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Digestion and importance of starch in ruminants

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ABSTRACT

Ruminants have a unique digestive physiology that heavily relies on microbial fermentation specifically in the rumen. The rumen, a complex microbial ecosystem, is the primary site for starch digestion. Enzymatic hydrolysis and microbial fermentation of starch in this compartment produce important by products, such as volatile fatty acids (VFAs) and microbial proteins. These by products are crucial sources of energy and protein, which affect the overall metabolic dynamics of ruminants. It is essential to have a comprehensive understanding of the factors that influence starch digestion rates to optimize ruminant nutrition. In this review, the complex mechanisms of starch digestion in ruminants and the various factors involved in starch digestion, including feed composition, microbial population and enzymatic activity, and how these contribute to the digestive process, are examined and its important role in shaping the nutritional environment is attempted to be explained. Additionally, identifying and characterizing starch fractions in concentrated feed sources is crucial for formulating well-balanced rations. In conclusion, this review synthesizes current knowledge on starch digestion in ruminants, offering insights into the complexities of the process. The collected information not only contributes to academic understanding but also has practical implications for optimizing feeding strategies, enhancing nutrient utilization, and promoting the overall well-being of ruminants.

Keywords: Ruminants, Starch, Starch digestion

INTRODUCTION

The main organic components of ruminant diets are carbohydrates, fats and proteins. Among these, carbohydrates play an important role for ruminants both as a source of energy and ballast and because they are present in almost 70% of the rations. Among carbohydrates, cellulose and starch are the most important components for ruminants (Saha et al., 2021; Wang et al., 2021). In modern farms, the cellulose content is kept low and the starch content is kept high in order to achieve and maintain high milk or meat production. In our country, barley and wheat are used as starch sources in rations, and maize has also started to take an important place. However, it

is known that due to the chemical properties of the starches they contain, care must be taken when using the otherwise they may cause serious metabolic problems such as acidosis in animal health. Carbohydrates are important for the health, energy and milk yield of ruminants in general and starch in particular (Hall, 2006a; Biliaderis, 2009).

1. Importance of carbohydrates in ruminant diets

The energy required by the animal's body is released when ingested nutrients are converted to carbon dioxide (CO₂) and water (H₂O) by burning oxygen in the body. Energy is obtained as a result of the metabolism of carbohydrates, fats, and proteins in the body. Among these carbohydrates, formaldehyde is produced from water and CO₂ by

photosynthesis with the action of sunlight and chlorophyll in green plants. Formaldehyde is converted to carbohydrates, which make up about 75% of plants (Baldwin and Connor, 2017). The carbohydrates found in plants are polysaccharides, cellulose, hemicellulose, pectins, fructans, and starches (Saha et al., 2021).

Although carbohydrates are present at the level of 1-1.5% in the animal body, they have an important place both as a source of energy in tissues and as an economic source of energy (Ergün et al., 2020).

In ruminants, protozoa and bacteria in the rumen microflora break down carbohydrates in an anaerobic environment to produce glucose. As a result of glucose degradation, CO₂, methane (CH₄), H₂O and volatile fatty acids (VFAs) are released (Saha et al., 2021). Volatile fatty acid, consisting of acetic acid, propionic acid, and butyric acid, each carry 2, 3, 4 carbon (C) atoms. In addition to providing approximately 70% of the energy requirements of ruminants, these VFAs also contribute in rumen maturation and digestion of carbohydrates such as cellulose and hemicellulose. Daily 2-4 kg of VFA are synthesized in a cattle rumen (Ergün et al., 2020).

2. Carbohydrate Types and Metabolism

Carbohydrates represent approximately 70% and above of the dry matter content of ruminant diets. These organic substances are biochemically classified into 4 types according to the number of simple sugars (monosaccharides) they contain: monosaccharides, disaccharides, oligosaccharides and polysaccharides. They are also classified as structural (cellulose, hemicellulose, lignin, beta-glucans, pectins), non-structural (starch, fructans, organic acids, mono-, di- and oligosaccharides) and non-starchy (cellulose, hemicellulose, lignin, fructans, beta-glucans, pectics). However, in 2001, the National Research Council (NRC) divided dietary carbohydrate sources into two categories: neutral detergent fiber (NDF) and non-fiber carbohydrates (NFC). Together, these two carbohydrates provide 70% or more of the dry matter and most of the energy in the diet. NDF consists of cellulose, lignin, and hemicelluloses, while NFC includes sugars (glucose, fructose, sucrose, lactose), starch, fructans, pectins, beta-glucans, galactans, and other carbohydrates (NRC, 2001; Hall, 2002; Hall, 2007a;) (Figure 1).

