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Starch in ruminant diets: a review^a

Almidones en la alimentación de rumiantes: revisión de literatura

Amido na alimentação dos ruminantes: revisão de literatura

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Summary

Background: starch is an important energy source for ruminants nutrition. This carbohydrate is often used to improve rumen fermentation, optimizing digestion of structural carbohydrates and increasing protein flow to the small intestine. Microbial and digestive enzymes are involved in starch digestion, generating products that can positively or negatively affect animal performance and health, depending on the starch contents of the diet. **Objective:** to describe the basic characteristics of starches, the factors affecting its nutritional availability, and its effects in ruminants. **Conclusion:** a number of factors affect starch digestibility, including granule size, amylose/amylopectin ratio, proportion of farinaceous and vitreous endosperm, presence of starch-lipid and starch-protein complexes, and physical-chemical processing of the feed. Ingestion of large amounts of starch can trigger ruminal acidosis. However, its rational use in the diet has positive effects on methane emissions, and in milk yield and composition.

Keywords: acidosis, amylopectin, amylose, digestibility, lactation, methanogenesis.

Resumen

Antecedentes: el almidón es un importante recurso energético para la alimentación de rumiantes. Este carbohidrato es frecuentemente empleado para el mejoramiento de los parámetros de fermentación ruminal, lo que optimiza el aprovechamiento de los carbohidratos estructurales e incrementa el flujo de proteína al intestino delgado. En su digestión participan enzimas microbianas y digestivas, las cuales generan diferentes

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productos que impactan positiva o negativamente el desempeño productivo y la salud del animal, dependiendo del nivel de almidón en la dieta. **Objetivo:** describir las características básicas de los almidones, los factores que afectan su disponibilidad nutricional y los efectos de su utilización en la alimentación de los rumiantes. **Conclusión:** existe un sinnúmero de factores que afectan la digestibilidad del almidón, entre ellos, el tamaño del gránulo, la relación amilosa/amilopéctina, la proporción de endospermo farináceo y vítreo, la presencia de complejos con lípidos y proteínas, y su procesamiento físico-químico. La ingestión de grandes cantidades de almidón puede desencadenar acidosis ruminal; no obstante, su empleo racional en la dieta de los rumiantes tiene efectos positivos sobre la emisión de metano, y la producción y calidad de la leche.

Palabras clave: acidosis, amilopectina, amilosa, digestibilidad, lactancia, metanogénesis.

Resumo

Antecedentes: o amido é uma importante fonte de energia na alimentação dos ruminantes. Este carboidrato é geralmente utilizado para melhorar os parâmetros de fermentação no rúmen, o que otimiza a utilização dos carboidratos estruturais e aumenta o fluxo de proteína para o intestino delgado do animal. Na sua digestão estão envolvidas enzimas digestivas e microbianas, as quais geram diferentes produtos que impactam positiva ou negativamente o desempenho produtivo e a saúde do animal dependendo do nível de amido na dieta. **Objetivo:** descrever as características básicas do amido, factores que afectam a sua disponibilidade nutricional e os efeitos da sua utilização na alimentação de ruminantes. **Conclusão:** diversos fatores afetam a digestibilidade do amido, incluindo o tamanho do grânulo, a relação amilose/amilopectina, a proporção de endosperma farináceo e vítreo, a formação de complexos com lipídeos e proteínas e o seu processamento físico-químico. A ingestão de grandes quantidades de amido pode provocar acidose ruminal, no entanto, a sua utilização racional na alimentação de ruminantes tem efeitos positivos sobre as emissões de metano, a produção de leite e a sua qualidade composicional.

Palavras chave: acidose, amilopectina, amilose, digestibilidade, lactação, metanogênese.

Introduction

Starch-the largest reservoir of plant polysaccharidesplays an important role in germination and growth, and its synthesis is second only to that of cellulose. Starch is the main energy component used in ruminant feeds due to its availability (Ortega and Mendoza, 2003). It is often included in the diet to improve ruminal fermentation, allowing for a better use of structural carbohydrates and to increase protein flow to the small intestine (Huntington et al., 2006). Starch sources are expensive, so they must be used wisely to be cost-effective. It is important to understand the structural characteristics of starch, its ruminal and post-ruminal digestion and the factors affecting its digestibility in order to improve performance and profit of livestock systems. This review describes starch, the factors affecting its nutritional availability, and its effects in ruminant feeding and nutrition.

