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Apparent digestibility of nutrients and energy from selected protein sources for tambaqui (*Colossoma macropomum*)

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ABSTRACT - This research aimed to evaluate the chemical composition and apparent digestibility coefficients (ADC) of dry matter (DM), gross energy (GE), crude protein (CP), and amino acids (AA) in plant and animal protein sources used in aquafeeds for tambaqui (*Colossoma macropomum*). Tested ingredients were soybean meal (SBM), cottonseed meal (CSM), corn gluten meal (CGM), fish meal (FM), meat and bone meal (MBM), and poultry by-product meal (PBM). A reference diet was formulated to contain 287 g kg^{-1} CP and 18.5 MJ GE kg diet^{-1}, and test diets were produced by incorporating test ingredients in a 70:30 ratio. Chromic oxide (Cr_2O_3) was used as an inert marker at 2 g kg^{-1}, and feces were collected by sedimentation. High variation in the ADC of DM (0.577 to 0.958) and GE (0.506 to 0.953) was observed between protein sources, while the ADC of CP was higher and showed less variation between the ingredients (between 0.834 and 0.978). The CGM, FM, and PBM treatments had the highest ADC values and appeared adequate for compounding aquafeeds for tambaqui, while CSM and MBM showed the lowest ADC values. Interestingly, the ADC of AA was variable among ingredients (from 0.272 to 0.989) and did not show the same trend as the other nutrients (mainly the CP). The present study demonstrates that tambaqui can efficiently digest both plant and animal protein sources. However, overall digestibility of plant protein sources appeared lower when extrusion was used to manufacture the diets.

Keywords: characidae, conventional ingredients, feed utilization, protein sources

1. Introduction

Tambaqui is the common name used in Brazil to designate *Colossoma macropomum* (Cuvier, 1818). This Neotropical omnivorous fish is widely farmed across Latin America due to its high growth potential and adaptability to different production systems. Tambaqui exhibits a variable natural feeding habit, shifting from seeds and fruits to plankton according to the season, which allows them to efficiently digest a wide range of feed materials (Silva et al., 2000; Silva et al., 2003). As Brazil's second most farmed fish species, tambaqui holds significant economic and social importance, particularly in regions surrounding the Amazon Forest. Despite its significance, few detailed studies are available on the nutrient requirements and feed ingredient digestibility for this species. The existing literature on the quantification of nutrient digestibility in tambaqui diets has been addressed in several studies (Silva et al., 1999, 2003; Soares et al., 2017; Araújo et al., 2018; Bicudo et al., 2018; Guimarães et al., 2014; Nascimento et al., 2020). Most studies have focused mainly on locally available alternative feed ingredients rather than on conventional feed ingredients commonly used in the aquafeed industry.

Proper nutrition is essential for the efficient growth and health of tambaqui, as it significantly influences its ability to thrive in intensive production systems. Previous research has highlighted the importance of balanced and highly digestible diets for sustainable fish production (Bicudo et al., 2018; Buzollo et al., 2018; Nascimento et al., 2020). The apparent digestibility coefficient of amino acids (ADC) is a key metric for assessing nutrient absorption efficiency in fish, directly influencing production performance and minimizing nutrient waste. Studies indicate that tambaqui can effectively digest protein and energy-rich ingredients, with notable differences in ADC values among various protein sources, such as soybean meal and corn gluten (Nascimento et al., 2020). Additionally, ingredients such as common bean by-products and mesquite pods have been found to exhibit lower digestibility coefficients due to their high fiber content and the presence of antinutritional factors, emphasizing the need for careful ingredient selection to optimize fish growth and health (Bicudo et al., 2018). A comprehensive assessment of ingredient digestibility, including bean by-products and other conventional ingredients like soybean meal, is essential for formulating cost-effective diets and promote sustainable aquaculture practices (Buzollo et al., 2018).

Producing sustainable aquafeeds is one of the key challenges for the future of the aquaculture industry (Béné et al., 2015; Regnier and Schubert, 2015). A crucial strategy to improve sustainability and develop cost-effective diets involves formulating feeds that meet the specific nutrient requirements of each species based on their digestible nutrient contents (Fagbenro, 1999; Gatlin et al., 2007). This approach can reduce nutrient waste and ensure that the nutrients are efficiently utilized by fish, thus improving growth performance. Given that nutrient digestibility is species-specific, it is essential to determine the nutrient digestibility values of different feed ingredients for each species.

Considering the above rationale, we performed a digestibility study to determine the nutritional value of six protein sources commonly used in compound diets for aquaculture: soybean meal, corn gluten meal, cottonseed meal, fish meal, meat and bone meal, and poultry by-product meal.

2. Material and methods

The experiment was carried out at the Laboratório de Pesquisa em Organismos Aquáticos (LAPOA) of the Pontifícia Universidade Católica de Goiás (PUC-GO), located in Goiânia, Goiás, Brazil (coordinates: 16°44'01.7"S, 49°12'51.6"W). All experimental procedures were reviewed and approved by the Animal Care and Use Committee of the Universidade Federal de Goiás (Protocol #149/10-CEUA). Fish were handled according to the guidelines described by the Brazilian Council for Controlling Animal Experiments (CONCEA, 2015).

