



## Starch Degradation Kinetics and Carbohydrate Composition of Tropical High-Starch Feed Ingredients for Ruminants

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### ABSTRACT

Starch-rich feeds are vital in ruminant diets because they provide readily fermentable energy, supporting growth, lactation, and overall productivity. This study evaluated the *in sacco* degradation patterns and carbohydrate fractions, based on the Cornell Net Carbohydrate and Protein System (CNCPS), of five high-starch feeds commonly used in ruminant diets, i.e., corn, cassava, sago, sorghum, and wheat. Analyses included chemical composition, carbohydrate fractions, and degradation dynamics of dry matter (DM) and starch. Cassava had the highest starch content ( $P < 0.001$ ), whereas wheat contained the lowest ( $P < 0.001$ ). Carbohydrate fractionation revealed distinct profiles among feeds, with cassava rich in the CB<sub>1</sub> fraction (slowly fermentable energy) and corn exhibiting the highest sugar (CA) content ( $P < 0.001$ ). *In sacco* evaluation showed considerable variability, in which wheat had the greatest DM degradability ( $P < 0.001$ ), while corn showed the highest starch degradability ( $P < 0.001$ ). Starch degradation rates differed significantly ( $P < 0.001$ ), with sorghum was degraded the fastest and sago the slowest. Effective degradability (ED) of starch was highest in corn and lowest in cassava. Corn provided rapidly available energy owing to its dominance in rumen degradable starch (RDS), whereas cassava, enriched in resistant starch (RS), degraded more slowly. Correlation analysis confirmed a significant negative relationship between RS and RDS ( $P < 0.05$ ), indicating that higher RS reduced the availability of rapidly fermentable starch in the rumen. These distinct degradation profiles highlight the potential complementary roles of high-starch feeds in precision diet formulation for tropical ruminants, supporting a balanced energy supply, improved fermentation efficiency, and sustainable livestock production.

**Keywords:** Carbohydrate, Feed, *In sacco*, Starch degradability, Resistant starch.

### INTRODUCTION

Achieving optimal energy supply is fundamental for ruminant performance, influencing muscle growth, lactation, and vital metabolic functions (Khejornsart et al. 2025). Among dietary energy sources, starch is widely utilized because of its high digestibility and substantial energy yield (Jin et al. 2025). Globally, corn (*Zea mays*) is the predominant starch-rich feed ingredient used in ruminant diets. Nevertheless, in many developing regions, including Indonesia, corn availability is constrained by fluctuating prices, competition with human consumption, and inconsistent supply. These challenges highlight the need to identify alternative starch sources that are locally

available, sustainable, and cost-effective.

In Indonesia, ruminant feeding systems predominantly depend on traditional grass forages. Inconsistent supply in terms of quality and quantity has been linked to reduced rumen fermentation efficiency, growth performance, and overall livestock productivity (Ali et al. 2023). To meet the energy demands of high-producing cattle, such as dairy and beef cattle, farmers commonly rely on high-starch feeds. Despite this practice, ration formulation in Indonesia is still largely based on the Total Digestible Nutrients (TDN) system, which estimates gross energy availability but overlooks the dynamics of carbohydrate fermentation in the rumen (McDonald et al. 2022). This conventional approach risks underestimating the variability in starch

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degradation rates among feed ingredients, thereby reducing the efficiency of energy utilization.

This gap emphasizes the importance of evaluating starch degradation characteristics to optimize feed formulation. Several starch-rich crops grown in tropical regions, such as cassava (*Manihot esculenta*), sorghum (*Sorghum bicolor*), sago (*Metroxylon sagu*) and wheat (*Triticum aestivum*), offer potential as alternatives to corn. Cassava is the third most important food crop globally after rice and maize and is notable for its agronomic resilience, including tolerance to acidic soils and the ability to propagate through vegetative growth (Howeler 2017; Parmar et al. 2017; Khejornsart et al. 2022; Unnawong et al. 2024). Sorghum is valued for its drought tolerance and high starch content, while wheat and sago are also widely used in certain regions as complementary starch sources. However, despite their availability, these ingredients differ considerably in starch composition, carbohydrate fractions, and ruminal degradation kinetics, all of which influence their nutritional value (Iommellii et al. 2022; Ma et al. 2022).

A systematic evaluation of these alternative starch sources within the framework of the Cornell Net Carbohydrate and Protein System (CNCPS) and *in sacco* technique is essential. Such an approach can provide insights into their degradation dynamics and energy release patterns, supporting precision feed formulation in tropical ruminant production systems (Palangi et al. 2020; Eslampeivand et al. 2022; Gleason et al. 2022). The CNCPS provides a framework for partitioning carbohydrates into four fractions based on solubility and degradation rate: Fractions A (rapidly soluble), B1 (slowly soluble), B2 (insoluble with slow degradation) and C (non-degradable) (Higgs et al. 2015; Gierus et al. 2024). Fraction A has a digestion rate of 40–60% per hour, fractions B1 and B2 from 20–40% per hour, and fraction C from 1–18% per hour (Hernández et al. 2020). *In sacco* evaluation of corn, cassava, sorghum, sago, and wheat allows starch to be classified into two primary fractions: Rumen degradable starch (RDS) and rumen undegradable starch (RUS). This partitioning provides insights into how different feeds contribute to ruminal fermentation and post-ruminal digestion (Jin et al. 2025). In addition, resistant starch (RS) further modulates this balance, functioning as a slowly digested carbohydrate fraction (Aguilar et al. 2023).