Description of starch

Composition

Starches are mainly α -glucans composed of two types of molecules: amylose and amylopectin

(Santana and Meireles, 2014; Table 1). Amylose is a linear D-glucose polymer containing about 99% α -1,4 links (Parker and Ring, 2001). Amylopectin, which has 95% α -1,4 links and 5% α -1,6 links (Stevnebo *et al.*, 2006), is the most abundant component of starches (Figure 1). On the other hand, amylose content in starch usually fluctuates from 200 to 300 g/Kg. Some starch-rich feeds such as waxy cereals usually contain negligible amounts of amylose, while high-amylose sources may contain up to 700 g amylose/Kg. Cereals such as wheat, maize, barley, and rice can contain a waxy gene derived from natural mutations of genes encoding granule bound starch synthase, which is required for amylose synthesis (Svihus *et al.*, 2005).

Structure

Starch granules are formed by concentrically growing layers alternating semi-crystalline and amorphous films (Figure 1). The semi-crystalline region is more abundant in amylopectin and is more impervious to enzymatic attack because of its resistance to entry of water. The amorphous region is rich in amylose and has lower density than the crystalline area, which facilitates water flow and enzyme attack; however, it is abundant in hydrogen bonds (Perez *et al.*, 2009).

Table 1. Properties of starch components.

Characteristic	Component	
	Amylose	Amylopectin
General structure	Linear	Branched
Branch sites	None ^a	1 per 20 to 25 glucose units
Polymerization degree ^b	~1.000	~10.000-100.000
Molecular weight	1 x 10 ⁵ -1 x 10 ⁶ g/mol	1 x 10 ⁷ -1 x 10 ⁹ g/mol
Stability in solution	Low	High

^a There is a type of branched amylose with 1 or 2 α -1,6 links per molecule.

^b Number of glucose residues per molecule.

Adapted from Parker and Ring, 2001.

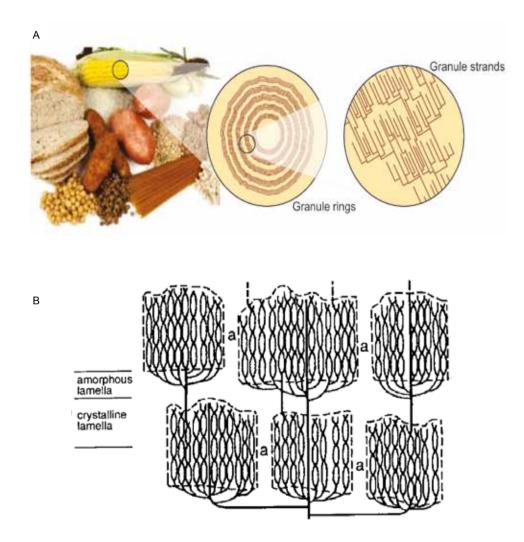


Figure 1. (A) Structure of starch granules, represented by organized laminar forms. Amorphous rings (composed mainly of amylose) separate layers in the semi-crystalline regions (composed primarily of amylopectin). Modified from Perez *et al.*, 2009. (B) Amylopectin structure according with the cluster model by Myers *et al.*, 2000. Glucan chains are depicted by solid lines while intersections between them indicate branch linkages. The dotted lines show the limit of amylopectin side chain clusters with unbranched chains associated in tightly packed double helices. a) depicts the amorphous areas separating amylopectin side chain clusters.

Structural alterations

Gelatinization. It is the permanent alteration of the granule structure by breaking its hydrogen bonds. Starch absorbs water during gelatinization, the expansion breaks the hydrogen bonds releasing some of the amylose by leaching, thus birefringence is reduced and starch becomes more soluble and exposed to enzyme activity (Rooney and Pflugfelder, 1986). In excess of water, most starches gelatinise at temperatures higher than 80 °C. The gelatinisation temperature is higher for small starch granules. Amylose-rich cereals are more resistant to gelatinisation than cereals with normal and high amylopectin levels (Svihus et al., 2005). Table 2 shows gelatinization values for several foods and processing methods. The degree of gelatinization is higher for extruded vs. pelleted food since the temperature used in the process is higher (up to 250 °C vs. 60-95 °C; Caballero, 2010).

Table 2. Starch gelatinization under several processing methodsin various feeds.

Food	Gelatinization (%) ¹	Processing
Corn	17.06	Unprocessed
Sorghum	12.47	Unprocessed
Yucca	7.59	Unprocessed
Concentrate 1	32.49	Pelleting
Concentrate 2	32.55	Pelleting
Concentrate 3	31.92	Pelleting
Corn	79. 3	Extruded

¹Assessed by an enzymatic method (Medel et al., 1999).

Retrogradation. It is defined as the reversible return of a solubilized, dispersed or amorphous state to a crystalline or insoluble form, which limits starch digestibility. Amylose is the main component that facilitates retrogradation (Biliaderis, 2009).