2.1. Non-Fiber carbohydrates (NFC)

Carbohydrates in this category include organic acids, sugars (monosaccharides and some

oligosaccharides), starch, and neutral detergent soluble fiber (NDSF) (Figure 1) (Hall, 2007a).

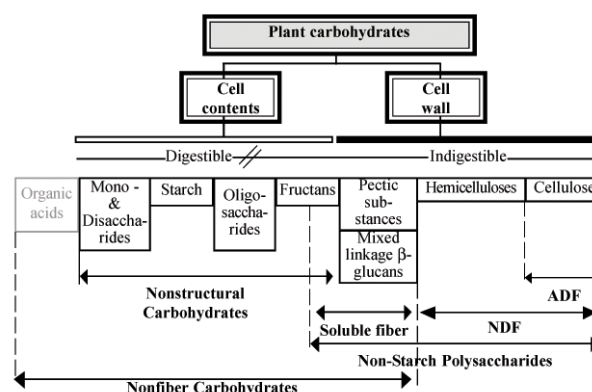


Figure 1. Carbohydrate components in plants (Hall 2007b).

2.1.1. Organic acids

These include fermentation acids found in silage (acetate, propionate, butyrate, lactate) and plant organic acids found in fresh forage and hay (malate, citrate, quinate, etc.). They are not carbohydrates, but are included in this group because they are included in the NFC calculations (Hall, 2007a).

2.1.2. Sugars (monosaccharides and disaccharides)

This includes both simple sugars (glucose, fructose, etc.) and disaccharides (sucrose, lactose). In plants, the main sugars are glucose, fructose, and sucrose. Lactose is found only in milk products. Sugars can form lactic acid as a result of fermentation, as well as butyrate more than other non-fibre carbohydrates (NFCs) and propionate near the starch level (Bhandari et al., 2023). Some sugars are also converted to microbial glycogen in the rumen (Weinert-Nelson et al., 2023).

2.1.3. Starch

Starch is composed of alpha-linked glucose chains stored by plants in crystalline granules. Starch digestion occurs in a wide range of species, from microorganisms to animals. However, there are large variations in the rate of fermentation or digestion depending on the processing, storage method or plant source of the digested starch. The finer the particle size of the forage, the faster the fermentation (Hall and Zanton, 2022). Smaller grains such as wheat, barley, and oats tend to ferment faster than coarser grains such as corn or sorghum (Slafer and Savin, 2023). Starch fermentation rates may increase as the starch content of the diet increases (Oba and Allen, 2003).

2.1.4. Soluble fibers

These include pectins, beta glucans, fructans and other non-starch polysaccharides not found in NDF. These carbohydrates cannot be digested by mammalian digestive systems, but can be digested by microbes. Soluble fibers tend to ferment very rapidly. Pectins, the major type of soluble fiber found in legume feeds, citrus pulp, and sugar beet pulp, can produce more acetate than other NFC (Bhandari et al., 2023). With the exception of fructans, little or no lactate is produced as a result of soluble fiber fermentation. Fermentation is also inhibited when the rumen pH is more acidic. Common sources of soluble fiber include legume forages, citrus pulp, beet pulp, soybeans, and soybean meal (Ma et al., 2021).

2.2. NDF

NDF is a carbohydrate source that cannot be digested by digestive enzymes but can be digested by rumen microorganisms and is essential for maintaining rumination and rumen function. NDF is composed of hemicellulose, cellulose and lignin. The cellulose and lignin portion is called acid detergent fiber (ADF). Volatile fatty acid is formed by the breakdown of cellulose. In addition, cellulose increases salivation and helps maintain optimal rumen pH. Hemicellulose also plays an important role in the development of rumen papillae and the formation of VFA. Lignin, on the other hand, is a substance that is not a true carbohydrate and is nearly indigestible, and its excess in feedstuffs reduces feed utilization. Dietary NDF is an important component of rumen pH, milk fat content, and dry matter intake in cattle (Hall, 2002; Hall, 2007a).

2.3. Carbohydrate metabolism in ruminants

Cellulose, hemicellulose, starch, sugars, pentosans, fructans, and pectins in forages are carbohydrate sources for ruminants. Cellulolytic bacteria use their enzymes to break down cellulose into glucose, cellobiose and short-chain oligosaccharides. Rumen microorganisms have enzymes that break down pentosan and hemicelluloses to xylose, arabinose, mannose and galactose. Starch, fructose and sugars ferment rapidly. Pectins are degraded to methanol and pectic acid by microbial enzymes. Lignin cannot be digested by rumen microorganisms (Dijkstra et al., 2005; Grev et al., 2017).