Although both approaches have been extensively employed worldwide to assess carbohydrate digestibility and enhance targeted ration formulation, their application to high-starch feed in Indonesia is limited. Existing CNCPS-based research in the country has primarily focused on agroindustrial by-products (Rahmadani et al. 2025a), leaving limited information on the carbohydrate fraction profiles of major ingredients, such as corn, cassava, sago, sorghum, and wheat. This knowledge gap constrains the development of precision feeding strategies that could optimize animal performance while reducing the dependence on imported feedstuffs. Therefore, this study aimed to characterize *in sacco* starch degradation, define CNCPS-based carbohydrate fraction profiles, and explore their interrelationships across RS and RDS of high-starch feed ingredients commonly used in Indonesia.

## MATERIALS AND METHODS

### Ethical Approval

This study was approved by the Animal Ethics Committee of IPB University, Indonesia (266-2024 IPB).

### Sample preparation

The study was performed at the Feed Science and Technology Laboratory, Faculty of Animal Science, IPB University, Indonesia. The feeds used in this study included corn and sorghum, which were obtained from Sukabumi, West Java; sago, which was obtained from local farmers in Riau; and cassava from local farmers in Bogor, West Java, Indonesia. Wheat was obtained from a local feed mill in Bogor, West Java. Each feed ingredient was ground using a grinder and then sieved through a 2mm mesh before chemical composition analysis and degradation testing via an *in sacco* study.

### Chemical composition

The chemical composition of the feed ingredients was determined in quadruplicate. Proximate analyses included dry matter (DM), ash, crude protein (CP), and ether extract, following the official methods of analysis. Fiber fractions (neutral detergent fiber/NDF, acid detergent fiber/ADF, cellulose, and lignin) were assessed according to Van Soest et al. (1991). Starch and amylose were determined using AOAC official method 996.11 (AOAC 2005), with amylopectin calculated as the difference between the total starch and amylose. Resistant starch was quantified using a Megazyme assay kit (Neogen, USA).

### Carbohydrate fraction

The carbohydrate fractions were determined according to Sniffen et al. (1992). The measured fractions included total carbohydrates (CHO), unavailable carbohydrates in fiber (CC), available carbohydrates in fiber (CB<sub>2</sub>), starch and non-starch polysaccharides (CB<sub>1</sub>), sugar content (CA), and non-structural carbohydrates (CNSC). Each fraction was determined using the equation proposed by Sniffen et al. (1992).

$$\text{CHO (\%DM)} = 100 - \text{CP(\%DM)} - \text{Fat (\%DM)} - \text{Ash (\%DM)}$$

$$\text{CC (\%CHO)} = \frac{100 (\text{NDF (\%DM)} \times 0.01 \times \text{Lignin (\%NDF)} \times 2.4)}{\text{CHO (\%DM)}}$$

$$\text{CB}_2 (\%CHO) = \frac{100((\text{NDF(\%DM)} - \text{NDICP(\%CP)} \times 0.01 \times \text{Lignin(\%NDF)} \times 2.4)}{\text{CHO (\%DM)}}$$

$$\text{CNSC (\%CHO)} = 100 - \text{CB}_2(\%CHO) - \text{CC(\%CC)}$$

$$\text{CB}_1 (\%CHO) = \frac{\text{Starch (\%NSC)} \times (100 - \text{CB}_2(\%CHO) - \text{CC(\%CHO)})}{100}$$

$$\text{CA (\%CHO)} = \frac{(100 - \text{Starch (\%NSC)}) \times (100 - \text{CB}_2(\%CHO) - \text{CC(\%CHO)})}{100}$$

### *In sacco* dry matter and starch degradability

The *in sacco* degradation experiment involved three rumen-fistulated Friesian Holstein bulls (average BW: 359±20kg). The animals were fed twice daily (morning and evening) with a diet composed of elephant grass and commercial concentrate at a 60:40 (w/w) ratio. The daily DM intake was set at 2% of the body weight. The forage

contained 11.06% crude protein (CP), 23.61% crude fiber (CF), and 69% total digestible nutrients (TDN), whereas the concentrate contained 10.04% CP, 23.10% CF, and 66% TDN. Fresh drinking water was provided ad libitum to the animals. A randomized complete block design (RCBD) 5×3 was applied, consisting of five feed ingredients (corn, cassava, sago, sorghum, and wheat) and three animals as blocks. Nylon bags (5×10cm) were oven-dried at 60°C for 2h, weighed, filled with 5g of sample, sealed, and incubated in the rumen at different time intervals (0, 3, 6, 12, 15, 24, and 48h). Each incubation was performed in triplicates.