Sources of starch

Cereal grains and roots

Cereal grains are a major source of starch used in animal feeds. Cereals are composed of pericarp, endosperm and germ (Figure 2). The pericarp comprises 3 to 8% of the kernel weight, although it can be up to 25% in oats (Evers *et al.*, 1999). It is mostly composed (90%) of highly lignified fiber and the starch content is less than 10% (Li *et al.*, 2007), thus pericarp digestibility does not exceed 40% (Van Barneveld, 1999).

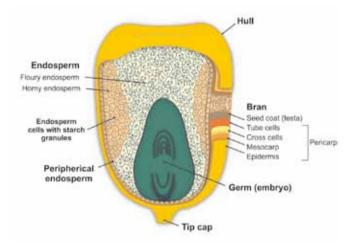


Figure 2. Corn kernel composition. Adapted from Eckhoff and Watson (2009).

The endosperm represents between 60 and 90% of the grain. It is the morphological structure containing the starch. It also contains proteins, phospholipids and ash, but little neutral detergent fiber (NDF) and phosphorus (P; Eckhoff and Watson, 2009). The endosperm layers, from the outside in, are aleurone, peripheral endosperm, horny (or vitreous) and floury. Both the peripheral and the horny endosperm have starch granules surrounded by a matrix abundant in hydrophobic proteins called prolamines and non-starch polysaccharides (PNAs; β-glucans, arabinoxylans, and pectins), which are relatively impermeable to water and enzymatic activity (Zeoula and Caldas Neto, 2001; Giuberti et al., 2014). Grains exhibiting high proportion of peripheral and horny endosperm are called vitreous or horny, while those abundant in floury endosperm are called opaque or soft (Zeoula and Caldas Neto, 2001).

Non-conventional sources

Starch represents an important fraction in many crops. Most cereals (i.e. corn, wheat, rice, oat, and barley) contain between 60 and 80% starch, while legumes (chickpea, bean, pea) contain from 25 to

50%, tubers (potato, cassava, cocoyam, arrowroot) from 60 to 90%, and some green fruit (banana, mango) contain as much as 70% (Santana and Meireles, 2014). As in cereals, the largest proportion of starch corresponds to amylopectin and the smallest to amylose (17-30%; Hu *et al.*, 2010). Amylose represents 14 to 19% of starch in cassava, between 2 and 22% in potato, and approximately 37% in plantain (Knowles *et al.*, 2012). Amylopectin in starch from potato is less branched compared to cereals (Alvani *et al.*, 2011). It is also highly expandable (Vasanthan and Bhatty, 1996) and gelatinizes at relatively low temperature (between 64.4 and 69.9 °C) compared to other starches (Hernandez-Medina *et al.*, 2008).

Table 3 shows amylose and amylopectin concentration in different starchy foods and concentrates fed to dairy cattle. Differences in amylose/amylopectin ratio affect the rate of ruminal or intestinal digestion. Digestion rate of amylopectin is usually higher than that of amylose (Knowles *et al.*, 2012).

Table 3. Amylose and amylopectin content in various feeds.

Source	Amylose (%)	Amylopectin (%)
Corn	29.24	70.76
Sorghum	29.55	70.45
Yucca	19.84	80.16
Concentrate 1 (C1)*	21.17	78.83
Concentrate 2 (C2)	22.22	77.78
Concentrate 3 (C3)	20.25	79.75
Concentrate 4 (C4)	24.89	75.10

*Isoenergetic and isoproteic concentrates (C) for dairy cattle formulated with four carbohydrate sources: corn (C1), sorghum (C2), yucca (C3), citrus pulp (C4). Assessed using the method described by Gibson *et al.* (1997).

Once it reaches the rumen, starch is degraded mainly by amylolytic bacteria and by fungi and protozoa to a lesser extent (Huntington, 1997). The α -1-4 and α -1-6 endo and exoamylases produced by rumen microorganisms have the ability to hydrolyze amylose and amylopectin glycosidic linkages, releasing different oligosaccharides (Table 4).

The post-ruminal process of starch degradation begins with pancreatic α -amylase secretion, which hydrolyzes amylose and amylopectin into dextrins and linear oligosaccharides with two to three glucose units. The process is completed by the action of oligosaccharidases (maltase and isomaltase) secreted in the intestinal membrane (Ortega and Mendoza, 2003).

