Chapter 11

# Digestion in Ruminants

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## 1. Introduction

Ruminants, cloven-hoofed mammals of the order *Artiodactyla*, obtain their food by browsing or grazing, subsisting on plant material (Hungate, 1966). Today, 193 species of living ruminants exist in 6 families: *Antilocapridae, Bovidae, Cervidae, Giraffidae, Moschidae* and *Tragulidae* (Nowak, 1999). The number of wild ruminants is about 75 million and of domesticated about 3.6 billion (Hackmann and Spain, 2010). Approximately 95% of the population of domesticated ruminants constitute species: cattle, sheep and goats, all of them belong to the *Bovidae* family. Cattle and sheep are the two most numerous species and cattle is of the most economic importance. The economic value of milk and beef production in the EU is almost 125 billion Euro per year and accounts for 40% of total agricultural production (FAIP, 2003). The dairy cows is unique among all other mammalian species because of the intense artificial transgenerational genetic selection for milk production during the last 50 yr, so that annual averages of more than 12,500 kg/cow of milk per lactation are not uncommon (Eastridge, 2006). The selection has increased their peak energy yield by about 250% (20 Mcal × $d^{-1}$ observed vs. 7.76 Mcal × $d^{-1}$ expected) (Hackmann and Spain, 2010). Genetic improvement is accompanied by increasing metabolic demands for energy. The efficient use of energy of the feed resources is the main reason for the numerous and multilateral studies on carbohydrates digestion processes in cattle.

## 2. Digestive tract

Ruminants digestive system is characterized by functional and anatomical adaptations that allowed them to unlock otherwise unavailable food energy in fibrous plant material, mainly in cellulose and others recalcitrant carbohydrates (Van Soest, 1994). This property gives them an advantage over nonruminants. An important characteristic of ruminants digestive system is the occurrence of the microbial fermentation prior to the gastric and intestinal digestion activity. Their unique digestive system integrates a large microbial population

with the animal's own system in the symbiotic relationship. The microbial fermentation occurs mainly in the rumen, the first chamber of the four-compartment stomach, which consists also of the reticulum and omasum (act as filters), and the abomasum (the true enzymatic stomach).

## 3. Rumen function

The feedstuffs consumed by ruminants are all initially exposed to the fermentative activity in the rumen, the place of more or less complete microbial fermentation of dietary components. Ruminal fermentation initially results in the degradation of carbohydrates and protein to short-term intermediates such as sugars and amino acids. The products of this initial degradation are readily metabolized to microbial mass and carbon dioxide, methane, ammonia and volatile fatty acids (VFA): primarily acetate, propionate and butyrate and to a lesser degree branched chain VFA and occasionally lactate. The rate and extent of fermentation are important parameters that determine protein, vitamins, and short-chain organic acids supply to the animal (Koenig et al., 2003; Hall, 2003). The host ruminant animal absorbs VFA (mostly through the rumen wall) and digests proteins, lipids, and carbohydrate constituents of microbes and feed residues entering the small intestine to supply its maintenance needs and for the production of meat and milk. Ruminant animals derive about 70% of their metabolic energy from microbial fermentation of feed particles and microbial protein accounts for as much as 90% of the amino acids reaching the small intestine (Nocek and Russell, 1988; Bergman, 1990).

The rumen has a complex environment composed of microbes, feed at various stages of digestion, gases, and rumen fluid. Rumen microorganisms usually adhere to feed particles and form biofilms to degrades plant material. The efficiency of ruminants to utilize of feeds is due to highly diversified rumen microbial ecosystem consisting of bacteria ($10^{10}$–$10^{11}$ cells/ml, more than 50 genera), ciliate protozoa ($10^4$–$10^6$/ml, 25 genera), anaerobic fungi ($10^3$–$10^5$ zoospores/ml, 5 genera) and bacteriophages ($10^8$–$10^9$/ml) (Hobson, 1989). The synergism and antagonism among the different groups of microbes is so diverse and complicated that it is difficult to quantify the role played by any particular group of microbes present in the rumen (Kamra, 2005). Bacterial numbers in the rumen are the highest and bacteria play a dominant role in all facets of ruminal fermentation. They are adopted to live at acidities between pH 5.5 and 7.0, in the absence of oxygen, at the temperature of 39-40$^{o}$C, in the presence of moderate concentration of fermentation products, and at the expense of the ingesta provided by ruminant (Hungate, 1966). Rumen digesta volume accounts for 8-14% of body weight of cows and is characterized by dry matter content about 15% (Dado and Allen, 1995; Reynolds et al., 2004; Kamra, 2005).