For the 0h control, nylon bags were rinsed under running water and dried identically to the incubated bags without being placed in the rumen. At the end of each incubation period, bags were withdrawn, washed for 5min under flowing water to remove remaining particles, rumen liquor, and microbes, and then oven-dried at 60°C for 72h until a constant mass was achieved. The residues were analyzed for DM and starch content according to AOAC (2005). The degradation kinetics of DM and starch were estimated using the exponential model of Ørskov and McDonald (1979).

$$\text{Dissappearance} = a + b(1 - e^{-c})$$

In this model, the parameter definitions are as follows: a, soluble fraction; b, potentially degradable fraction; e, natural logarithm; c, fractional degradation rate of b; and t, incubation time. The effective degradability (ED) of DM or starch was determined using the following equation:

$$\text{ED} = a + \frac{b \times c}{k + c}$$

As described earlier, a, b, and c represent the soluble, degradable, and rate parameters, respectively, while k indicates the ruminal outflow rate, assumed to be 0.06h<sup>-1</sup>. The value of rumen undegradable starch (RUS) was obtained using the following formula:

$$\text{RUS} = 100 - \text{RDS}$$

### Data Analysis

Data were subjected to analysis of variance (ANOVA), and significant differences among means were further tested using Duncan's multiple range test (DMRT) at P<0.05. Pearson's correlation analysis was conducted to determine the relationship between resistant starch and rumen-degradable starch. Statistical analysis was performed using SAS OnDemand for Academics.

## RESULTS

### Chemical composition

Table 1 summarizes the chemical compositions of the evaluated high-starch feeds, revealing significant differences among all parameters (P<0.001). Sorghum had the highest crude protein level (14.2%), whereas cassava had the lowest (6.46%). Corn had the highest fat content (4.72%), while the lowest value was again observed in sago (0.39%). Significant differences were observed in the fiber fractions of the feed ingredients (P<0.001). Sago had the highest ADF (12.1%) and NDF (44.4%) concentrations, whereas corn had the lowest (3.97% and 11.6%, respectively). The NDICP fraction was most abundant in sago (3.02%) and least abundant in cassava (0.865%). Lignin was recorded highest in corn (7.55%) and lowest in sorghum (0.862%). The cellulose content ranged from 2.56% in corn to 8.20% in sago. This variation indicated considerable diversity in the chemical composition of the high-starch feed materials tested.

Table 2 presents the starch and resistant starch contents of the high-starch feed ingredients, which differed significantly among the materials (P<0.001). Cassava (78.1%) and sorghum (70.4%) had the highest starch levels, indicating their role as major energy sources. Sorghum also showed the highest resistant starch content (16.3%), followed by cassava (11.4%) and sago (9.19%). Conversely, wheat and corn were recorded as having the lowest resistant starch content, at 7.02 and 8.84%, respectively. These variations are largely attributable to the structural differences in the starch of each material.

Table 3 presents the compositional profiles of starch, specifically amylose and amylopectin fractions, in the high-starch feeds. Sago had the highest amylose content (26.3%), whereas wheat had the lowest (4.27%). Conversely, wheat had the highest amylopectin content (60.9%), whereas corn had the lowest (39.6%). These results indicate differences in the starch profiles of feed ingredients, which have implications for their functional properties and potential utilization in feed formulations.

### Carbohydrate fractionation

Carbohydrate fractionation from various high-starch feed materials showed significant compositional differences (P<0.001), as presented in Table 4. Cassava was recorded as having the highest total carbohydrate (CHO) content (91.5%), whereas corn showed the lowest value (79.8%). In the carbohydrate fraction, sago had the

**Table 1:** Chemical composition of high-starch feeds (%DM)

Feeds	DM	Ash	OM	CP	Fat	ADF	NDF	NDICP	Lignin	Cellulose
Cassava	87.4 <sup>b</sup>	1.50 <sup>c</sup>	85.9 <sup>b</sup>	6.46 <sup>c</sup>	0.50 <sup>d</sup>	5.35 <sup>d</sup>	15.8 <sup>bc</sup>	0.87 <sup>c</sup>	0.97 <sup>c</sup>	4.33 <sup>d</sup>
Corn	87.1 <sup>b</sup>	1.79 <sup>b</sup>	85.3 <sup>b</sup>	13.7 <sup>a</sup>	4.72 <sup>a</sup>	3.97 <sup>c</sup>	11.6 <sup>d</sup>	0.99 <sup>c</sup>	7.55 <sup>c</sup>	2.56 <sup>e</sup>
Sago	85.9 <sup>c</sup>	5.14 <sup>a</sup>	80.8 <sup>c</sup>	7.86 <sup>b</sup>	0.39 <sup>d</sup>	12.1 <sup>a</sup>	44.4 <sup>a</sup>	3.02 <sup>a</sup>	3.01 <sup>a</sup>	8.20 <sup>a</sup>
Sorghum	89.2 <sup>a</sup>	1.19 <sup>d</sup>	88.0 <sup>a</sup>	14.2 <sup>a</sup>	1.44 <sup>c</sup>	6.76 <sup>c</sup>	16.6 <sup>b</sup>	1.25 <sup>b</sup>	0.86 <sup>c</sup>	5.77 <sup>c</sup>
Wheat	89.4 <sup>a</sup>	1.38 <sup>cd</sup>	88.1 <sup>a</sup>	13.8 <sup>a</sup>	2.05 <sup>b</sup>	9.38 <sup>b</sup>	12.6 <sup>cd</sup>	1.08 <sup>bc</sup>	1.37 <sup>b</sup>	7.85 <sup>b</sup>
Average	87.8	2.20	85.6	11.2	1.82	7.51	20.2	1.44	1.39	5.74
SEM	0.328	0.342	0.623	0.775	0.362	0.672	2.84	0.186	0.195	0.488
P-value	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001

DM= dry matter; OM= organic matter; CP= crude protein; ADF= acid detergent fiber; NDF= neutral detergent fiber; NDICP= neutral detergent insoluble protein; SEM= standard error of the mean; a-e= values in the same column with different letters are significant (P<0.05).

