implications of these findings extend beyond individual species management. Grass carp's herbivorous adaptations align well with the global push for sustainable aquaculture practices, offering a model for reducing environmental impact while maintaining productivity. By utilizing grass carp in integrated systems, aquaculture producers can promote nutrient recycling, reduce waste, and lower dependency on limited natural resources such as fishmeal and fish oil (Mugwanya et al 2022). These practices not only improve the ecological footprint of aquaculture but also provide cost-effective solutions to feed formulation challenges.

The digestive adaptations of grass carp, including elongated intestines, specialized gut microbiota, and efficient enzyme systems, enable the species to effectively utilize fibrous plant materials. These traits make grass carp a vital component of sustainable aquaculture systems, which emphasize reducing reliance on unsustainable feed resources while promoting environmental and economic sustainability. By optimizing feed formulations to align with the natural capabilities of grass carp, aquaculture systems can achieve better growth performance, reduced costs, and improved environmental outcomes.

Omnivorous fish. Omnivorous fish, like Nile tilapia, have intestinal structures that reflect their mixed diet, situated between those of carnivorous and herbivorous species (Jiao et al 2023; Gioda et al 2017). The intestines of Nile tilapia are longer than those of carnivorous fish but shorter than those of herbivorous species, allowing them to efficiently digest both animal proteins and plant carbohydrates (Jiao et al 2023; Gioda et al 2017). This intermediate intestinal length supports a versatile digestive process, while the presence of microvilli in the intestinal lining improves nutrient absorption from various dietary sources (Jiao et al 2023).

The intestinal morphology of Nile tilapia is particularly well-suited for processing fibrous plant materials, though not as efficiently as that of herbivorous fish (Jiao et al 2023). Studies suggest that dietary supplements, such as yeast nucleotides, can improve intestinal structure in tilapia by increasing villi height and surface area, leading to enhanced nutrient absorption (Xu et al 2015). This adaptability to diverse diets makes tilapia highly suited for aquaculture practices incorporating plant- and animal-based feed ingredients (Gule & Geremew 2022).

Tilapia’s ability to digest plant and animal matter is pivotal in its success as an aquaculture species (Temesgen et al 2022). Research shows that tilapia can effectively utilize plant-based diets, which is essential for sustainable aquaculture aimed at reducing dependence on fishmeal (Gule & Geremew 2022; Sarker et al 2020). For instance, the inclusion of fermented yeast extracts in tilapia diets has been shown to improve growth performance while enhancing intestinal health. These benefits are attributed to increases in villi length and goblet cell numbers, which will enhance nutrient absorption and immune function (Pisuttharachai et al 2022; Hassaan et al 2018). Optimizing feed formulations for Nile tilapia, involves balancing plant and animal ingredients to meet their nutritional needs while supporting environmental sustainability (Soudah et al 2023).

Incorporating plant-based ingredients not only reduces reliance on fishmeal but also minimizes the environmental impact of aquaculture practices (Gule & Geremew 2022; Sarker et al 2020; Pérez-Fuentes et al 2018). This approach aligns with global efforts to promote eco-friendly aquaculture without compromising fish growth and health.

The intestinal microbiota of Nile tilapia also plays a critical role in its digestive efficiency and overall performance. Specific dietary components have been shown to influence gut health, with the potential to further enhance feed formulations (Ou et al 2024; Vale Pereira et al 2024). By modulating the gut microbiota through targeted nutrition, aquaculture practices can improve not only fish growth and health but also feed utilization efficiency.

In summary, Nile tilapia's intestinal adaptations make it a versatile and sustainable aquaculture species. Its ability to digest a wide range of feed ingredients supports the development of balanced diets that optimize growth while reducing environmental impacts associated with traditional fishmeal production. Advances in understanding intestinal health and microbiota can further refine feed strategies, promoting resilience and efficiency in tilapia aquaculture.