2.1. Feed ingredients and diet preparation

Test ingredients were mixed with a reference diet (Table 1) in a 70:30 ratio. Thus, seven compound diets were evaluated: six containing the test ingredients and a reference diet. The reference diet was formulated to slightly exceed the protein and energy requirements for tambaqui, containing 280 g kg^{-1} of crude protein and 15 MJ kg^{-1} of digestible energy (DE) (Guimarães and Martins, 2015). Chromic oxide (Cr_2O_3) was used as an external inert marker at 2 g kg^{-1} diet. A feed mill facility provided all ingredients, vitamins, and mineral mixes (Guabi Nutrição Animal S.A.). Soybean meal (SBM), corn gluten meal (CGM), cottonseed meal (CSM), fish meal (FM) derived from freshwater fish processing waste, meat and bone meal (MBM), and poultry by-product meal (PBM) were evaluated. All ingredients were ground to a particle size of 400 µm.

Table 1 - Chemical composition of the reference diet (dry matter basis)

Ingredient	g kg^{-1}
Soybean meal	490.0
Fish meal	50.0
Corn	271.5
Wheat middlings	60.0
Soybean oil	65.0
DL-Methionine	1.0
Dicalcium phosphate	56.0
Vit/min supplement[1]	2.5
Ascorbic acid[2]	0.8
NaCl[3]	1.0
Chromic oxide III	2.0
BHT[4]	0.2
Proximate analysis (dry matter basis)[5]	g kg^{-1}
Crude protein	287.0
GE (MJ kg^{-1})	18.5
Lipid	81.1
Ash	93.9
Crude fibre	55.4
NDF[6]	87.6

1 Vitamin and mineral mix provided the following (IU or mg kg^{-1} diet): folic acid 10 mg, biotin 10 mg, niacin 170 mg, calcium pantothenate 80 mg, vit. A 16,060 IU, vit. B1 32 mg, vit. B12 0.032 mg, vit. B2 32 mg, vit. B6 32 mg, vit. C 350 mg, vit. D3 4,510 IU, vit. E 250 IU, vit. K3 30 mg, cobalt 0.5 mg, copper 20 mg, iron 150 mg, iodine 1 mg, manganese 50 mg, selenium 0.7 mg, zinc 150 mg; supplied by Mogiana Alimentos Ltda.
2 Ascorbyl polyphosphate (DSM Stay C 35.0% activity).
3 Sodium chloride.
4 Antioxidant: butylated hydroxytoluene.
5 Analysed.
6 Neutral detergent fiber with a heat stable amylase and expressed exclusive of residual ash.

The chemical composition and amino acid profile compositions of the test ingredients were analyzed (Table 2). Diets were mixed with distilled water at 45 °C (25% of dry weight); the moist mixture was extruded at 99–120 °C in a single-screw extruder (Ex Micro Laboratorio, Exteec, Ribeirão Preto, Brazil) to obtain 7.0 mm diameter pellets. Diets were oven-dried at 55 °C for 24h and stored at −18 °C until use.

2.2. Fish and experimental conditions

Fifty-six tambaqui juveniles (initial weight of 300 ± 30 g and 5 months old) purchased from a commercial fish farm (Aquicultura São Paulo, Brejinho de Nazaré/TO, Brazil) were randomly stocked into seven 310 L aquaria (eight fish per aquarium), where each group of fish was fed a different diet (CGM, CSM, SBM, PBM, FM, MBM, and the reference diet). This aquarium set was used for the feeding procedure and was connected to a recirculating water system. Another set of four conical-bottomed 300 L aquaria was used to collect feces by sedimentation following a modified procedure of the Guelph system procedure, which was described previously by Guimarães et al. (2008) and adapted to collect tambaqui feces collection (da Mota et al., 2015). Both systems were connected to a biological filter, and a thermostat controlled the water temperature. However, each fecal collection had its own biological filter to avoid contamination.

The seven experimental diets (six test diets plus the reference diet) were randomly assigned to feeding aquaria, and fish were fed seven days before fecal collection (acclimation period) after which the first collection cycle began. During the feces collection, fish were fed twice daily until apparent satiation. For the feces collection procedure, four groups of fish were transferred to four conical-bottom fecal collection aquaria, and feces were collected every 30 min to reduce nutrient leaching. These groups of fish remained in these aquaria set for 8 h and were then transferred back to the respective aquaria for

Table 2 - Chemical composition and amino acid content of the test ingredients and reference diet (g kg^{-1} otherwise stated, mean of two samples)[1]