**Table 2:** Starch and resistant starch contents of high-starch feeds (%DM)

Feeds	Starch	Resistant Starch
Cassava	78.1 <sup>a</sup>	11.4 <sup>b</sup>
Corn	65.4 <sup>b</sup>	8.84 <sup>c</sup>
Sago	67.0 <sup>b</sup>	9.19 <sup>c</sup>
Sorghum	70.4 <sup>b</sup>	16.3 <sup>a</sup>
Wheat	65.2 <sup>b</sup>	7.02 <sup>d</sup>
Average	69.2	10.6
SEM	1.28	0.744
P-value	<0.001	<0.001

SEM= standard error of the mean; a-c= values in the same column with different letters are significant (P<0.05).

**Table 3:** Starch characterization of high-starch feeds (%DM)

Feeds	Amylose	Amylopectin
Cassava	20.5	57.6
Corn	25.8	39.6
Sago	26.3	40.7
Sorghum	21.0	49.4
Wheat	4.27	60.9

highest CC content (3.71%), whereas cassava had the lowest (0.405%). The CB<sub>2</sub> fraction was highest in wheat (65.3%) and lowest in corn (0.885%). Conversely, corn had the highest CNSC content (96.5%), and wheat had the lowest (32.3%). The CB<sub>1</sub> fraction was significantly higher in cassava (67.0%) and lowest in wheat (21.1%). The CA fraction was the largest in corn (33.4%) and the smallest in wheat (11.2%).

#### In sacco dry matter and starch degradability

This study assessed the degradation dynamics of dry matter (DM) and starch in five starch-rich feed ingredients

over incubation times of 0, 3, 6, 12, 15, 24, and 48h (Table 5). At 0h rumen incubation, the highest DM loss through nylon bag washing (P<0.001) was found in sago (4.24%) and the lowest in sorghum (1.55%). Throughout the incubation period, wheat consistently showed the highest DM degradation, with a peak value of 82.6% at 48h, significantly exceeding that of the other feeds (P<0.001). In contrast, sorghum exhibited relatively low degradation rates during the incubation period. Cassava exhibited a more significant increase in DM degradation after 24h of incubation.

The extent of starch degradation at 0h ranged from 6.56% in cassava to 18.5% in corn (P<0.001), indicating substantial variability among feed materials at the initial incubation stage. Consistently, corn showed the highest degradation throughout the incubation period, with a maximum value of 94.1% at 48h, followed by wheat (87.3%) and sago (73.9%). Meanwhile, cassava and sorghum showed moderate levels of starch degradation at 71.9% and 68.4%, respectively, after 48h. Significant differences in starch degradation among these high-starch feed materials (P<0.001) indicated variations in their fermentability levels.

The kinetics of *in sacco* DM and starch degradation in various high-starch feeds showed significant variation between the feed materials (Table 6). Wheat had the highest DM degradation potential (a+b=99.8%), soluble fraction (4.22%), and effective degradation value (39.1%). Conversely, sorghum had the lowest soluble fraction and effective degradation, at 0.00% and 19.7%, respectively, whereas sago had the lowest degradation potential (52.2%). In terms of starch degradation, the trend differed from that of DM, with sorghum showing the highest soluble fraction

**Table 4:** Carbohydrate fractions of high-starch feeds

Feeds	CHO (%DM)	CC (%CHO)	CB <sub>2</sub> (%CHO)	CNSC (%CHO)	CB <sub>1</sub> (%CHO)	CA (%CHO)
Cassava	91.5 <sup>a</sup>	0.405 <sup>c</sup>	13.8 <sup>c</sup>	85.8 <sup>b</sup>	67.0 <sup>a</sup>	18.8 <sup>c</sup>
Corn	79.8 <sup>c</sup>	2.63 <sup>b</sup>	0.885 <sup>d</sup>	96.5 <sup>a</sup>	63.1 <sup>b</sup>	33.4 <sup>a</sup>
Sago	86.6 <sup>b</sup>	3.71 <sup>a</sup>	39.4 <sup>b</sup>	56.9 <sup>c</sup>	38.3 <sup>d</sup>	18.6 <sup>c</sup>
Sorghum	83.2 <sup>c</sup>	0.410 <sup>c</sup>	15.9 <sup>c</sup>	83.6 <sup>b</sup>	58.9 <sup>c</sup>	24.8 <sup>b</sup>
Wheat	82.7 <sup>cd</sup>	2.48 <sup>b</sup>	65.3 <sup>a</sup>	32.3 <sup>d</sup>	21.1 <sup>e</sup>	11.2 <sup>d</sup>
Average	84.8	1.93	27.1	71.0	49.7	21.4
SEM	0.928	0.327	5.70	5.84	4.35	1.85
P-value	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001

CHO= total carbohydrates; CC= non-degradable fraction; CB<sub>2</sub>= insoluble and slowly degradable fraction, CNSC= non-structural carbohydrates; CB<sub>1</sub>= soluble and slowly degradable fraction; CA= readily soluble fraction; SEM= standard error of the mean; a-e= values in the same column with different letters are significant (P<0.05).