The end products of the main fermentation of carbohydrates in ruminants are VFA, CO₂ and CH₄. Acetic acid is produced from pyruvic acid,

propionic acid is mostly produced by the reduction of lactic acid, and butyric acid is produced by the condensation of acetic acid and acetyl-CoA. Of the gases produced in the rumen, 70% is CO₂ and 30% is methane gas. Most of the methane gas is excreted through the rumen (Einsmenger et al., 1990; Dijkstra et al., 2005).

Acetic acid and butyric acid from VFA are converted to acetyl-CoA in the liver. Acetyl-CoA is involved in the formation of milk fat and other fats in the body. Acetic acid and butyric acid make up half of milk fat, and triglycerides absorbed from the intestines make up the other half. Propionic acid is converted in the liver to oxalacetic acid and glucose. Glucose is used as a source for the synthesis of lactose from mammary tissue. Approximately 2 kg of lactose must be produced in the liver for 20 kg of milk per day. Therefore, the amount of glucose produced in the liver plays an important role in the amount of milk produced per day. In addition, in the rumen of cattle, propionic acid is converted to propionate, which is the main substance for gluconeogenesis. Approximately 30-70% of the energy source glucose is provided by propionate (Hall, 2006a; Hall, 2007a).

The ratio of roughage to concentrates in ruminant diets significantly affects the ratio of VFA between them. In ruminants fed roughage, VFA is composed of 60-70% acetic acid, 15-20% propionic acid, and 10-15% butyric acid. As the amount of degradable carbohydrates in the diet increases, the amount of acetic acid and propionic acid reaches 40%, so the amount of propionic acid increases and the amount of acetic acid decreases. While the decrease in the amount of acetic acid causes a decrease in the fat content of the milk, the increase in propionic acid reduces the energy loss during rumen fermentation in fattening cattle. Therefore, an increase in propionic acid is desirable in beef cattle, while a decrease in acetic acid is undesirable in dairy cattle. In addition, when roughage is added to the ration in finely ground form, the amount of acetic acid decreases, resulting in a decrease in the fat content of the milk. However, in high yielding cows, it is not possible to meet the nutritional needs of the animals with large amounts of roughage, so it is recommended that the ration be adjusted so that the roughage content is not less than 40% (Hall, 2006a; Hall, 2007a).

3. Starch Types and Their Digestion Mechanism in Rumen

3.1. Importance of starch and starch digestion

Starch is stored in plant organs such as roots, seeds, and fruits and makes up about 80% of these organs. It is found in smaller amounts in the stems and leaves of plants. Starch particles consist of 20-30% amylose and 70-80% amylopectin. The amount of amylose increases as the plant matures. In amylose, the glucose units are linked by α -1,4 glycosidic linkages and in amylopectin, they are linked by α -1,4 linkages to the glucoses in the backbone chain and by α -1,6 linkages at the branching points and are the most abundant part of starch. From Perez et al. (2009) chemical structure of amylose and amylopectin in starch has shown in Figure 2. Compounds with α -1,4 bonds are degraded to maltose, those with α -1,6 bonds to isomaltose, and the end product is usually glucose. Since all α -1,4 bonds in plants can be degraded by the enzyme α -amylase, all amylose can be degraded, but only 60% of amylopectin can be degraded (Tester et al., 2004; Perez et al., 2009; Wang et al., 2024).

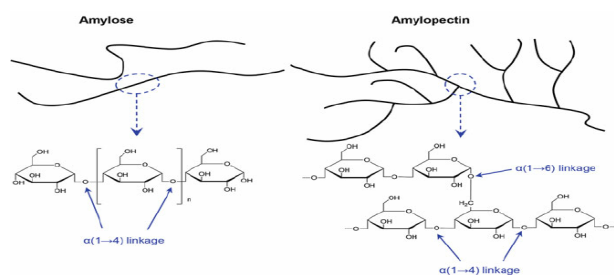


Figure 2. Chemical structure of amylose and amylopectin in starch (Perez et al., 2009).

Starch is deposited in granules within the endosperm. Depending on the grain type, granules vary widely in shape (round, lenticular, polygonal), size distribution (unimodal or bimodal), and whether they are single (simple) or clusters of granules (compound) (Tester et al., 2004). Starch granules are formed by the accumulation of growth rings composed of alternating semi-crystalline and amorphous sheets. These rings extend from the center of the granule (hilum) to the surface of the granule, similar to the layers of an onion. The amorphous regions in starch granules are thought to represent the branching points of amylopectin, while the crystalline region is thought to represent the more compact double helix structure of amylopectin. The semicrystalline regions are more abundant in amylopectin and are resistant to enzymatic

degradation because they are resistant to water ingress. In contrast, amylose has more amorphous layers and is therefore more susceptible to enzymatic degradation and water ingress. Starches are defined as waxy when the ratio of amylose to amylopectin is <15%, normal when the amylose content is 16-35% of the granule, and high amylose when the amylose content exceeds 36% of the granule (Svihus et al. 2005; Perez et al., 2009).