## 4. Techniques for estimating rumen digestibility

The rumen digestibility of feeds can be estimated by biological methods. The "basic model" which gives the value utilized for defining the nutritive value of a feed is the *in vivo* digestibility, which represents the entire process occurring in the gastro-intestinal tract. *In*

*vitro* methods which simulate the digestion process, have being less expensive and less time-consuming, and they allow to maintain experimental conditions more precisely than do *in vivo* trials. Three major *in vitro* digestion techniques currently available to determine the nutritive value of ruminant feeds are: digestion with rumen microorganisms (Tilley and Terry, 1963; Menke et al., 1979), digestion with enzymes (De Boever et al., 1986), and *in situ* the nylon bag technique (Mehrez and Ørskov, 1977). The nylon bag technique *(in sacco)* has been used for many years to provide estimates of both the rate and the extent of disappearance of feed constituents. Those characteristics are measured by placing feedstuffs in fabric bag and then incubating the bag by certain time intervals in the rumen of animal. However, the single technique does not provide accurate estimation of *in vivo* digestion. Judkins et al. (1990) compared 11 techniques for estimating diet dry matter digestibility across six different diets in experiment with rams. Authors found, that the rumen digestibility of feeds nutrients was influenced by diets composition, feeding conditions and physiological status of animals. It therefore seems appropriate that the developments and use of various modification of mentioned experimental techniques have enabled much progress in rumen studies.

## 5. Carbohydrates classification in ruminants feeds

Carbohydrates constitute the highest proportion of diets and are important for meeting the energy needs of animals and of rumen microbes, and are important for maintaining the health of the gastrointestinal tract. Typically, carbohydrates make up 70 to 80% of the diets fed to dairy cattle and are composed of mixture of numerous monomers and polymers (Nocek and Russell, 1988). The carbohydrates fraction of feeds are defined according the chemical or enzymatic methods used for their analysis and availability to the ruminants. Broadly, carbohydrates are classified as nonstructural that are found inside the cells of plants or structural that are found in plant cell walls, but these fractions are not chemically uniform (Van Soest et al., 1991).

Fraction of nonstructural carbohydrates (NSC) includes organic acid, mono- di- and oligosaccharides, starches, and other reserve carbohydrates. Total NSC includes pectin is referred as nonfibrous carbohydrates (NFC), calculated as 100−(CP+ether extract+ash+NDF) (Mertens, 1992). NFC are the highly digestible and are the major source of energy for high producing cattle. Fraction of structural carbohydrates is characterized by neutral detergent fiber (NDF) and acid detergent fiber (ADF) contents. NDF includes the crosslinked matrix of the plant cell wall with cellulose, hemicellulose, and lignin as the major components and ADF does not include hemicelluloses (Van Soest, 1963). NDF, ADF, and cellulose content are measured according to methods described by Van Soest et al. (1991). The content of hemicellulose was calculated as NDF – ADF (Mertens, 1992).

Fractions of carbohydrates described above are subdivided by chemical composition, physical characteristics, ruminal degradation, and postruminal digestibility characteristics, because of these factors, various modifications of the analytical methods have been proposed (Hall et al., 1999; Nie et al., 2009).