In ruminants, the site of starch digestion affects the substrates absorbed. Ruminal digestion generates volatile fatty acids (VFA) for absorption and provides energy for microbial protein synthesis (Huhtanen and Sveinbjörnsson, 2006). Decreased rumen digestibility of starch is desirable to prevent from acidosis and to increase the supply of glycogenic substrates (Svihus et al., 2005). Starch digestion in the small intestine implies greater energetic efficiency compared with ruminal digestion due to reduced methane production and fermentation heat losses and higher efficiency of metabolisable energy utilisation (Huhtanen and Sveinbjörnsson, 2006). Nevertheless, the increased energy efficiency from higher starch digestion in the small intestine is offset by the increase in hindgut fermentation, because only VFA are absorbed from the hindgut whereas microbial matter is excreted in feces. A decrease in ruminal starch digestion is not associated with an increase in its small intestinal

Enzyme	Link	End product
Phosphorylase	α -1-4 glycosyl	Glucose 1 phosphate
Alpha-amylase	α -1-4 glycosyl	Linear and branched oligosaccharides
Beta-amylase	α -1-4 glycosyl	Maltose and limit dextrins
Amyloglucosidase	α -1-4 glycosyl and α -1-6 glycosyl	Glucose
Isoamylase	α -1-6 glycosyl	Lineal chains of α -1-4 glucans
Pullulanase	α -1-6 glycosyl	Lineal chains of α -1-4 glucans

Table 4. Enzymes involved in starch hydrolysis.

Adapted from Tester et al., 2004.

digestion, but it is associated with higher hindgut and lower total tract digestibility (Larsen *et al.*, 2009).

For this reason, rumen is considered the primary site of starch digestion. Ruminal digestion usually accounts for 75 to 80% of the intake, and about 35 to 60% of the starch entering the small intestine is degraded. About 35 to 50% of the starch that escapes digestion in the small intestine is degraded in the hindgut (Harson, 2009). According to a meta-analysis by Moharrery *et al.* (2014), ruminal starch digestibility varies greatly (from 224 to 942 g/Kg). The authors also noted that starch consumption adversely affected ruminal starch digestibility, obtaining a negative slope of 1.4% per Kg increase in daily starch intake. Table 5 presents the content and ruminal digestibility of various starch sources used in livestock.

Table 5. Starch content and ruminal digestibility of several starch sources commonly used as feed supplements in dairy cattle.

Grain	Starch (%)	Rumen digestibility (%) ^a
Corn ^{1,2}	76.0	72 - 89.9
Sorghum ^{1,2}	71.3	60 - 78.4
Wheat ^{1,2}	70.3	88.3 - 88.1
Barley ^{1,2}	64.3	80.7 - 84.6
Oats ^{1,2}	58.1	92.7 - 94.0
Yucca ³	80.0	91.0

^a Variability is explained by grain treatment (grinding, rolling, flaking).

¹Herrera-Saldana et al., 1990. ²Huntington, 1997. ³Vearsilp and Mikled, 2001.

Factors affecting starch digestibility

Granule size

This is a limiting factor in starch digestion because the relationship between starch volume and surface area, and thus substrate-enzyme contact, decreases as granule size increases (Svilus *et al.*, 2005). Cereals with small granules, such as oats and rice, are more digestible than corn, wheat and potato, which have long granules (Bednar *et al.*, 2001; Svilus *et al.*, 2005).

Amylose/amylopectin ratio

Several studies have shown that amylose/ amylopectin ratio is negatively correlated with starch digestion (Bednar *et al.*, 2001). Amylose is inserted into amylopectin molecules increasing the amount of hydrogen bonds within the starch molecule, which negatively impacts the ability of expansion and enzyme activity (Caldas-Neto *et al.*, 2000). Likewise, starch granules with high amylose content are more prone to retrogradation (Svilus *et al.*, 2005).

Floury versus vitreous endosperm

Several researchers (Correa *et al.*, 2002; Ngonyamo-Majee *et al.*, 2008) have reported an inverse relationship between starch digestibility and vitreousness. Allen *et al.* (2008), studied ruminal and duodenal-fistulated cows using corn with vitreous endosperm content varying between 25 and 66%. They found that feeding corn with 66% of vitreous endosperm reduced ruminal digestion in 19.1% and overall digestion in 7.1%.

Starch-lipid complexes

Quantitatively, lipids are the major non-starch compounds in starch granules and can be found as free fatty acids (mostly palmitic and linoleic acid) and lysophospholipids (Svihus *et al.*, 2005). In cereal grains, a portion of amylose has insoluble starch-lipid complexes, which form helical structures that provide greater adhesion between molecules, dininish starch swelling (Vasanthan and Bhatty, 1996), decrease their solubility (Rooney and Pflugfelder, 1986) and reduce the rate of enzymatic digestion (Crowe *et al.*, 2000). Cassava and potato starch contain a smaller percentage of lipids compared with cereal starch (Zeoula and Caldas Neto, 2001; Alvani *et al.*, 2011).