Nutrients	Soybean meal	Corn gluten meal	Cottonseed meal	Fish meal	Poultry by-product meal	Meat and bone meal	Reference diet
IFN[2]	5-04-612	5-28-242	5-01-619	-	5-03-798	5-09-322	-
Dry matter	898.5	894.4	911.6	879.0	943.5	904.3	
Crude protein	456.8	626.8	441.2	515.9	559.8	468.1	
Gross energy (MJ/kg)	18.8	22.4	18.4	18.8	21.3	15.7	
Lipid	17.2	23.8	14.5	78.2	138.9	111.0	
Crude fibre	63.3	13.3	260.0	-	-	-	
NDF[3]	71.6	126.0	263.4	-	-	-	
Ash	12.0	31.9	56.6	296.2	93.9	343.9	
Amino acids							
Essential							
Arginine	30.0	19.8	27.9	23.6	23.0	22.9	17.0
Histidine	11.3	8.9	8.6	7.7	6.9	7.0	6.7
Isoleucine	21.0	16.6	12.7	14.0	12.2	12.2	11.9
Leucine	35.8	48.2	23.4	25.1	31.3	23.0	21.7
Lysine	27.5	15.6	17.3	21.9	18.7	18.6	14.0
Phenylalanine	23.4	22.2	17.2	15.5	14.3	14.5	13.6
Methionine	6.0	7.6	5.4	7.8	5.3	5.4	4.7
Threonine	18.3	14.5	11.9	14.1	11.8	11.8	10.8
Valine	21.5	18.2	14.9	15.8	14.4	14.5	12.7
Non-essential							
Alanine	19.9	26.7	14.7	21.3	20.7	20.4	13.3
Aspartic acid[4]	54.1	34.8	34.0	35.6	32.1	32.0	29.8
Cysteine	5.4	5.1	4.2	3.3	2.9	2.8	3.4
Glycine	21.0	15.8	15.8	28.9	33.7	33.6	14.4
Glutamic acid[5]	88.1	81.5	64.2	58.1	54.0	53.8	51.1
Tyrosine	15.0	15.8	9.9	10.1	8.9	9.1	8.6
Serine	24.8	21.1	16.3	17.0	15.8	15.7	14.5

[1] The chemical composition of feed ingredients is expressed in dry matter, while amino acids are expressed as-is.
[2] International Feed Number.
[3] Neutral detergent fiber with a heat-stable amylase and expressed exclusive of residual ash.
[4] Aspartic acid + asparagine.
[5] Glutamic acid + glutamine.

the feeding procedure. The feces-collecting aquaria were cleaned, and the water was exchanged before the following feces-collection procedure. On a consecutive day, three groups of fish were transferred to three fecal collection aquaria, and feces were collected (for a schematic view of the procedure, see Araújo et al., 2018). This procedure was repeated three times to obtain sufficient feces to represent a replicate (each group of fish). Then, the diets were reassigned to the feeding aquaria for another round. The acclimation, feeding procedure, and fecal collection processes (one round) were repeated four times to obtain quadruplicate measurements for each diet. After the first fecal collection, the other acclimatization periods were reduced to 3 days to ensure evacuation of the previously ingested food and to avoid any metabolically adaptive response to the diets (da Mota et al., 2015; da Silva Reis et al., 2019; Sugiura et al., 1998). For each round, feces were pooled by tank, oven-dried at 55 °C, ground, and stored at −18 °C until chemical analysis was performed.

During the experiment, a natural photoperiod was maintained. The dissolved oxygen content was 6.1 ± 0.43 mg L^{-1}, the pH was 6.6 ± 0.18, and the total ammonia–nitrogen was 0.11 ± 0.02 mg L^{-1}. The temperature was 27.5 ± 0.9 °C. These parameters remained within the recommended range for the growth of tambaqui (Barbosa, 2022).

2.3. Chemical analysis

The chemical composition of diets and ingredients (dry matter, ash, crude protein, crude fiber, and total lipid content) was determined according to standard AOAC methods (2000). From that analysis, only dry matter and crude protein content were analyzed in the feces due to the limited amount of samples. i) The dry matter was dried in an oven at 105 °C until a constant weight; ii) ash was incinerated in a muffle furnace at 600 °C for 2 h; iii) the protein (N × 6.25) was analyzed by the Kjeldahl method after acid digestion; iv) lipids were analyzed by ether extraction in a Soxtec system. Van Soest et al. (1991) procedure with the addition of sodium sulfite and alpha-amylase was used to determine the neutral detergent fiber (NDF). Chromic oxide was determined in diets and feces according to Bremer Neto et al. (2005), and the gross energy content was determined in diets, ingredients, and feces using a calorimeter (Parr Instrument Company, Moline-IL, USA). Amino acids were determined in ingredients, diets, and feces by high-performance liquid chromatography after acid and base digestion using an ion exchange chromatographic analysis method. After digestion, solutions of the free amino acid pools were vacuum filtered, diluted to 0.25 M with 0.02 N HCl for adjustment to pH 8.5, and filtered through a Millipore membrane (0.45 mm). Amino acids were quantified photocolorimetrically after staining with ninhydrin (Sindirações, 2009).