Starch digestion varies with grain type, grain processing methods, preservation methods, diet composition, and animal species. Starch from barley, wheat and oats is more rapidly digested than starch from corn, while starch from sorghum is the most resistant to digestion. These differences are due to the structure of the endosperm rather than the amylose and amylopectin in the starch. Mealy and glassy endosperm are both resistant to enzymes and digestion, but for different reasons: mealy endosperm contains soluble proteins, while glassy endosperm contains insoluble proteins called prolamins (Hoffman and Shaver, 2010; Trotta et al., 2021). Starch sources vary according to the amount and proportion of germ and vitreous endosperm, and there are significant differences between vitreous endosperm in some cereal species. For example, vitreous endosperm in dried corn ranges from 0% to 75%, and corn with more vitreous endosperm is more resistant to grinding and digestion than corn with waxier endosperm. Vitreous content increases as the crop dries in the field, so the difference between field-dried hybrid corn is large. Because corn silage is harvested earlier than high moisture corn, the kernels will be moister and have less vitreous endosperm. However, for similar products, there can be a 30-40% difference in dry matter when harvesting corn silage with high vitreous endosperm and a 60-75% difference in dry matter when harvesting high moisture corn (Hoffman and Shaver, 2010; Fernandes et al., 2021).

When grain is ensiled, starch fermentation in the rumen is affected by both the moisture concentration in the grain and the storage time. This is because ensiling dissolves endosperm proteins over time. This risk is greater in high moisture grains such as corn silage. Therefore, corn silage should be stored in the silo for several months before feeding (Allen, 1998; Allen et al., 2003).

Cattle can digest about 90% of starch, depending on the rate at which it passes through the rumen and the amount in the ration. Starch is a

carbohydrate that can ferment quickly without stimulating too much rumen movement and without remaining in the rumen for a long time. For these reasons, if the ration contains high amounts of easily digestible carbohydrates such as starch and molasses, cellulose digestion in the rumen is reduced, and therefore the amount of milk fat is reduced. In addition, lactic acid formation increases along with propionic acid in ruminants fed high starch diets, leading to problems such as acidosis and laminitis. If starch reaches the large intestine without being fermented in the rumen, it is fermented there and can cause diarrhea because the VFAs stimulate the intestinal wall (Du et al., 2021; Palmonari et al., 2021).

The outer surface of cereal grains consists of a thick, multilayered pericarp that protects the inner layers of the grain and endosperm from microbial attack. In addition to the pericarp, which accounts for 3% to 8% of the total kernel weight, barley and oats have a fibrous stem, or tegument, which accounts for up to 25% of the total kernel weight (Evers et al., 1999). Chemically, about 90% of the pericarp and tegument are fibers, and their digestibility is about 40% due to their lignified structure (Van Barneveld, 1999). The ruminal digestibility of the hull and pericarp is further reduced by the low ruminal pH (<6.2) associated with high grain diets.

The endosperm consists of two distinct tissues, the starchy endosperm and the aleurone. The aleurone consists of 1 to 3 layers, depending on the type and genetics of the grain (Narwal et al., 2020). The endosperm cell walls of wheat and maize consist mainly of arabinoxidants, while those of oats and barley consist mainly of β -glucans. Endosperm cell walls are largely devoid of lignin and, given the high arabinoxylanase and β -glucanase activity of rumen microorganisms, are not a significant barrier to starch digestion (McAllister et al., 2001).

Endosperm cell walls surround starch granules embedded in a protein matrix. The endosperm has two distinct regions in both maize and sorghum grain. In the vitreous endosperm region, starch granules are densely packed within a protein matrix, whereas in the endosperm region, starch granules are loosely associated with the protein matrix. In maize, the starch granules are very closely associated with the protein. In barley and wheat, the protein matrix is loosely associated with starch granules throughout the endosperm (Ergün et al., 2020).

3.2. Effects on rumen digestion mechanism

Rumen bacteria are responsible for the majority of starch digestion in the rumen. *Streptococcus bovis*, *Ruminobacter amylophilus*, *Prevotella ruminicola*, *Butyrivibrio fibrisolvens*, *Succinimonas amylolytica* and *Selenomonas ruminantium* are the major starch digesters (Trotta et al., 2021; Wang et al., 2022). Although TIC enzymes have a significant effect on the ability to digest starch (Zhang et al., 2006), this change in digestion is less pronounced when isolated starch granules are subjected to digestion by a mixed rumen microbial population (Fondevila and Dehority 2001; Iommelli et al., 2022).