Starch-protein complexes

The proteinaceous matrix surrounding starch granules affects starch digestibility. Digestibility is negatively associated with the presence of prolamins. Prolamins are storage proteins that receive a different name for each cereal, namely zein (corn), kafirins (sorghum), gliadin (wheat), hordeins (barley), secalins (rice), and avenines (oats). Usually, wheat, oats, rice and barley have fewer prolamins than corn and sorghum (Momany *et al.*, 2006; Giuberti *et al.*, 2014).

Zeins account for 50 to 60% of the protein in the whole grain and are located at the periphery of the cell. Floury endosperm is low in zein compared with vitreous endosperm (Giuberti *et al.*, 2014). Zeins are not soluble in the rumen environment (Lawton, 2002). Starch digestion requires that rumen bacteria degrade zeins first via proteolysis, before starting the amylolytic activity (Cotta, 1998).

Processing of cereal grains

Grain processing using temperature, humidity and pressure facilitate binding of bacteria to starch granules, increasing its digestibility (Huntington *et al.*, 2006). Common processing includes grinding, pelleting, dry rolling, steam rolling (addition of water before rolling), and steam flaking. All these processes aim to break grain barriers such as the pericarp and the protein-starch matrix, allowing access of microorganisms to starch granules. These processes also reduce the particle size, and increase surface area and microbial colonization (Giuberti *et al.*, 2014). The response to processing varies with different grains, with sorghum > corn > oats = barley > wheat (Huntington *et al.*, 2006).

Gelatinization of starch makes it more water-soluble and digestible. According to Huntington (1997), steam flaking of corn improves ruminal, post-ruminal and total tract digestibility compared with dry rolling (85 vs. 70%, 92 vs. 69%, and 99 vs. 90%, respectively). According to Sveinbjörnsson *et al.* (2007), heat treatment increases starch degradation during 8 h of *in vitro* incubation, as follows: 0.155 vs. 0.870 for pure potato starch, 0.491 vs. 0.815 for peas, 0.686 vs. 0.913 for barley, and 0.351 vs. 0.498 for maize.

Only a fraction of starch is gelatinazed during steam conditioning and pelleting of feeds (from 10 to 200 g starch/Kg). The expander processing, on the other hand, adds up to 80 g water/Kg while the diet reaches a high pressure and temperatures above $100 \,^{\circ}$ C, thus resulting in between 220 and 350 g starch/Kg gelatinized during this process. The extrusion adds even more water (up to 180 g water/Kg) and the diet is subjected to even higher temperatures (>110 $\,^{\circ}$ C) under high pressure, thus resulting in more complete gelatinisation and disintegration of starch granules (Svihus *et al.*, 2005). This was evidenced by Offner

et al. (2003), who reported 0.607, 0.663, 0.743, 0.746, 0.819, 0.830, and 0.867 effective degradabilities for untreated, cracked, ground, pelleted, expanded, steam flaked and extruded corn, respectively (passage rate 0.04 h⁻¹). Grain type also influences the results. Steam flaking of corn eliminated the adverse effects of vitreous endosperm and protein-starch matrix on digestibility in comparison with dry rolling. This was contrary to the results obtained for barley, a grain with a highly digestible protein-starch matrix, where no difference was observed between both treatments (Engstrom *et al.*, 1992).

Starch source

The highest effective degradability of starch in cereal grains was obtained for oats, wheat and barley, being lower for corn and sorghum. Corn and especially sorghum have a high proportion of peripheral and horny endosperm resulting in increased resistance to microbial activity (Rooney and Pflugfelder, 1986), unlike wheat and oats, which have higher proportion of floury endosperm. In addition, corn and sorghum have a denser protein matrix (Kotarski *et al.*, 1992). The *in vitro* experiment by Lanzas *et al.* (2007) measured fractional gas rates, as a measure of starch digestion (Huhtanen and Sveinbjörnsson, 2006), reporting 0.26, 0.24, 0.15, and 0.06 h⁻¹ rates for wheat, barley, corn and sorghum, respectively (p<0.001).

Cassava has higher effective degradability than corn and sorghum due to its lack of pericarp, protein matrix, horny and peripheral endosperm; as well as low proportion of lipids, lack of associations between starch and protein, less amylose, more amylopectin, less hydrogen bonding, and greater swelling when subjected to chemical processes. Cassava starch is composed exclusively of amylopectin in the crystalline region and amylose in the amorphous region, which prevents excessive formation of hydrogen bonds with amylopectin, allowing amylose to be readily leached. This is contrary to cereals, which have amylose in the crystalline region (Zeoula and Caldas Neto, 2001). Effective degradability of corn, sorghum and cassava, reported by Offner et al. (2003), was 0.597, 0.603 y 0.802, respectively (passage rate 0.06 h^{-1}).