The ADC values of the test diets were calculated according to the equation described by Cho (1993):

$$ADC_{(n)} = 100\left[100\left(\frac{\%Cr_2O_{3_d}}{\%Cr_2O_{3_f}}\right) \times \left(\frac{\%N_f}{\%N_d}\right)\right]$$

in which $ADC_{(n)}$ = the apparent digestibility coefficient of a nutrient or energy in the test diets; $Cr_2O_{3_d}$ = % chromic oxide of the diet; $Cr_2O_{3_f}$ = % chromic oxide of the feces; N_d = nutrient or energy in the test diet; and N_f = nutrient or energy in feces.

The ADC of nutrients from each ingredient was calculated according to the equation proposed by Bureau and Hua (2006):

$$ADCN_{ing} = \frac{[(a + b) \times ADCN_{test} - a \times ADCN_{ref}]}{b}$$

in which a = nutrient or energy contribution of the reference diet to nutrient or energy content of the test diet; b = nutrient or energy contribution of test ingredients to nutrient or energy content of combined diet; $a + b$ = level of nutrient or energy in combined diet (%); $ADCN_{test}$ = apparent digestibility coefficients of a nutrient or energy in combined diet; and $ADCN_{ref}$ = apparent digestibility coefficients of a nutrient or energy in the reference diet.

2.4. Experimental design

The trial consisted of six treatments (test diets) and four replicates (groups of fish) arranged in a randomized block design for the ADC of dry matter, crude protein, and gross energy. In contrast, three replicates were used for the ADC of individual amino acids due to the limited sample from the last fecal collection. To facilitate comparison of feedstuffs, we divided the ingredients into plant and animal protein sources. Each block was considered as one round of fecal collection. Differences between the ingredients were analyzed according to the following model:

$$Y_{ijk} = \mu + T_i + B_j + e_{ijk}$$

in which Y = the observed response; μ = the overall mean; T = the effect of ingredients; B = the effect of the fecal collection period; and e = the residual error.

2.5. Data processing and statistical analysis

All percentage data were arcsine transformed before analysis. A nested effect was tested to determine a temporal effect of feces collection on the ADC of nutrients. The ADC values for dry matter, protein, energy, and individual amino acids were subjected to ANOVA using the PROC GLM procedure of SAS (Statistical Analysis System, version 8.12). Differences in ADC values between the tested ingredients were determined using the Student-Newman-Keuls multiple range test at P<0.05. Additionally, the ADC data of all test diets and their nutrient composition were analyzed by linear correlation using the PROC CORR procedure of SAS to investigate nutrient interactions. The digestible amino acid content of the feed ingredients was calculated using the following equation: Digestible amino acid = ADC of the amino acid in the ingredient × amino acid content of the ingredient. The digestible amino acid values were plotted in a graph using Excel. The estimated amino acid requirements of tambaqui (Martins et al., 2024) was included to evaluate whether the protein sources were limiting in one or more essential amino acids.

3. Results

The CGM treatment had the highest protein (626.8 g kg^{-1}) and energy content (22.4 MJ kg^{-1}) compared to the other plant protein products, while the fiber content was the lowest (13.3 g kg^{-1}) among these products (Table 2). The SBM and CSM treatments showed a similar chemical composition, except for fiber, ash, and NDF, which were higher in CSM (Table 2). Except for leucine and methionine, SBM showed the highest EAA content. Arginine was the most abundant EAA in SBM and CSM, while leucine was the most abundant in CGM (Table 2). Glutamic acid was the most abundant non-essential amino acid (NEAA) in all plant protein sources (Table 2). PBM showed the highest gross energy, protein, and lipid content and the lowest ash content among the animal protein sources. MBM showed the highest ash content (Table 2). Except for leucine, FM showed the highest EAA levels among the animal protein sources, slightly higher than the other sources (Table 2). A similar trend was observed for the NEAA content, except for glycine, which was higher in MBM and PBM (33.7 and 33.6 g kg^{-1}, respectively, versus 28.9 g kg^{-1}).

No effect of fecal collection period (round) was observed (P = 0.1093). Differences in the ADC of DM, CP, and GE were observed between the feed ingredients (Table 3). CGM and FM showed the highest GE (0.953 and 0.935), CP (0.978 and 0.930), and DM digestibility values among the plant and animal protein sources. In contrast, the CSM and MBM showed the lowest ADC values for DM (0.597 and 0.577) and GE (0.506 and 0.858), except for protein in the MBM. The ADC of gross energy was noticeably lower for cottonseed meal (CSM) among the plant protein sources (0.506). However, no differences between SBM and CSM were observed for the ADC of CP and DM. The ADC of protein ranged from 0.870 to 0.978 among the plant protein sources, while animal protein sources showed ADCs ranging from 0.834 to 0.930.