**Table 5:** Dry matter and starch degradation (%) of high-starch feeds at different times of ruminal incubation

Feeds	0	3	6	12	15	24	48
Dry matter							
Cassava	4.03 <sup>a</sup>	7.43 <sup>b</sup>	9.72 <sup>c</sup>	21.6 <sup>b</sup>	24.9 <sup>c</sup>	49.6 <sup>a</sup>	63.7 <sup>b</sup>
Corn	3.49 <sup>a</sup>	8.00 <sup>b</sup>	13.3 <sup>b</sup>	24.1 <sup>b</sup>	28.3 <sup>b</sup>	34.8 <sup>b</sup>	62.3 <sup>b</sup>
Sago	4.24 <sup>a</sup>	6.31 <sup>c</sup>	10.5 <sup>c</sup>	22.7 <sup>b</sup>	23.1 <sup>c</sup>	37.9 <sup>b</sup>	44.0 <sup>c</sup>
Sorghum	1.55 <sup>b</sup>	3.44 <sup>d</sup>	5.40 <sup>d</sup>	13.6 <sup>c</sup>	19.3 <sup>d</sup>	35.8 <sup>b</sup>	47.5 <sup>c</sup>
Wheat	1.64 <sup>b</sup>	16.9 <sup>a</sup>	23.7 <sup>a</sup>	34.2 <sup>a</sup>	43.6 <sup>a</sup>	55.0 <sup>a</sup>	82.6 <sup>a</sup>
SEM	0.332	1.22	1.66	1.84	2.28	2.30	3.70
P-value	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
Starch							
Cassava	6.56 <sup>d</sup>	16.9 <sup>c</sup>	17.8 <sup>c</sup>	31.7 <sup>b</sup>	39.1 <sup>b</sup>	51.8 <sup>c</sup>	71.9 <sup>b</sup>
Corn	18.5 <sup>a</sup>	29.1 <sup>b</sup>	34.2 <sup>a</sup>	47.3 <sup>a</sup>	55.3 <sup>a</sup>	72.5 <sup>a</sup>	94.1 <sup>a</sup>
Sago	15.1 <sup>b</sup>	19.7 <sup>d</sup>	21.2 <sup>b</sup>	32.0 <sup>b</sup>	39.5 <sup>b</sup>	60.3 <sup>b</sup>	73.9 <sup>b</sup>
Sorghum	17.1 <sup>a</sup>	31.1 <sup>a</sup>	34.6 <sup>a</sup>	37.8 <sup>b</sup>	52.0 <sup>a</sup>	55.2 <sup>bc</sup>	68.4 <sup>b</sup>
Wheat	8.41 <sup>c</sup>	26.8 <sup>c</sup>	34.2 <sup>a</sup>	46.4 <sup>a</sup>	55.0 <sup>a</sup>	60.4 <sup>b</sup>	87.3 <sup>a</sup>
SEM	1.29	1.48	2.00	2.04	2.32	2.03	2.86
P-value	<0.001	<0.001	<0.001	0.002	0.009	<0.001	<0.001

SEM= standard error of the mean; a-d= values in the same column with different letters are significant (P<0.05).

**Table 6:** *In sacco* degradation kinetic parameters of dry matter and starch

Variable	Cassava	Corn	Sago	Sorghum	Wheat	SEM	P-value
<b>DM</b>							
a (%)	0.700 <sup>d</sup>	2.98 <sup>b</sup>	1.70 <sup>c</sup>	0.00 <sup>d</sup>	4.22 <sup>a</sup>	0.421	<0.001
b (%)	97.6 <sup>a</sup>	89.9 <sup>ab</sup>	50.5 <sup>c</sup>	81.8 <sup>b</sup>	95.5 <sup>a</sup>	4.70	<0.001
a + b (%)	98.3 <sup>a</sup>	92.9 <sup>a</sup>	52.2 <sup>c</sup>	81.8 <sup>b</sup>	99.8 <sup>a</sup>	4.81	<0.001
c (%/hour)	0.022 <sup>c</sup>	0.020 <sup>c</sup>	0.043 <sup>a</sup>	0.191 <sup>b</sup>	0.033 <sup>b</sup>	0.003	<0.001
ED <sub>6</sub> (%)	27.5 <sup>b</sup>	26.3 <sup>c</sup>	22.5 <sup>d</sup>	19.7 <sup>e</sup>	39.1 <sup>a</sup>	1.78	<0.001
<b>Starch</b>							
a (%)	6.69 <sup>c</sup>	18.5 <sup>a</sup>	12.1 <sup>b</sup>	19.9 <sup>a</sup>	12.8 <sup>b</sup>	1.29	<0.001
b (%)	87.7 <sup>ab</sup>	97.6 <sup>a</sup>	92.4 <sup>ab</sup>	54.1 <sup>c</sup>	82.4 <sup>b</sup>	4.26	<0.001
c (%/hour)	0.030 <sup>b</sup> <sup>c</sup>	0.030 <sup>b</sup> <sup>c</sup>	0.027 <sup>c</sup>	0.047 <sup>a</sup>	0.043 <sup>ab</sup>	0.003	<0.001
ED <sub>6</sub> (%)	35.4 <sup>c</sup>	52.2 <sup>a</sup>	39.0 <sup>c</sup>	43.8 <sup>b</sup>	47.6 <sup>b</sup>	1.68	<0.001

DM= dry matter; a= soluble fraction; b= insoluble but potentially soluble fraction; a + b= degradation potential; c= degradation rate; ED<sub>6</sub>= effective degradability at a degradation rate of 6%/hour; RDS= rumen degradable starch; RUS= rumen undegradable starch; SEM= standard error of the mean; a-d= values in the same row with different letters are significant (P<0.05).