Physiological restrictions of the small intestine

Starch digestibility in the small intestine is limited. As digesta flow increases, starch digestibility decreases (Huntington *et al.*, 2006). Factors that limit starch digestibility include controlled glucose absorption, deficient enzyme accessibility to starch granules, alterations in ruminal and intestinal pH, and lack of synchrony between starch flow through the intestine and amylase secretion (Owens *et al.*, 1986).

Starch digestion efficiency in the small intestine varies between sources. Tothi *et al.* (2003) reported higher digestibility for barley starch in the small intestine compared with cornstarch, resulting in higher small intestine absorption in terms of g/Kg starch ingested.

Starch and ruminal acidosis

Starch fermentation increases volatile fatty acids (VFA) and lactate production, which can reduce ruminal pH and kill cellulolytic microorganisms, leading to decreased fiber digestibility and dry matter (DM) intake. Additionally, it can cause metabolic disorders such as acute and sub acute ruminal acidosis, rumenitis, laminitis, liver abscesses and polyencephalomalacia (Plaizier *et al.*, 2009).

The risk of ruminal acidosis increases when starch digestion rate increases. This rate varies with grain type and processing and generally occurs in the following order: wheat (32% h) > oat > barley (29% h)> potato (5% h) > corn (2% h) and sorghum (Callison *et al.*, 2001; Mosavi *et al.*, 2012). Krause *et al.* (2002) reported lower ruminal pH in lactating cows fed high moisture corn vs. dried corn. Gulmez and Turkmen (2007) observed a decrease of ruminal pH (<6) in lactating cows when corn was replaced by wheat. They also observed low pH (<5.8) over 13 continuous hours when wheat was the only source of starch.

Cassava is used as a readily fermentable energy source for ruminants. It has a high rate and extent of ruminal degradation, as evidenced by Khampa and Wanapat (2006) who compared cassava vs. corn supplementation at 1 and 2% of live weight. They found that 2% cassava supplementation lowered ruminal pH (5.3 vs. 6.4) and cellulolytic bacteria (2.3 vs. 5.9×10^7).

Starch and methanogenesis

Ruminal digestion of fiber-rich diets increases hydrogen and carbon dioxide production, which are substrates for methanogenesis. Moreover, starch-rich diets change the bacterial ecology by favoring propionic-acid producing bacteria over methanogens (Bannink et al., 2006; Ellis et al., 2008). Propionic acid production from dicarboxylic acids (aspartate, malate, fumarate) via the succinate pathway is thermodynamically more efficient than methanogenesis (Offner and Sauvant, 2006). Moreover, rapidly-fermenting diets reduce methane production by decreasing ruminal pH, which affects the growth of methanogens, protozoa (Hook et al., 2011) and cellulolytic bacteria (Sung et al., 2007), and increases passage rate, which reduces protozoans and, thereby, interspecies hydrogen transfer (Kumar et al., 2013).

Agle et al. (2010) reported that diets with higher proportion of non-structural carbohydrates (52 and 72%) resulted in numerically lower methane emissions (1.5 vs. 3.4 g/hour, respectively), although results showed no difference due to high variability. A recent study in grazing Holstein Friesian cows found that concentrate level (2, 4, 6, and 8 Kg/cow/day) had no impact on methane emissions (287, 273, 272, and 277 g/day, respectively). However, when it was associated with DM and energy consumption, methane decreased with increasing levels of concentrate ($g CH_4/Kg DM: 20, 19.3$, 17.7, and 18.1; CH₄-E/gross energy intake: 0.059, 0.057, 0.053, and 0.054, respectively). They demonstrated that concentrate supplementation to grazing cows increased milk production and decreased methane emissions per unit of milk produced (Jiao et al., 2014). Aguerre et al. (2011) found that changing forage: supplement ratio (F/S) from 68:32 to 47:53 reduced methane emissions from 648 to 538 g/cow/day. Pirondini et al. (2015) evaluated the effect of starch (23.7 and 27.7% DM) on methane emissions in dairy cows, finding lower emissions for starch-rich diets (415 vs. 396 g/d, respectively). Finally, Hatew et al. (2015) investigated the effect of starch (270 vs. 530 g/Kg concentrate DM) and fermentation rate (fast vs. slow) in dairy cows. They found no differences in methane produced per Kg of fat-corrected milk and protein, or per Kg DM consumed, or as a fraction of the gross energy consumed. However, the high starch diet (46.9 vs. 43.1 g/Kg) had less ruminal methane per Kg of fermentable organic matter (42.6 vs. 47.4 g/Kg). Hales et al. (2012) evaluated the effect of corn processing. They found that Jersey animals eating steamed corn flakes produced less methane than those eating dry rolled corn (58.77 vs. 74.31 L/animal, 11.65 vs. 14.06 L/Kg DM intake, 2.47 vs. 3.04% of gross energy consumed, and 3.30 vs. 4.18% of digestible energy consumed). The reduction was explained by differences in ruminal fermentation, changing the place of digestion (from the rumen to the intestine), or decreased ruminal pH. Scarce literature is available on the effect of starch source and processing on methane emissions. In a study reported by the CCRP (2012) a reduction of methane emissions in cows fed ground wheat (219 g methane/day, 11.1 g methane/Kg of DM consumed) vs. ground corn (424 and 19.5 g methane, respectively).