Among the animal protein sources, a positive correlation coefficient were observed between the gross energy and crude protein content and ADC of DM (Table 4). In contrast, high ash content was negatively correlated to the ADC of DM. Nonetheless, a negative correlation was observed between lipid

Table 3 - Apparent digestibility coefficients of gross energy, crude protein, and dry matter of conventional protein sources for tambaqui, *C. macropomum* (n = 4 aquaria)

Ingredient	Gross energy	Crude protein	Dry matter
	Plant protein sources		
Corn gluten meal	0.953±0.026A	0.978±0.020A	0.958±0.021A
Soybean meal	0.661±0.020B	0.918±0.039B	0.610±0.030B
Cottonseed meal	0.506±0.024C	0.870±0.020B	0.597±0.034B
	Animal protein sources		
Fish meal	0.935±0.034a	0.930±0.025a	0.766±0.036a
Poultry by-product meal	0.898±0.039ab	0.834±0.028b	0.803±0.023a
Meat and bone meal	0.858±0.033b	0.878±0.019b	0.577±0.030b

Means ± SD with different letters in the same column are statistically different by the SNK test (P<0.05). Capital letters compare plant protein sources, while lowercase letters compare animal protein sources.

content and protein ADC. No significant correlation was observed between the other nutrition factors among animal protein sources. Conversely, test diets' fiber, gross energy, lipid, and protein content significantly affected the ADC of DM, CP, and GE in plant protein sources. Crude fiber was negatively correlated to all ADC values evaluated in this trial (P<0.05). In contrast, gross energy, lipids, and crude protein levels were positively correlated to all ADC values in plant products (P<0.01; Table 4).

The ADC of essential amino acids (EAA) and non-essential amino acids (NEAA) of the feed ingredients evaluated for tambaqui is shown in Table 5. CSM showed the lowest ADC of all EAA and NEAA among

Table 4 - Correlation coefficients among nutrient content and apparent digestibility coefficients (ADC) of dry matter, crude protein and gross energy of conventional protein sources for tambaqui, *C. macropomum*[1]

Components	ADC DM	ADC CP	ADC GE
	Animal protein sources		
Gross energy	0.92**	−0.35	0.41
Lipid	0.10	−0.88**	−0.37
Crude protein	0.91**	−0.38	0.39
Ash	−0.81**	0.55	−0.24
	Plant protein sources		
Crude fibre	−0.67*	−0.81**	−0.87**
Gross energy	0.99**	0.81**	0.96**
Lipid	0.96**	0.86**	0.99**
Crude protein	0.99**	0.81**	0.96**
Ash	−0.09	−0.44	−0.40

[1] Each value corresponds to a correlation coefficient between the nutrient concentration of the test diets and the ADCs of nutrients. One and two asterisks are statistically significant at P<0.05 and P<0.01, respectively.

Table 5 - Apparent digestibility coefficients of amino acids from protein sources for tambaqui, *C. macropomum* (n = 3 aquaria)

Amino acids	Plant protein sources			Animal protein sources		
	CGM	CSM	SBM	MBM	PBM	FM
Essential						
Arginine	0.967±0.002A	0.808±0.005B	0.941±0.003A	0.789±0.003c	0.710±0.003b	0.946±0.003a
Histidine	0.964±0.003A	0.804±0.004B	0.919±0.002A	0.721±0.004a	0.660±0.001b	0.900±0.003a
Isoleucine	0.972±0.002A	0.854±0.002B	0.968±0.001A	0.921±0.002a	0.819±0.003b	0.957±0.003a
Leucine	0.958±0.002A	0.782±0.003B	0.960±0.001A	0.855±0.004b	0.689±0.004c	0.937±0.004a
Lysine	0.964±0.002A	0.768±0.004B	0.977±0.001A	0.875±0.002a	0.792±0.003b	0.922±0.003a
Phenylalanine	0.961±0.001A	0.790±0.003B	0.967±0.001A	0.851±0.003a	0.699±0.004b	0.947±0.004a
Methionine	0.982±0.001A	0.796±0.003B	0.988±0.001A	0.913±0.003a	0.809±0.001b	0.924±0.003a
Threonine	0.946±0.001A	0.753±0.003B	0.946±0.002A	0.795±0.003b	0.641±0.004c	0.888±0.003a
Valine	0.964±0.001A	0.841±0.003B	0.962±0.001A	0.858±0.003b	0.697±0.003c	0.945±0.003a
Mean EAA	0.964	0.799	0.959	0.842	0.724	0.930
Non-essential						
Alanine	0.962±0.001A	0.781±0.003B	0.962±0.001A	0.821±0.003b	0.620±0.004c	0.937±0.003a
Aspartic acid[1]	0.976±0.001A	0.911±0.002B	0.989±0.000A	0.865±0.001a	0.811±0.002b	0.971±0.001a
Cysteine	0.937±0.003A	0.773±0.002B	0.934±0.001A	0.650±0.005b	0.272±0.003c	0.941±0.003a
Glycine	0.976±0.001A	0.902±0.003B	0.987±0.001A	0.869±0.002b	0.814±0.003c	0.946±0.003a
Glutamic acid[2]	0.962±0.002A	0.854±0.003B	0.965±0.001A	0.824±0.003b	0.660±0.003c	0.876±0.004a
Tyrosine	0.949±0.001A	0.818±0.004B	0.954±0.001A	0.800±0.003b	0.638±0.004c	0.928±0.003a
Serine	0.973±0.001A	0.842±0.004B	0.965±0.001A	0.878±0.003b	0.745±0.004c	0.946±0.004a
Mean NEAA	0.962	0.840	0.894	0.815	0.651	0.935
Mean AA	0.963	0.817	0.930	0.830	0.692	0.932