Gut microbiota and its influence on digestibility. The gut microbiota, the community of microorganisms living in the digestive tract of fish, plays a crucial role in digestion and nutrient absorption (Hasan et al 2023). This complex microbial ecosystem varies significantly among carnivorous, herbivorous, and omnivorous fish, reflecting their different dietary needs and digestive capacities (Huang et al 2020). Gut bacteria assist in breaking down food components that the host's digestive enzymes cannot process efficiently, particularly in the case of plant-based materials (Sidhu et al 2023). Understanding the composition and function of gut microbiota across fish species provides valuable insights into their digestive efficiency and their ability to utilize plant-based ingredients in aquaculture.

Carnivorous fish. In carnivorous fish, such as North African catfish or other protein-dominated species, the gut microbiota is dominated by bacteria that are specialized in aiding protein digestion. One of the most prevalent species in the gut of carnivorous fish is *Acinetobacter*, which plays a key role in breaking down proteins into simpler molecules such as amino acids (Jiang et al 2018; Zhou et al 2018). This bacterial dominance reflects the high-protein diet typical of carnivorous species, which rely heavily on these microorganisms to efficiently process and absorb animal-based nutrients (Jiang et al 2018).

Because carnivorous fish primarily consume animal matter, their gut microbiota is less diverse compared to that of herbivorous and omnivorous species (Huang et al 2020). The microbiota is specialized to handle the digestion of proteins and fats, making it less equipped to process carbohydrates and fibrous plant materials (Huang et al 2020). As a result, carnivorous fish often struggle with digesting plant-based ingredients, which can limit the use of plant-based feed in aquaculture for these species (Li et al 2014a).

Herbivorous fish. Herbivorous fish, such as grass carp, possess a gut microbiota that is well-adapted for breaking down fibrous plant material. The bacterial community in herbivores is dominated by species like Bacteroides, which are known for their ability to digest cellulose and other complex carbohydrates found in plant cell walls (Hao et al 2017; Xie et al 2018). These bacteria produce enzymes that break down cellulose into simpler sugars, which can then be absorbed and utilized by the fish (Jiang et al 2018; Huang et al 2020). The gut microbiota of herbivorous fish is essential for maximizing the nutritional value of plant-based diets. Without these cellulose-digesting bacteria, herbivores would struggle to extract sufficient energy from the fibrous plants they consume (Hao et al 2017). The presence of specialized bacteria like Bacteroides highlights the evolutionary adaptation of herbivorous fish to plant-based diets, enabling them to efficiently digest and thrive on fibrous plant materials (Hao et al 2017).

Omnivorous fish. Omnivorous fish, such as grass carp, exhibit the highest microbial diversity in their gut compared to carnivorous and herbivorous species. This diversity reflects the omnivorous diet, which includes both plant and animal matter. The gut microbiota of omnivores contains a broad spectrum of bacteria capable of digesting proteins, carbohydrates, and fibers, allowing these fish to process a wide range of food types (Jiang et al 2018; Huang et al 2020).

The adaptability of omnivorous fish to different food sources is largely due to the versatility of their gut microbiota. While they possess bacteria similar to those found in carnivorous fish for protein digestion, they also harbor bacteria like Bacteroides for breaking down plant-based carbohydrates (Li et al 2014b). This microbial diversity makes omnivorous fish more flexible in terms of diet, allowing them to efficiently digest both animal and plant ingredients (Hao et al 2017).

Comparative digestibility of plant-based ingredients in Nile tilapia, North African catfish, and grass carp. The digestibility of plant-based feed ingredients is a fundamental aspect of aquaculture nutrition, impacting feed efficiency, growth, and sustainability. Nile tilapia, North African catfish, and grass carp represent distinct feeding habits-omnivorous, carnivorous, and herbivorous, respectively, each with unique digestive adaptations influencing their capacity to process various plant-based feeds. The following tables summarize the apparent digestibility coefficients (ADCs) of various plant-based feed ingredients for Nile tilapia (Table 1), North African catfish (Table 2), and grass carp (Table 3), accompanied by supporting literature. These tables provide a comprehensive overview of each species' ability to utilize these ingredients effectively in aquaculture diets.