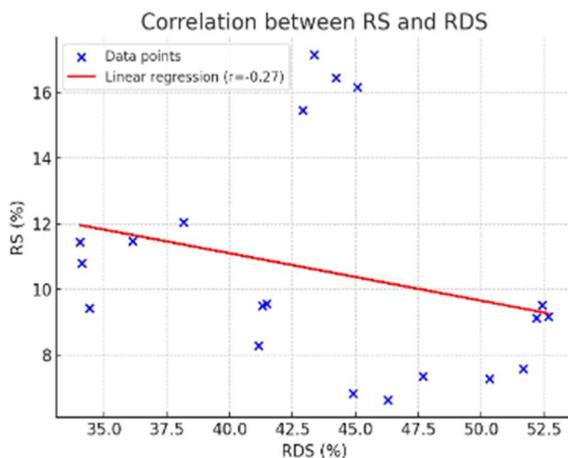
(19.9%) and degradation rate (0.047%/h), whereas cassava showed the lowest values (6.69% and 0.030%/h, respectively). Corn exhibited the highest effective starch degradability (52.2%), whereas cassava had the lowest (35.4%).

The estimated values of RDS and RUS from *in sacco* degradation of various high-starch feeds are presented in Table 7. The differences in RDS and RUS values among the feeds were significant (P<0.001). The estimation of these two parameters was based on the effective degradation and starch composition of each feedstuff. Corn had the highest RDS value (46.9%), while sago had the lowest value (25.8%). Conversely, cassava recorded the highest RUS value (50.8%), while wheat showed the lowest value (37.7%).

**Table 7:** Estimated rumen degradable starch (RDS) and rumen undegradable starch (RUS)

Feeds	RDS (% of starch)	RUS (% of starch)
Cassava	27.9 <sup>d</sup>	50.8 <sup>a</sup>
Corn	46.9 <sup>a</sup>	43.0 <sup>c</sup>
Sago	25.8 <sup>de</sup>	40.3 <sup>d</sup>
Sorghum	37.5 <sup>b</sup>	48.2 <sup>b</sup>
Wheat	34.3 <sup>c</sup>	37.7 <sup>e</sup>
SEM	2.17	1.40
P-value	<0.001	<0.001

SEM= standard error of the mean; a-e= values in the same column with different letters are significant (P<0.05).



**Fig. 1:** Correlation between rumen degradable starch and resistant starch.

**Correlation between rumen degradable starch and resistant starch**

Correlation analysis between resistant starch (RS) and rumen-degradable starch (RDS) revealed a negative relationship (Fig. 1). An increase in RDS content tended to be followed by a decrease in RS (r = -0.27), indicating an inverse relationship between the rapidly rumen-degradable starch fraction and the starch fraction that persists as RS. However, the relatively low correlation value suggests that the contribution of RDS to RS variation is still limited.

**DISCUSSION**

Understanding starch degradation in high-starch feeds is essential not only for maximizing nutrient utilization but also for preventing digestive disorders associated with rapid ruminal fermentation. This study demonstrates how variations in chemical composition, carbohydrate fractions, and degradation kinetics shape the utilization of selected feed resources. By linking chemical characterization with starch degradation dynamics, the findings provide critical insights for selecting and processing feed ingredients to balance ruminal and post-ruminal energy supply, thereby improving both animal performance and feed efficiency.

The analysis of the chemical composition of high-starch feeds revealed substantial variability across multiple nutritional parameters (Table 1), reflecting differences in nutritional value and potential utilization in the ruminant digestive system. Sago exhibits the highest ADF and NDF content with a relatively low lignin level, but is dominated by cellulose, a profile indicating its potential to support rumen fermentation and improve the digestibility of fiber fractions. Conversely, corn has a higher lignin content, which can be a limiting factor for fiber digestibility and can reduce its nutritional quality (Wang et al. 2021). In contrast, sorghum stands out for its higher CP and OM content than other feed ingredients. A high CP concentration has the potential to increase rumen microbial activity and, in turn, improve digestibility (Tulu et al. 2025).

Starch, a major natural polysaccharide, is widely distributed in cereals and tubers. In this study, cassava exhibited the highest starch concentration (78.061%), supporting its role as a major energy source, consistent with its reported carbohydrate content of approximately 73–85% (Chamorro et al. 2025). Sorghum also has a relatively high starch content of 70.388%, but this is accompanied by

a significant amount of RS. This finding aligns with that of a previous study by Aguiar et al. (2023), who reported that sorghum is rich in resistant starch; therefore, most of its carbohydrates are not digested in the rumen. The presence of RS plays an important physiological role as it bypasses ruminal fermentation and undergoes slower degradation in the hindgut, which contributes to improved nutrient absorption and more efficient energy utilization (Pereira and Leonel 2014; Rahmadani et al. 2025b). Conversely, corn and wheat had significantly lower starch and RS contents than cassava and sorghum.