## 6. Degradation and utilization of carbohydrates by rumen microbial ecosystem

Dietary carbohydrates are the main rumen microbial fermentation substrates. Microbial yields are related primarily to the growth rate that carbohydrate permits. The individual carbohydrates characterized by faster rumen degradation rates result in greater microbial yield (Hall and Herejk, 2001). The enzyme systems produced by microorganisms for carbohydrates hydrolysis are complex; they usually comprise hydrolases from several families, and there may be multiple enzymes hydrolysing each polysaccharide. Nearly all carbohydrate digestion occurs (>90%) within the rumen, but under certain circumstances (e.g., high rate of passage), a significant amount of carbohydrate digestion can occur in the small and large intestine.

## 7. Nonfibrous carbohydrates

Nonfiber carbohydrates may provide 30 to 45% of the diet on a dry matter basis (Hall et al., 2010). The NFC fraction is considered a source of readily available energy for microbial growth (Ariza et al., 2001).

### 7.1. Mono- di- and oligosaccharides

The concentration of monosaccharides, glucose and fructose was estimated from 1% to 3% (in grasses and herbage) and of sucrose from 2% to 8% (Smith, 1973). Sucrose formed from α-D-glucose and β-d-fructose linked by 1, 2 glycosidic linkage is digested by enzyme sucrose phosphorylase (EC 2.4.1.7, according to the IUB-MB enzyme nomenclature; Stan-Glasek et al., 2010). Maltose formed from two units of glucose joined with an $\alpha$(1–4) bond is digested by enzyme $\alpha$–glucosidase (EC 3.2.1.20). Oligosaccharides concentration in the different plants ranges between 0.3% and 6% and represent a wide diversity of biomolecules (including stachyose and raffinose), they are chains of monosaccharides that are two to approximately 20 units long. The enzymes belonging to the group of polysaccharide hydrolases (EC 3.2.1.-) which hydrolyse the glycosidic bond between two or more carbohydrates utilize oligosaccharides (Courtois, 2009).

Mono-and disaccharidesare rapidly fermented within the rumen to yield VFA. The rate of glucose fermentation after glucose dosing varied from 422 to 738% $h^{-1}$ and the rate of fermentation of monosaccharides originating from disaccharide hydrolysis was 300 to 700% $h^{-1}$(Wejsberg et al., 1998).

Ruminal bacteria that ferment sucrose include *Streptococcus bovis, Lachnospira multiparus, Lactobacillus ruminis, Lactobacillus vitulinis, Clostridium longisporum, Eubacterium cellulosolvens,* and some strains of *Eubacterium ruminantium, Butyrivibrio fibrisolvens, Ruminococcus albus, Ruminococcus flavefaciens, Megaspaera elsdenii, Prevotella spp., Selenomonas ruminantium, Pseudobutyrivibrio ruminis* strain A and *Succinivibrio dextrinosolvens* (Stewart et al., 1997, Martin and Russell, 1987, Stan-Glasek et al., 2010). Maltose utilize *Ruminobacter amylophilus*)

and oligosaccharides *Actinomyces ruminicola* as a sources of energy (Anderson, 1995; An et al., 2006).

## 7.2. Pectic substances

Pectic substances are a group of galacturonan polymers with neutral sugars (largely arabinose and galactose) substitutions (Jung, 1997). Pectic substances are found in the middle lamella and other cell wall layers (Van Soest, 1994). The most important pectinolytic activity represents pectin lyase (EC 4.2.2.10) (Wojciechowicz, 1982).

Grasses contain from 3 to 4% of pectin in the dry matter, leguminous plants from 5 to 12%, and sugar beet pulp 25% (Aspinall, 1970; Van Soest, 1983; Cassida et al., 2007). The utilization of pectin varied from 79.4 to 95.9% (Marounek and Dušková, 1999). Most of pectin degrades at a rate of 13% $h^{-1}$ (Hall et al., 1998).