CGM - corn gluten meal; CSM - cottonseed meal; SBM - soybean meal; MBM - meat and bone meal; PBM - poultry by-product meal; FM - fish meal.
Means ± SD with different letters in the same column are statistically different by the SNK test (P<0.05); capital letters are for comparisons between plant protein sources, while lowercase letters are for comparisons between animal protein sources.
[1] Aspartic acid + asparagine.
[2] Glutamic acid + glutamine.

the plant protein products. In contrast, PBM showed low ADC values for essential and non-essential amino acids among animal protein sources. In this study was observed a relatively low ADC of cysteine (0.272) for PBM. FM, SBM, and CGM showed the highest ADC of amino acids (higher than 0.85) among all feed ingredients evaluated for tambaqui. Despite discrepancies between the average ADC values for all amino acids and the ADC of protein in PBM, all other protein sources showed a significant positive correlation between the ADC of all amino acids and the ADC of crude protein (average 0.7617, $P<0.001$).

4. Discussion

This study comprehensively assessed the apparent digestibility coefficients (ADC) of dry matter (DM), gross energy (GE), crude protein (CP), and amino acids (AA) in conventional plant- and animal-based protein sources for tambaqui (*Colossoma macropomum*). The results revealed significant variation among ingredients. For instance, corn gluten meal (CGM) and fish meal (FM) exhibited the highest ADC values for GE, CP, and DM within their respective categories, while cottonseed meal (CSM) and meat and bone meal (MBM) showed the lowest digestibility values. These findings corroborate previous digestibility studies on tambaqui that evaluated both conventional and alternative ingredients (Nascimento et al., 2020; Buzollo et al., 2018), and emphasize the need for updated digestibility data for key protein sources currently used in commercial diets.

The chemical composition of the ingredients can partially explain the observed differences in digestibility. For example, CGM presented the highest protein and energy content and the lowest fiber content among the plant ingredients, factors commonly associated with improved digestibility. In contrast, the higher ash and fiber levels in CSM and MBM may have contributed to their lower ADC values. These patterns are consistent with previous findings reporting that high fiber and ash contents impair nutrient digestibility and utilization in fish (Hertrampf and Piedad-Pascual, 2000; Guimarães et al., 2012). The chemical composition of the ingredients used in this study was generally similar to values reported in the literature (Abimorad et al., 2008; Gonçalves and Furuya, 2004; NRC, 2011), although slight differences were observed. For instance, the poultry by-product meal (PBM) used here had a slightly lower ash content compared with those described by Buzollo et al. (2018) and Nascimento et al. (2020), while FM showed a chemical profile consistent with filleting residue–based products (Abimorad et al., 2008; Guimarães et al., 2012). Furthermore, the amino acid composition was variable among ingredients, but in general, the levels observed in this study were higher than those reported for similar feedstuffs in other studies (Köprücü and Özdemir, 2005; Zhou and Yue, 2012; Yamamoto et al., 1998). These comparisons underscore the importance of combining digestibility and compositional analyses in evaluating feed ingredient quality, especially since differences in macronutrient profiles may influence the efficiency of nutrient absorption and fish growth across species.

Previous studies have reported that tambaqui can efficiently digest plant protein products better than animal proteins (Van der Meer et al., 1997). However, our results showed very low dry matter digestibility for most of the evaluated plant proteins, while only MBM showed a low ADC of DM among the animal protein sources. This suggests that tambaqui may not be as efficient using plant protein sources. The fiber and ash contents in plant and animal protein sources appear to be the main components negatively affecting overall digestibility, as indicated by the negative correlation coefficients (Table 4). Similar results were found for tambacu, a hybrid of tambaqui (*Colossoma macropomum*) and pacu (*Piaractus mesopotamicus*), which exhibited a low capacity to digest ingredients with high fiber and antinutritional factor contents, impacting overall nutrient absorption (Bicudo et al., 2018). While the ability to digest animal protein sources might be related to the feeding habits of fish, the bulk of the evidence shows that a high ash content (mainly from bones) can depress growth, dry matter, and energy digestibility in fish. High ash content, particularly from ingredients rich in bone-derived minerals such as hydroxyapatite, can accumulate in the intestinal lumen and act similarly to fiber, increasing digesta passage rate and reducing nutrient digestibility. This effect is commonly observed in low-quality animal by-product meals, such as meat and bone meal or poorly processed fish and poultry by-product meals (Guimarães et al., 2012; Hertrampf and Piedad-Pascual, 2000; Sugiura et al., 1998, 2000). Recent studies have shown that tambaqui is highly efficient in digesting protein and energy-rich ingredients. Nascimento et al. (2020) reported that among the energetic ingredients, corn and wheat bran exhibited the highest apparent digestibility coefficients for essential amino acids (ADC_EAA) at 0.946 and 0.919, respectively. Corn gluten meal and soybean meal were noted for their high ADC for essential amino acids, with values ranging from 0.795 to 0.985 for various protein ingredients, except for alcohol yeast, which had the lowest ADC EAA of 0.684.