Variations in starch content among feed materials are influenced by their structural composition, particularly the relative proportions of amylose and amylopectin. Starch generally contains approximately 20–30% amylose and 70–80% amylopectin (Tharanathan 2005). Amylose consists of linear chains of glucose joined by  $\alpha$ -1,4 glycosidic bonds (Pfister and Zeeman 2016), whereas amylopectin is characterized by a branched structure with  $\alpha$ -(1 $\rightarrow$ 6) linkages occurring approximately every 20 glucose units (Masina et al. 2017). In this study, cassava contained 20.50% amylose and 57.56% amylopectin, which is different from corn and sorghum, which have higher amylose contents. The high proportion of amylose in cereals is related to its role as an energy reserve during germination (Rahmadani et al. 2025a).

Characterization of starch from various high-starch feed materials has indicated that the chemical structure of starch significantly influences its digestibility and RS formation. High-amylose feeds, such as sago (26.31%), corn (25.84%), and sorghum (21.03%), tend to have greater RS levels, consistent with Ma et al. (2025), who observed a positive association between amylose concentration and RS digestibility. Amylose tends to form double-helical structures with ordered molecular arrangements, resulting in inclusion complexes that resist enzymatic hydrolysis by ruminal microbes (Zheng et al. 2020). This renders amylose more resistant to amylolytic enzymes and contributes to RS formation. Conversely, feed materials with high amylopectin content, such as wheat (60.93%), are relatively easier to digest because the branched structure of amylopectin allows for faster and more efficient enzyme access.

The utilization of starch derived from agricultural products as ruminant feed relies on its high carbohydrate content, making it a major energy source. Variations in feed quality are largely influenced by differences in chemical composition, particularly the distribution of carbohydrate fractions. Such different carbohydrate fractions also influence the magnitude of enteric methane emissions from ruminants (Sofyan et al. 2022; Della Rosa et al. 2025), which contribute to global warming. Cassava had the highest total carbohydrate (CHO) content, primarily contributed by the CB<sub>1</sub> fraction. The CB<sub>1</sub> fraction is a soluble carbohydrate that is slowly degraded, providing fermentable energy in the rumen. This finding aligns with a report (Mafaldo et al. 2024) stating that cassava contains highly soluble starch, which is associated with the characterization of cassava starch, dominated by amylopectin. Conversely, corn had the lowest CHO content but a high proportion of CNSC and CA fractions. This indicates that most of the carbohydrate fraction in corn consists of simple sugars, which act as a rapidly degradable

but limited source of energy in the rumen (Rodríguez-Espinosa et al. 2021).

The CC fraction is a carbohydrate that cannot be degraded in the rumen. Sago had the highest CC fraction content, indicating the presence of lignin-bound fiber, which reduces its digestibility. This aligns with the high NDF content in sago, where lignocellulose and indigestible fiber components can limit its role as a rapidly fermentable energy source. Thus, although sago is rich in starch, its high NDF and CC fractions indicate digestibility limitations due to some of its fiber being bound by lignin and difficult to utilize optimally. Conversely, wheat exhibited a more balanced carbohydrate profile, with a high CB<sub>2</sub> fraction and low CA fraction. The high CB<sub>2</sub> content supports a slower degradation rate, thus providing sustained energy for rumen microbes while potentially reducing the risk of acidosis (Pan et al. 2021).

Insoluble fiber contributes to increasing feed bulk and mass, whereas soluble fiber is rapidly fermented, providing quick energy to rumen microbes (Nabeshima et al. 2020). However, excessive consumption of highly degradable starch can trigger acidosis in ruminants (Owens et al. 1998). This finding confirms the importance of understanding the functional roles of feed ingredients, particularly fiber and starch profiles, in rumen fermentation. Energy efficiency in ruminant nutrition may be enhanced by establishing a balance between fast-fermenting carbohydrates (e.g., CB<sub>1</sub> from cassava) and slowly degradable carbohydrates (e.g., CB<sub>2</sub> from wheat), while integrating the role of indigestible fractions (e.g., CC from sago). Feed formulations based on an understanding of the chemical composition of high-starch materials can improve microbial efficiency, alter the composition of rumen bacterial communities, suppress methanogen growth, and mitigate metabolic disorders (Hook et al. 2011; Herliatika et al. 2024).

The nutrient fraction degraded at 0h represents the water-soluble components that are released before any ruminal microbial activity occurs. The disappearance of DM at this initial stage is mainly influenced by factors such as the degree of grinding, which determines particle size and affects the uniformity of particle distribution (Darma et al. 2023). In this study, DM loss at 0h ranged from 1-4%, while starch loss ranged from 6-18%, indicating that starch, particularly soluble starch, constitutes most of the feed DM (Shen et al. 2015). After 48h of incubation, the digestibility of DM in all high-starch feed materials remained below 85%, indicating that not all DM could be fully utilized by rumen microbes. Wheat showed the highest DM digestibility (82.638%), whereas sago showed the lowest (43.988%). This difference is closely related to variations in the chemical composition that affect microbial activity. The high starch content in wheat, especially that dominated by amylopectin, likely contributes significantly to the high digestibility of DM, as reported by Feyisa et al. (2024). Conversely, the degradation of DM in sago occurs more slowly, which is believed to be due to the high proportion of the CB<sub>2</sub> fraction and the dominance of amylose, thus limiting its role as a rapidly fermentable energy source but still contributing to rumen volume.