The difference in methane production per starch vs. cellulose unit does not depend on the chemical composition, as both carbohydrates are hydrolyzed to glucose before fermentation. Conversely, hemicellulose polymer includes sugars with 5 to 6 carbons, which could lead to changes in the fermentation profile (different proportions of VFA) and methane emissions. Rather than the chemical composition, the differences in methane production from starch, cellulose and hemicellulose appear to be a function of the microbial species that degrade each substrate. Fermentation patterns and methane production vary as microbial species adapt to changes in dietary substrates and ruminal conditions. Additionally, associative effects between nutrients influence methane production, which means that this gas can be estimated for the diet and not for individual ingredients (Knapp et al., 2014).

Relationship between starch and milk composition and yield

Effect on milk yield and fat content

Milk yield response depends on the starch source (Khorasani *et al.*, 2001) and its degradation

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rate. Mosavi et al. (2012) compared milk yield in Holstein cows consuming wheat, barley, maize or potatoes. They found a reduced milk yield for the diet added with potatoes, and attributed it to its lower digestibility. Supplementation with rapidly degradable starches in rumen -such as barley, wheat or cassava- increases yield but reduces milk fat (Sutton, 1989). Poore et al. (1993) found a milk vield increase of 3.4 Kg/day and 0.4% fat reduction when ruminal digestibility increased from 48 to 72%. Milk fat reduction is associated with changes in the fermentation profile, caused by a relative reduction in lipogenic vs. glycogenic precursors (Reynolds et al., 1997). Rumen propionate increases while acetate and butyrate decrease when ingestion of rapidly degradable starch exceeds 7 Kg/day (Casper et al., 1990). Jurjanz et al. (1998) evaluated starch source and level (wheat or potato peels; <5, 6, or >7.5 Kg/d) on milk yield and composition. High starch consumption from potato peels (>7.5 Kg/day) lead to slower ruminal degradation and increased milk fat content (+ 3.3 g/Kg) compared to wheat. Fed in lower amounts, the starch source did not affect milk fat synthesis. The lower rate of starch degradation could have released more fat precursors. Mosavi et al. (2012) also observed slower ruminal degradation for corn starch compared with wheat, barley or potato, as well as increased acetate and butyrate production along with higher milk fat (3.43%) vs. 3.12, 3.09, and 3.13%, respectively). Contrary to these findings, Chanjula et al. (2004) did not observe differences in milk production and compositional quality by adding corn (low degradability) or cassava (high degradability) at two inclusion levels (55 vs. 75%).

According to Kennelly and Glimm (1998), milk fat is reduced due the inhibitory effect of methylmalonyl CoA (synthesized from propionic acid) on fatty acid synthesis in the mammary gland. Methylmalonyl CoA accumulation competitively inhibits malonyl CoA (Van Soest, 1994).

Reynolds *et al.* (1997) associated milk fat decrease with increased levels of plasma glucose and insulin in animals fed high amounts of the supplement. Insulin lowers lipolysis and promotes lipogenesis in adipose tissue, reducing fatty acids availability to the mammary gland, thus decreasing milk fat. According to Van Soest (1994), lipogenesis in adipose tissue is insulin dependent, which is not the case for the mammary gland.

The reduction in milk fat can also be explained by increased trans-unsaturated fatty acids in the rumen (Gaynor *et al.*, 1995). Cereal grains are high in linoleic and oleic acid. A ruminal pH decrease due to the diet can disturb biohydrogenation of unsaturated 18 carbon fatty acids increasing *trans* C18:1 fatty acid (*trans* isomers result from incomplete microbial biohydrogenation of linoleic acid into stearic acid). It is known that ruminal and milk increase in *trans* C18:1 is correlated with low milk fat levels in cows fed high grain diets (Griinari *et al.*, 1998). Corn contains a high concentration of linoleic (C18:2) and octadecanoic acid (*trans* C18:1), which inhibit biohydrogenation and reduce lipogenesis in the mammary gland.