Pectin-utilizing bacteria include *Butyrivibrio fibrisolvens* and *Prevotella ssp.*(the principal rumen pectin-utilizing bacteria) and *Fibrobacter succinogenes, S. bovis* and *Lachnospira multiparus* (Czerkawski and Breckenridge, 1969; Gradel and Dehority, 1972; Baldwin and Allison, 1983). Pectin is reported to ferment primarily to acetate (Czerkawski and Breckenridge, 1969; Marounek and Dušková, 1999).

## 7.3. Starch

Starch is a complex of two structurally distinct polymers: amylose and amylopectin (Chesson, 1997). Amylose is chemically composed of α-*1,4*- linked polymers of glucose. It is degraded by α-amylases (EC 3.2.1.1), which releases oligosaccharides maltodextrins, and β-amylases (EC 3.2.1.2), which remove maltose units. Amylopectin is a highly branched molecule of α-*1,4*- linked polymers of glucose joined *1,6* at intervals along the backbone moleculr. Amylopectin is degraded to maltose by β-amylases action (in 50%), glucanohydrolases (EC 3.2.1.3 and EC 3.2.1.41) and isoamylase (EC 3.2.1.68). Maltose and maltodextrins are degraded to glucose by α-glucosidase (EC 3.2.1.20) (Hobson, 1989). Starch can be degraded by ruminal microbial enzymes as well as enzymes in the small intestine of the ruminats.

Of the nonfibrous fraction, starches are the highest proportion in the diet, and cereal grains is the major source of starch in ruminants diet. The cereal grains differ in their starch content, with wheat containing (on dry matter basis) 77% starch, corn 72%, and barley and oats 57 to 58% (Huntington, 1997). Differences exist among cereal grains in their extents and rates of ruminal starch degradation. In the rumen has been digested from 55 to 70% of corn starch, 80 to 90% of barley and wheat starch, and 92 to 94% of oats starch (Huntington, 1997). The degradation rates is estimated from 4.0 to 6.4% $h^{-1}$ for corn starch and from 14.7 to 24.5% $h^{-1}$ for barley starch (Herrera-Saldana et al., 1990; Tamminga et al., 1990). On average, 5 to 20% of starch consumed is digested postruminally, mainly in the small intestine (from 45 to 85% of starch entering the duodenum), this capacity is limited by the supply of pancreatic amylase (Hunhington, 1997).

The bacteria *Ruminobacter amylophilus, Prevotela ruminicola, Streptococcus bovis, Succinimonas amylolytica* and many strains of *Selenomonas ruminantium, Butyrivibrio fibrisolvens, Eubacterium ruminantium* and *Clostridium* ssp., all of the entodiniomorph protozoa and the chytrid fungi are amylolitic (Chesson, 1997). The high-starch concentrate diets favor the development of propionate producing bacteria species (Ørskov, 1986; France and Dijkstra, 2005). The fermentation of starch in the rumen depending on factors such as structure (amylose/amylopectin ratio), plant source, mechanical alterations (grain processing, chewing), diet composition, amount of feed consumed per unit time and degree of adaptation of ruminal microbiota to the diet (Piva and Masoero, 1996, Huntington, 1997; Eastridge, 2006).

## 8. Structural carbohydrates

Structural carbohydrates is less digestible than NFC and is negatively correlated with energy concentration in the diet for ruminants, but is important for rumination, saliva flow, ruminal buffering, and health of the rumen wall, however, high dietary concentrations can limit dry matter intake by increased rumen fill. The retention time of plant fiber in the rumen is sufficiently long (48 h or more in some species) to allow the growth of a fibrolytic microbial population whose extensive fiber utilization contributes a major portion of the energy for the animal (Van Soest, 1994). The cellulose fibers are embedded in a matrix of other structural biopolymers, primarily hemicelluloses and lignin (Lynd, 1999; Marchessault and Sundararajan, 1993; Van Soest, 1994). The high-fibre forage diets encourage the grown of acetate producing bacterial species, the acetate : propionate : butyrate molar proportion would typically be in region 70:20:10 (France and Dijkstra, 2005). Fiber digestion may be reduced due to decreased rumen pH (the fiber digesters are most active at a pH of 6.2 to 6.8), and the availability of surface area for colonization (Sutton et al., 1987; Chesson and Forsberg, 1997). Fungi plays an active and positive role in fiber degradation (Williams and Orpin, 1987).