Table 1

Digestibility and the inclusion levels of plant-based ingredients in Nile tilapia (*O. niloticus* (Linnaeus, 1758))

Ingredients	*Digestibility (Source)*	*The Mininimum; (Optimum); Maximum Inclusion (Source)*
Soybean Meal (SBM)	91.12% (Koprucu & Özdemir 2005; Ribeiro et al 2011; Vidal et al 2015)	10; (25); 30 (El-Sayed 1999)
Duckweed (Lemna spp.)	88.4–93.9% (El-Shafai et al 2004)	5; 15; 20; (15-20) (Opiyo et al 2022)
Rapeseed Meal	Varied, up to 92.2% (Tran-Ngoc et al 2019)	10; (25); 30 (El-Sayed 1999)
Sunflower Meal	90.2% (Tran-Ngoc et al 2019)	5; (10); 15 (Olvera-Novoa et al 2002)
Corn Gluten Meal	89.0% (Koprucu & Özdemir 2005)	10; (20); 30 (Shiau et al 1990)
Wheat Bran	82.87% (Ribeiro et al 2011)	5; (15); 20 (El-Sayed 2003)
Chickpea	Higher ADCs (Montoya-Mejía et al 2016)	5; (10); 15 (Siddhuraju & Becker 2001)
Beans	Lower ADC, 69.41% (Montoya-Mejía et al 2016)	5; (10); 15 (Mbahinzireki et al 2001)

Table 2
Digestibility and the inclusion levels of plant-based ingredients in North African catfish (*C. gariepinus* (Burchell, 1822))

Ingredients	*Digestibility (Source)*	*The Mininimum; (Optimum); Maximum Inclusion (Source)*
Soybean Meal (SBM)	90-95% (with amino acid/protease) (Elesho et al 2021; Oyedokun 2022)	-
Lima Bean (Phaseolus lunatus)	Varied with processing (Falaye et al 2014)	5; (10); 15 (Fagbenro et al 2004)
Moringa oleifera Seed Meal	High at moderate levels (Haruna et al 2019)	5; (10); 20 (Richter et al 2003)
Roquette (Eruca sativa) Seed Meal	Comparable to SBM at 20% (Fagbenro et al 2004)	-
Sunflower Meal	Good digestibility (Tran-Ngoc et al 2019)	5; (10); 20 (Olvera-Novoa et al 2002)
Local Ingredients (e.g., Leucaena)	High (Farahiyah et al 2016)	-

The three tables allow for an analysis of key points regarding the digestibility of plant-based ingredients. Below is an in-depth review of how these ingredients are utilized across the species, informed by Tables 1, 2, and 3.

Soybean meal (SBM). Soybean meal is widely recognized for its high protein content and favorable digestibility in aquaculture feeds:

Nile tilapia. Demonstrates excellent digestibility for SBM, with apparent digestibility coefficients (ADCs) for protein up to 91.12%. This indicates its suitability as a primary plant protein source, as supported by Koprucu & Özdemir (2005), Ribeiro et al (2011), and Vidal et al (2015). The findings in Table 1 corroborate its effectiveness in tilapia diets.

North African catfish. Although primarily carnivorous, catfish adapt well to SBM, particularly with enzyme or amino acid supplementation, achieving ADCs up to 95%. This adaptability is backed by research from Elesho et al (2021) and Oyedokun et al (2019), as shown in Table 2.

Grass carp. While specific ADCs are not detailed, SBM is generally accepted as a high-protein option in grass carp diets, indicating potential as highlighted in Table 3.