According with Montoya et al. (2004), the optimal content of nonstructural carbohydrates (NSC) for maximizing milk yield is between 30 and 38% of the diet. Those researchers supplemented cows with 4 Kg of a commercial concentrate and 0, 6, and 12 Kg of fresh potatoes, thus NSC accounted for 7.2, 12.4, and 17.9% of DM intake. Milk yield was higher for the potato treatments (17.2 vs. 15.8 liters/cow/day; p = 0.004). Nevertheless, no difference was observed for the inclusion of 6 vs. 12 Kg potatoes, which could be associated with a limited ability to use potato NSC. Their study found no difference between treatments for fat percentage and production (p>0.05). Pimentel et al. (2006) also evaluated cassava supplementation on milk yield and composition. They replaced 0, 25, 50, and 75% of corn with cassava, finding a linear decrease of 30 and 1.15 g/day in milk yield (corrected for 3.5% fat) and fat production, respectively. According to the authors, the viability and level of corn substitution with cassava will depend on a low cost of substitution that compensates for the expected decrease in production.

Dann *et al.* (2014) evaluated three starch levels (17.7, 21.0, and 24.6%) in Holstein cows using increasing levels of ground corn. They found that solids-corrected milk yield was not affected by the diet, averaging 40.8 Kg/d. They concluded that starch content did not affect rumen fermentation or performance. Their highest starch level (on a DM basis) was between 23 to 30%, which follows within the recommended range for lactating cows (Grant, 2005).

Delahoy *et al.* (2003) conducted two experiments assuming that supplements such as steam-flaked corn (SFC) and non-forage fiber (NFF) sources may provide benefits over corn. In the first experiment, animals were assigned to a cracked-corn (CC) or to a steam-flaked corn (SFC) supplement. In the second experiment, animals were offered ground corn (GC) or no forage sources of fiber (NFF). No differences were observed in milk yield (24.3 and 27.5 Kg/d for experiments 1 and 2, respectively), explained by a lack of difference in net energy consumption for lactation, which exceeded the requirements (Experiment 1). Another factor that could explain these results is the quality of the pasture, which did not reduce the pH, a target to improve by NFF inclusion in Experiment 2.

Effect on the protein content

Diets rich in nonstructural carbohydrates increase ruminal ammonia nitrogen utilization and microbial protein synthesis (Svihus et al., 2005). Therefore, when dietary energy increases, metabolizable protein is also increased. Mosavi et al. (2012) evaluated the effect of four starch sources on milk protein in Holstein cows. While protein levels of milk were similar (3.03, 3.10, 3.14, and 3.04%) for wheat, barley, corn and potato supplements, respectively, milk protein differed in favor of wheat, barley and corn, compared to potato (1.08, 1.06, 1.06, and 0.98 Kg/d, respectively; p = 0.02). Gozho and Mutsvangwa (2008) found no difference in milk protein for animals fed diets based on wheat, barley or corn, but higher milk protein was observed for diets based on corn vs. oats. On the contrary, other studies comparing slow versus fast ruminal degrading starches found no differences in milk protein (Khorasani et al., 2001; Silveira et al., 2007; Cabrita et al., 2009).

It has been suggested by Huhtanen and Sveinbjörnsson (2006) that enhanced starch digestion in the small intestine increases milk protein, perhaps by sparing amino acids from being used for gluconeogenesis in the liver. They report a study in which milk protein yield was slightly but significantly higher for maize compared with barley supplements. Contrary to this concept, increasing starch digestion in the rumen is considered advantageous in terms of milk protein yield, since it increases the energy supply for microbial protein synthesis and the metabolisable protein flow to the small intestine (Thair, 2012). Finally, Reynolds (2006) reports a study in which there was no evidence that the site of starch digestion increased milk production or changed its composition.

Final thoughts

Rumen fermentation of starch -although it reduces energy efficiency over the enzymatic digestion in the intestine- determines its nutritional value for ruminants. The rate and extent of ruminal starch digestion alters pH, cellulolytic activity, microbial protein synthesis, methane emissions and, eventually, animal production. There is a considerable body of research on degradation potential of various cereal grains, but little information on non-traditional sources of starch that could replace cereal grains when availability and costs are competitive. The structural traits of starch from these sources, their interaction with other components, and the effect of processing should be examined. In vitro digestion techniques constitute a starting point for studying the extent and kinetics of starch degradation from non-conventional sources.

Starch is the main energy component used in ruminants feed to modulate ruminal fermentation and promote sync with the nitrogen sources. More research is required to evaluate the effect of using one or more sources of starch —with different degrees of degradability and processing— on protein use efficiency, milk yield and compositional quality. Studies should focus on addition levels and nutrient composition of the forage base according with the stage of lactation and energy requirements of the animal.

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Conflict of interest

The authors declare they have no conflicts of interest with regard to the work presented in this report.

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