### 8.1. Cellulose

Cellulose content is in the range from 35 to 50% of plant dry weight (Lynd et al., 1999). It is chemically composed of a homogenous polymers of β-1,4-D-glucose linked through β-1,4-glycosidic bonds. Native cellulose exists as fibrils which are composed of amorphous and crystalline regions formed from cellulose chains, each of them contains between 500 and 14,000 b-1,4D-glucose units (Bazooyar et al., 1012). The digestion of cellulose necessitates a combination of many classes of cellulases. The digestion process including activity of endoglucanases (EC 3.2.1.4), that cut randomly at internal amorphous sites in the cellulose chain; exoglucanases (cellodextrinases EC 3.2.1.74 and cellobiohydrolases EC 3.2.1.91), that act processively on the reducing or non-reducing ends of cellulose chains, releasing either cellobiose or glucose as major products; and glucosidases (EC 3.2.1.21) that hydrolyze soluble cellodextrins and cellobiose to glucose (Lynd et al., 2002).

*Fibrobacter succinogenes, Ruminococcus flavefaciens* and *R. albus* are considered to be the predominant cellulolytic bacteria present in the rumens, these species gain selective advantage in the rumen is by optimizing two catabolic activities: cellulose hydrolysis (depolymerization) and efficient utilization of the hydrolytic products (cellodextrins) (Weimer, 1996; Koike and Kobayashi, 2001). *F. succinogenes* has a potent ability to solubilize crystalline chains of cellulose (Halliwell and Bryant, 1963; Shinkai and Kobayashi, 2007). *F. succinogenes* produces primarily succinate (a propionate precursor), and lesser amounts of acetate, *R. flavefaciens* produces primarily acetate and lesser amounts of succinate converts to propionate by *Selenomonas ruminantium* (Weimer at al., 1999).

The predominant ruminal cellulolytic species digest cellulose at rate approximately from 5 to 10% $h^{-1}$, however, the extent to which native cellulose is utilizes by ruminal microorganisms is limiting by the cellulose association with lignin (Weimer, 1996; Chesson, 1993). Cellulose degradability of forages varies from 25 to 90% (Pigden and Heaney, 1969).

### 8.2. Hemicelluloses

Hemicellulose concentration varies from 6 to 22% (on dry matter basis) in leaves of grasses and herbs (Schädel at al., 2010). Hemicelluloses are composed of complex heteropolymers that vary considerably in primary composition, substitution and degree of branching, and can be grouped into four classes: xylans, xyloglucans, mannans and mixedlinkage $\beta$-glucans (Ebringerova et al., 2005).

*Bacteroides (Fibrobacter) succinogenes, Ruminococcus albus,* and *Ruminococcus flavefaciens* and same strains of *Butyrivibrio fibrisolvens* and *Bacteroides ruminicola* are considered to be the organisms responsible for most of the degradation of hemicelluloses (Hespell, 1988). Rumen degradation of hemicelluloses varies from 16 to 90%, depending on their composition (Pigden and Heaney, 1969; Coen and Dehority, 1970).

### 8.3. Lignin

Lignin, a complex phenolic polymer, is indigestible by rumen microbes, but their concentration limits digestibility of structural carbohydrates (Van Soest, 1994). The main reason for reduction of accessibility for the hydrolases secreted by ruminal microbes is the presence of strong covalent bonds between lignin and the cell wall polysaccharides (Chesson, 1993).

## 9. Interactions between energy and protein metabolism in rumen

Manipulation of rumen fermentation through proper diet formulation changes microbial population in a way that improved efficiency of microbial protein synthesis. A major factor in maximizing microbial protein synthesis is the ruminally available energy and N in the diet. There are many interactions of dietary conditions on bacterial populations and on protein and carbohydrates digestion in rumen. For instance: microbial fermentation releases

organic acids that readily dissociate to decrease pH that influence on the microbial ecosystem and determining the selective growth of certain microbial species, and the types and quantities of fermentation products (Russell and Rychlik, 2001).