Although the diets were extruded, a process known to enhance nutrient availability, no apparent increase in dry matter and energy digestibility was observed for SBM and CSM in this study. These values were positively correlated (r = 0.70 and 0.95 for animal and plant protein sources, respectively). It is likely that the extrusion conditions and starch content of these products were not sufficient to significantly improve carbohydrate digestibility. Nonetheless, the hypothesis of increased dry matter and energy digestibility in extruded SBM and CSM cannot be entirely dismissed, as previous studies have observed an increase in non-starch polysaccharides solubility after the extrusion process (Anguita et al., 2006; Sagum and Arcot, 2000).

In general, the ADC of CP was high for all protein sources (above 0.80), while the ADC of DM (from 0.577 to 0.958) and GE (from 0.506 to 0.953) was highly variable among feed ingredients. Our study's ADC values of DM, CP, and GE from CGM were notable. However, it is important to clarify that CGM, as a protein source, should not be directly compared with corn, an energy source. Although CGM is a by-product of corn, their different nutritional roles must be considered. For instance, while the ADC_CP of CGM in our study is comparable to values reported by Buzollo et al. (2018) for corn, these ingredients serve distinct nutritional purposes in aquafeeds. Additionally, the ADCs of GE (0.661 versus 0.786) and DM (0.610 versus 0.843) from SBM were lower than those reported for soybean meal (Bicudo et al., 2018) in tambaqui juveniles, yet similar to the ADC_CP (0.918 versus 0.951) reported for soybean meal (Buzollo et al., 2018) in tambaqui juveniles.

The apparent digestibility coefficients (ADC) for dry matter (DM), crude protein (CP), and gross energy (GE) in CGM were similar to those reported for pacu (*Piaractus mesopotamicus*), a closely related species with similar feeding habits (Abimorad et al., 2008). For Nile tilapia, Guimarães et al. (2012) reported ADC values of 0.862 for DM and 0.881 for GE, which were slightly lower than those observed in the present study. In contrast, the ADCs of GE (0.661 versus 0.781) and DM from SBM were lower than those reported for pacu (Abimorad et al., 2008) and similar to those reported for Nile tilapia (Guimarães et al., 2012). The CSM treatment exhibited slightly higher ADC values for nutrients than values reported for Nile tilapia (Guimarães et al., 2012), reflecting its relatively high fiber content, which both tambaqui and pacu are adapted to process effectively. These findings indicate that tambaqui and pacu share similar digestive capacities for conventional plant-based ingredients due to their phylogenetic proximity and omnivorous feeding habits.

For juvenile tambacu hybrids, the ADC values for DM, CP, and GE decreased as the fiber content of the ingredients increased (Bicudo et al., 2018). Conventional ingredients, such as corn and soybean meal, were more digestible than alternative feedstuffs, such as common bean residue and mesquite meal, due to the latter's high fiber content and antinutritional factors. Tambacu exhibited reduced efficiency in digesting fiber-rich plant ingredients compared with tambaqui, likely due to subtle differences in the activity of digestive enzymes (e.g., proteases) and/or gut microbiota between the two species. However, a comparative study would be necessary to confirm this hypothesis.

Comparisons with Nile tilapia (*Oreochromis niloticus*) revealed slight differences in digestibility patterns. These comparisons are relevant due to the species' similar feeding habits, digestive physiology, and their shared importance in tropical aquaculture (Araújo-Lima and Goulding, 1998; Tesfahun and Alebachew, 2023). For example, the ADC of dry matter (DM) and gross energy (GE) in poultry by-product meal (PBM) for Nile tilapia were 0.811 and 0.888, respectively, which were higher than those observed in the present study for tambaqui. Similarly, tilapia exhibited higher values for most essential amino acids in MBM, with MBM-460 exceeding 90% in apparent availability coefficients (AAC), as reported by Xavier et al. (2014). In contrast, tambaqui demonstrated superior digestibility for fibrous materials, suggesting species-specific adaptations to dietary fiber, such as the presence of gut microbiota specimens capable of efficiently digesting these materials (Nascimento et al., 2020; Guimarães et al., 2014).

Additionally, (Vidal et al., 2017) reported ADC values for soybean coproducts in tilapia, with DM values ranging from 0.842 for low-protein soybean meal (LPSBM) to 0.884 for soy protein concentrate (SPC), and CP values from 96.8 for full-fat soybean meal to 0.979 for high-protein soybean meal. These values highlight tilapia's efficiency in digesting soybean coproducts with lower fiber content. On the other hand, tambaqui consistently showed higher digestibility for cysteine in cottonseed meal (CSM), which was 10% less digestible in Nile tilapia (Zhou et al., 2012). It is worth noting that this ability to digest fibrous materials seems to be better in tambaqui compared to other omnivorous fish species, although a comparative study is needed to test this hypothesis. Still, the trend of reduced nutrient digestibility according to the increase in dietary fiber content is similar to other aquaculture fish species. The ADC values of all amino acids observed for SBM, CGM, and FM in this study were high and very similar to the digestibility values reported for Nile tilapia (Guimarães et al., 2008; Köprücü and Özdemir, 2005) and pacu (Abimorad et al., 2008). Conversely, tambaqui demonstrated a unique advantage in processing fibrous materials, reinforcing its dietary specialization compared to tilapia.