Microbial digestion of wheat and barley starch granules spreads inward from the microbial attachment point on the surface of the granule. In contrast, corn starch granules are digested from the inside out by tunneling amylolytic bacteria. As a result, when digestion is complete, the interior of the granule is empty, leaving only the outer surface layer. In addition, using very high concentrations of grain in the diet can cause a decrease in the diversity and number of protozoa, which can lower ruminal pH and increase the risk of acidosis in cattle (Faichney et al., 1997).

The structure of the protein matrix surrounding the starch granules of cereals commonly used in cattle diets has a much greater effect on the rate and amount of starch digestion than the properties of the starch itself (Iommelli et al., 2022). In hard maize, rumen bacteria preferentially colonize around starch granules within the glassy protein matrix. As digestion progresses, they hydrolyze the starch granules, passing them into the endosperm cells but leaving the protein matrix intact. As a result, with prolonged exposure to rumen bacteria, all starch granules are digested, leaving only the surrounding protein matrix and endosperm cell wall (Fernandes et al., 2021). Many of the differences in digestion between more slowly fermented grains (e.g. maize, sorghum) and more rapidly fermented grains (e.g. wheat, barley) may depend on the properties of the protein matrix between these grains (Khan et al., 2015).

3.3. Starch' importance in ruminant diets

It may seem logical to increase the energy content of the ration by feeding more cereals and less roughage in order to increase milk production and thus meet the nutritional needs of cows. However, instead of improving performance, this situation leads to low milk fat, acidosis, decreased milk production, digestive disorders, laminitis and

situations that can lead to death. The starch in wheat ferments faster than the starch in corn. Therefore, when fed in excess, it causes digestive upset, decreased rumen pH, acidosis, laminitis, decreased feed digestibility, diarrhea, and decreased feed intake (Hall, 2006b).

4. Applications to Modify Starch Structure

Two basic processes are used to increase the digestibility of starch in feed ingredients in the ration.

4.1. Gelatinization

Permanent modification of the granular structure by breaking hydrogen bonds. During gelatinization, starch absorbs water, expands, breaks hydrogen bonds, releases some amylose, and thus becomes more soluble and subject to more enzyme activity (Pan et al., 2021). In water, most starches gelatinize at temperatures above 80°C. The gelatinization temperature is higher for small starch granules. Grains rich in amylose are more resistant to gelatinization than grains with normal and high amylopectin content (Svihus et al., 2005).

4.2. Retrogradation

It is the reversible conversion of the dissolved, dispersed or amorphous form of starch into the crystalline or insoluble form that limits starch digestibility. Retrogradation is a desirable process in certain applications, including the production of breakfast cereals, parboiled rice, dehydrated mashed potatoes, and Chinese rice vermicelli, because it modifies their structural, mechanical, and sensory properties. The retrogradation of starch is desirable for nutritional reasons because it slows down the enzymatic digestion of starch and moderates the release of glucose into the blood stream. In Western countries, starch contributes to over 50% of the average caloric intake, and up to 90% in the developing world. As one of the major carbohydrate components in many foods, the digestion of starch has significant health implications. As discussed later, the digestibility of starch is of nutritional interest in relation to the rising incidence of obesity and diet-related diseases (Wang et al., 2015). In short, it is the recrystallization of starch. Amylose is the main component that facilitates retrogradation (Biliaderis, 2009).

CONCLUSION

As a result, determining the starch content, fractions and degradation rates in dense feed sources used in ruminant diets is of great importance in terms of healthy animal growth, productive metabolism and overall implementation of an optimal nutritional strategy. The digestive systems of ruminants allow them to obtain energy-rich substances by effectively breaking down starch, particularly through the microorganisms in their stomachs. This process plays a vital role in ensuring that animals meet their energy requirements and have a healthy growth process. In addition, determination of starch fractions in concentrated feed sources provides guidance for optimizing the nutrient content of rations and meeting the specific nutritional needs of animals. These analyses ensure that animals receive the nutrients they need in the most effective way, thereby improving their overall health. In-depth knowledge of starch content, fractions and degradation rates in ruminant diets is critical from a sustainable agriculture and animal welfare perspective. As a result, this analytical information plays a key role in the development of ruminant feeding strategies, a better understanding of the nutritional needs of animals, and improving the productivity of the livestock industry in general.

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