## 10. "Synchrony" hypothesis

The purpose of proper nutrition is "nutritional synchrony" refers to provision of dietary protein (N sources, true protein) and energy (ruminally fermented carbohydrates) to the rumen in such a manner that they are available simultaneously in proportions needed by the ruminal microorganisms (Hall and Weimer, 2007). Synchronous nutrient availability should allow more efficient use of nutrients, thus enhancing production of microbial products, increasing nutrient supply to the animal, and potentially improving animal production performance (Sinclair et al., 1993; Hall and Huntington, 2008).

### 10.1. Production efficiency

A number of studies have been conducted to evaluate the effects of "nutritional synchrony" conception on production efficiency, but the results are not consistently. There are many results which confirm increase in the yield of microbial protein when highly degradable carbohydrates were synchronized with rapidly degraded protein (Kovler et al., 1998; Charbonneau et al., 2006). Result from the *in sacco* study confirms that the better synchronization also affects degradation rate of diet components (Niwinska, 2009; Niwińska and Andrzejewski, 2011). However, nutrient synchrony has generally not resulted in improved animal performance (Yang et al., 2010). The fundamental reason is the following: ruminants animal have the ability to recycle N from blood and saliva to the gastrointestinal tract during periods of dietary protein deficiency or during periods of asynchronous carbohydrate and protein supply. Hall and Huntington (2008) suggested that for the optimal use of "nutritional synchrony" conception we may need to look at the whole animal, not just the rumen, and that a term such as the optimal balance may be more appropriate when considering the complexity of the ruminant animal.

### 10.2. Product composition

Volatile fatty acids, produced in the rumen, can have a major effect on fat composition of ruminant products. Results of studies with animal models, in tissue culture systems and in clinical research indicate that the functional health-related properties of milk and beef fat appear to be linked to the presence of rumenic acid and vaccenic acid (Parodi, 2005; Lee, 2008; Field et al., 2009). Milk fat provides 30% of fat consumed by humans and is the richest natural dietary source of those valuable fatty acids (Ritzenthaler et al., 2001). Research undertaken over the past decade has indicated, that concentration of those favorable fatty acids in milk fat may be controlled by the starch/fibre ratio in the diet of dairy cows (Niwińska et al., 2011).

### 10.3. Pollution emissions

An excessive supply of feed nutrients results in an increase in waste excreted to the environment. The pollutants produced by ruminants are nitrogen and methane, their production is dependent on carbohydrate composition of diet. Improved efficiency of microbial protein synthesis is considered as the most important target in reduction emissions of N, while synchronization of carbohydrate and protein supply in the rumen has been suggested as one possible solution to achieve this aim (Kaswari et al., 2007; Reynolds and Kristensen, 2008; Yang et al., 2010). The rumen microbial ecosystem produces methane as a result of anaerobic fermentation. Methane production results in losses of 5 to 12% of gross energy of diet and is estimated to be about 15% of total atmospheric methane emissions (Reid et al., 1980; Moss et al., 2000). The proper selection of carbohydrates in the ration, taking into account the structural and nonfibrous carbohydrates content, can reduce the formation of carbon dioxide, hydrogen and formate the major precursors of methane production in the rumen (Mitsumori and Sun, 2008).

## 11. Conclusion

The current data indicated, that the world production of dairy products is expected to grow 26% by 2020 and beef production worldwide grew by 30 million tons during 1965-2005 (OECD, 2011; FAO; 2006). The projected increase in cattle production directs our attention to the better utilization of feed resources. Understanding the effects of carbohydrates types and rumen microbial population shifts in response to nutrients contained in different feeds may be valuable to improve production efficiency, to modify the composition of the product and to minimize pollution emissions.

## Author details

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