Differences in nutrient digestibility among tambaqui, pacu, and tilapia may also result from anatomical and physiological differences, feed processing methods, and the quality of raw materials (Cho and Bureau, 2001; Guimarães et al., 2012). Although tambaqui and pacu share a close phylogenetic proximity, the ability to digest animal and plant protein sources appears to be more similar between tambaqui and tilapia. This observation highlights the need for caution when extrapolating ADC values from one species to another, even among closely related fish.

The ADC values of all amino acids observed for SBM, CGM, and FM in this study align closely aligned with those reported for juvenile tambaqui by Nascimento et al. (2020), except for methionine, which was significantly less digestible in CSM (0.796) compared to CGM (0.982) and SBM (0.988). Conversely, the ADC of cysteine in PBM was notably lower (0.272) than those observed for other protein sources in both studies. The ADC values of different amino acids in MBM were also consistent with the values reported by Nascimento et al. (2020), except for aspartic acid, which was higher in FM (0.971) compared to MBM (0.865).

Interestingly, cysteine showed a markedly lower ADC in PBM. Although it has been reported that the quality of animal-rendering protein products had improved by the late 1990s (Bureau et al., 1999), it is still possible to find low-quality products on the market. The low cysteine digestibility is a clear indication of the inadequate raw material processing in meat and bone meal, as previously reported in studies on poultry (Parsons et al., 1997; Wang et al., 1997; Wang and Parsons, 1998). Low cysteine digestibility, specifically in MBM and probably in PBM as well, is a combined effect of a high temperature within the processing system and the duration of cooking, probably forming lanthionine and reducing cysteine digestibility (Wang and Parsons, 1998). Since these products limit sulfur amino acids, this increases the imbalance in amino acids and dramatically reduces the quality of protein and the digestibility of the other amino acids. Although one could argue that the PBM used in this study might have been contaminated with feathers, this is not likely to be possible because raw feathers are rich in cysteine (Moritz and Latshaw, 2001), while the PBM used in this study showed cysteine levels similar to high-quality PBM (Bureau et al., 1999; Cheng and Hardy, 2002; Dong et al., 1993; Guimarães et al., 2008; Hertrampf and Piedad-Pascual, 2000). Altogether, this may explain the low amino acid digestibility in this product compared with the reported ADC values for omnivorous and carnivorous fish species and the low correlation between the mean ADC of all amino acids and the ADC of protein (Bureau et al., 1999; Cheng and Hardy, 2002; Chi et al., 2017; Guimarães et al., 2008).

After calculating the digestible amino acid content of the ingredients used in this study and comparing it with the amino acid requirement of tambaqui (Costa et al., 2020), we observed that most of the ingredients used in this study seem to be deficient in sulfur amino acids (specifically methionine) and lysine. Notably, most of the amino acids in FM used in this study seem to be deficient for tambaqui, emphasizing the need to supplement specific crystalline amino acids, even when using a traditional protein source in aquaculture diets. This finding also highlights the need to formulate diets based on digestible amino acid levels.

5. Conclusions

Our study demonstrates that tambaqui can efficiently digest plant and animal protein sources. However, lower apparent digestibility coefficients (ADC) for dry matter (DM) and gross energy (GE) in plant protein sources highlight the need for careful formulation to minimize environmental impacts in aquaculture systems. As observed in PBM, the variability in the quality of rendered animal proteins underscores the importance of monitoring ingredient quality to ensure adequate amino acid supply for optimal fish growth. These findings contribute to the development of species-specific feed formulations, supporting sustainable aquaculture practices.

Data availability

The entire dataset supporting the results of this study is available upon request to the corresponding author. The dataset is not publicly available due to privacy concerns, as it contains sensitive information that could compromise the confidentiality of research participants. Specifically, the dataset includes personal or identifiable data, which are protected under privacy regulations. To ensure compliance with ethical guidelines and data protection laws, access to the dataset is restricted and will only be granted on a case-by-case basis, subject to the approval of the corresponding author.

Author contributions

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Conflict of interest

The authors declare no conflict of interest.

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Declaration of generative AI in scientific writing

In this manuscript, AI-assisted tools, specifically Grammarly, were used to aid in grammatical corrections and improve textual fluency, and Mendeley was utilized for reference management. It is emphasized that these tools were employed solely for language editing and organizational purposes under strict human supervision, ensuring that the use of the software did not introduce inaccuracies, incomplete thoughts, or biases. The full responsibility for the content of this work lies entirely with the authors.

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