High-starch feed materials showed starch degradation after 48h of incubation, with corn exhibiting the highest and sorghum the lowest digestibility. Starch degradation is

influenced by various factors, including starch granule structure, starch type, protein interactions, and anti-nutritional factors such as tannins (Rooney and Pflugfelder 1986; Hidayat et al. 2021). The high digestibility of corn is linked to its solubility and non-structural carbohydrate content, which provides rapid energy to rumen microbes (Zhang et al. 2021). Corn is also dominated by the non-structural carbohydrate fraction, which acts as a quick energy source and can be directly utilized by ruminal microbes for fermentation. In contrast, the limited starch degradation in sorghum corroborates earlier findings (Pan et al. 2021), as its high resistant starch content and phenolic compounds, particularly tannins, can form complexes with starch and inhibit its enzymatic breakdown (Barros et al. 2012).

The DM degradation kinetics differed significantly among fractions a and b and the ED. Although all high-starch feedstuffs had relatively similar DM degradation rates (c), starch degradation showed significant variation, with sorghum recording the highest rate and sago the lowest. This contrasts with the findings of Shen et al. (2015), who reported that DM is largely starch, which positively affects the degradation rate and ED. These discrepancies may be attributed to differences in DM content, protein fractions, and starch composition (Wachirapakorn et al. 2016; Huang et al. 2022). The high amylose content in sago contributes to slower degradation due to its linear chain resistance (Zhao et al. 2018) and protein-starch interactions further influence starch degradation via protein solubility and ruminal breakdown (Krieg et al. 2017).

The ED value at a degradation rate of 6%/h is an important indicator in feed formulation, as it reflects the extent to which feed can be utilized within a limited time in the rumen. The results showed that wheat had the highest ED value for DM, whereas sorghum had the lowest. The low ED value in sorghum was mainly due to the high fraction b, which is related to the presence of tannin compounds. In starch degradation, corn had the highest ED value, whereas cassava had the lowest. These results emphasize that the structural and chemical properties of each high-starch feed material play critical roles in determining its degradation rate and the extent of energy released in the rumen.

High-carbohydrate feeds are commonly used in high-producing ruminant diets to support milk yield and promote weight gain (Srakaew et al. 2021). RDS can intensify rumen fermentation, accumulating short-chain fatty acids and lactic acid, which lowers the pH and increases the risk of subacute acidosis (Metzler-Zebeli et al. 2013; Rahmadani et al. 2025a). In contrast, RUS is slowly or not degraded in the rumen. Excess RUS can reduce starch digestibility and ruminal nitrogen efficiency, but RUS can be digested in the small intestine, improving glucose absorption and reducing energy losses (Kathrin et al. 2013). This study emphasizes the importance of balancing RDS and RUS: corn is rich in RDS, cassava in RUS, and a combination, such as corn with wheat, can enhance energy efficiency without severely lowering rumen pH while supporting weight gain (Zheng et al. 2020; Srakaew et al. 2021).

This study underscores the negative association between RS and RDS. Enhanced RDS availability

coincides with reduced RS, reflecting the greater susceptibility of starch to enzymatic hydrolysis (Ramli et al. 2025). This was supported by *in sacco* digestibility, which showed a progressive reduction in RS with increasing RDS content. These findings suggest that a higher dietary RS can limit ruminal starch degradation while promoting post-ruminal digestion in the duodenum. Moreover, measuring the RS fraction of a feed ingredient can also serve as an indirect indicator of its RUS value, thereby providing useful insights into starch utilization dynamics across digestive sites.

Nonetheless, several limitations of this study should be considered. The *in sacco* methodology inherently involves biological variability arising from differences in the rumen environment, microbial population dynamics, and animal-specific factors such as rumen motility and retention time. In addition, methodological factors, including the type of nylon bag and the physicochemical characteristics of feed ingredients, such as starch granule structure, amylose-to-amylopectin ratio, and prior processing history, may have influenced starch degradation patterns (Offner et al. 2003). These sources of variability can affect the precision of the measurements and limit the extrapolation of results to broader feeding systems. Future studies should employ standardized feed characterization, controlled processing conditions, and multi-environment validation to improve the reliability and predictive accuracy of starch degradation models in tropical ruminant nutrition.

## Conclusion

This study provides an integrated understanding of starch degradation kinetics and carbohydrate fractionation in tropical high-starch feeds commonly used in Indonesia. The findings highlight that differences in rumen degradable and resistant starch among feed ingredients can be strategically utilized to balance energy release and improve feed efficiency in tropical ruminant diets. These insights support the refinement of feed evaluation systems beyond TDN based approaches and encourage further investigation into processing methods or feed combinations that optimize starch utilization and rumen fermentation dynamics.

## DECLARATIONS

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**Data Availability:** The data that support the findings of this study are available from the corresponding author upon

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**Ethics Statement:** This study was conducted in accordance with the guidelines for the care and use of animals and was approved by the Animal Ethics Committee of IPB University, Indonesia (Approval No. 266-2024 IPB).

**Author's Contribution:** MR conducted the conceptualization, methodology, investigation, analysis, data curation, visualization, and drafting. FRA contributed to analysis and drafting. NN, LK, EBL, EP and RF contributed to supervision, data curation, and review/editing. AJ provided supervision, resources, funding acquisition, validation, and review/editing. All authors approved the final manuscript.

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