Table 3

Digestibility and the inclusion levels of plant-based ingredients in grass carp (*C. idella* (Valenciennes, 1844))

Ingredients	*Digestibility (Source)*	*The Mininimum; (Optimum); Maximum Inclusion (Source)*
Soybean Meal (SBM)	Commonly high 68% (Referenced in overall reviews)	-
Azolla (Cooked)	Pathansali & Zainol 1976; (Arya et al 2024)	-
Napier and Grass Meals	Better than maize (Pathansali & Zainol 1976; Law et al 1986)	-
Maize Leaves	84.7% (Dongmeza et al 2010)	-
Barnyard Grass	60.9% (Dongmeza et al 2010)	-
Duckweed (Lemna spp.)	50% (Protein) GE 61%, (Van Dyke & Sutton 1977)	5; (15); 20 (Leng et al 1995)
Cottonseed Meal	Protein: 83.2% to 86.8% (Köprücü 2012)	5; (10); 15 (Robinson & Li 1995)
Sunflower Meal	78.9% to 83.1% (Köprücü & Sertel 2012)	-

Sunflower meal. Sunflower meal is another viable plant protein alternative:
Nile tilapia. Shows strong digestibility performance, with ADCs of up to 90.2% (Koprucu & Sertel 2012) as noted in Tabel 3.

Duckweed. Is valued for its sustainable production and nutrient content:
Nile tilapia. Demonstrates high ADCs for protein, ranging from 88.4% to 93.9%, making it a suitable supplemental feed (El-Shafai et al 2004). Table 1 confirms its potential as a reliable plant-based ingredient.
Grass carp. Shows lower protein digestibility for duckweed, approximately 50%, due to structural complexities in its cell walls (Gan et al 2012; Köprücü 2012). This is highlighted in Table 3, underlining the need for processing to improve its nutritional value.

Wheat bran. Wheat bran is commonly used as a supplemental feed:
Nile tilapia. Shows an ADC for protein at 82.87%, indicating its utility as a secondary ingredient (Ribeiro et al 2011). This aligns with the data in Table 1.
Comparison with other species. Detailed ADCs for North African catfish and grass carp are not provided in Tabel 2 or 3, suggesting its limited primary use for these species.

Other Notable Ingredients

Chickpea (for Nile Tilapia**)**. This legume displays high digestibility and outperforms beans (lower ADCs of 69.41%, Montoya-Mejía et al 2016), as seen in Table 1.

Lima bean (for North African catfish). Processing significantly impacts its digestibility, with variable ADCs (Falaye et al 2014), as shown in Table 2.

Maize leaves (for grass carp). Achieves good digestibility at 84.7%, noted as a promising feed option in Tabel 3 (Dongmeza et al 2010)**.** Soybean meal consistently shows high digestibility across all three species, serving as a cornerstone plant protein. Nile tilapia and North African catfish demonstrate broader adaptability to various plant-based ingredients, supported by data in Tables 1 and 2. Grass carp, with its herbivorous nature, exhibits more variability in digestibility, especially with fibrous ingredients like duckweed, as seen in Table 3. This comparative analysis underscores the importance of matching plant-based feed ingredients to the digestive profiles of Nile tilapia, North African catfish, and grass carp. Optimizing feed formulation requires consideration of both the species' natural adaptations and the processing of ingredients to enhance digestibility. This understanding fosters sustainable aquaculture practices by leveraging plant-based feeds to balance nutrition, cost, and environmental sustainability.

Conclusions. This review highlights the comparative digestibility of plant-based feed ingredients in Nile tilapia, North African catfish, and grass carp, showcasing their varying adaptations and enzyme activities. Soybean meal consistently emerges as the most effective plant protein source across all three species, with high apparent digestibility coefficients. Nile tilapia and North African catfish demonstrate broader adaptability to plant-based feeds, benefiting from strategic supplementation and balanced enzymatic profiles. In contrast, grass carp, as an herbivorous species, requires carefully selected and processed ingredients to achieve optimal digestibility, particularly with fibrous materials. This understanding underscores the importance of tailoring feed formulations to the unique digestive capabilities of each species to support sustainable and efficient aquaculture practices.

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