Chapter

Sheep Digestive Physiology and Constituents of Feeds

Samir Medjekal and Mouloud Ghadbane

Abstract

Sheep have a gastrointestinal tract similar to that of other ruminants. Their stomach is made up of four digestive organs: the rumen, the reticulum, the omasum and the abomasum. The rumen plays a role in storing ingested foods, which are fermented by a complex anaerobic rumen microbiota population with different types of interactions, positive or negative, that can occur between their microbial populations. Sheep feeding is largely based on the use of natural or cultivated fodder, which is exploited in green by grazing during the growth period of the grass and in the form of fodder preserved during the winter period. Ruminant foods are essentially of plant origin, and their constituents belong to two types of structures: intracellular constituents and cell wall components. Cellular carbohydrates play a role of metabolites or energy reserves; soluble carbohydrates account for less than 10% dry matter (DM) of foods. The plant cell wall is multi-layered and consists of primary wall and secondary wall. Fundamentally, the walls are deposited at an early stage of growth. A central blade forms the common boundary layer between two adjacent cells and occupies the location of the cell plate. Most of the plant cell walls consist of polysaccharides (cellulose, hemicellulose and pectic substances) and lignin, these constituents being highly polymerized, as well as proteins and tannins.

Keywords: cell wall, rumen microbiota, sheep feeding, tannins

1. Introduction

Food is, in general, one of the main factors affecting animal production. Its effects can be noted on both the quantity and quality of animal products. Although this idea is easily accepted by technicians and breeders, especially aware of the negative effects of poor, inadequate or unbalanced nutrition. Ruminant farming depends mainly on the availability and the quality of the fodder. In developing countries, the low forage potential, linked to the limitation of water and arable area, has great difficulties in producing sufficient high-quality animal protein for the human population and involves a massive use of imports of animal products such as dairy and meat products [1].

Herbivores, and especially ruminants, occupy a prominent place in the world, among domestic animals bred for production. Their contribution to satisfying humanity's food needs through the milk and meat they are made to produce is of paramount importance. Ruminant animals have the advantage over monogastric animals of being able to extract and use the energy contained in a plant biomass which cannot be used directly by man because of its high lignocellulose content. As such, ruminant animals cannot be regarded as a direct competitor of man to his food biomass [2].

Ruminants counting the sheep are mammals that are able to procure nutrients from plant-based food by fermenting it in a specialized stomach earlier to digestion, principally through microbial actions. The process, which takes place in the front part of the digestive system and therefore is called foregut fermentation, typically requires the fermented ingesta (known as cud) to be regurgitated and chewed again. The process of rechewing the cud to further break down plant matter and stimulate digestion is called rumination. The digestive system of the ruminant may be considered sterile at birth. Colonization of the digestive tract, particularly of the rumen, will occur gradually with the successive installation of different populations of microorganisms in a well-defined order [3]. As the ecosystem develops, it becomes more complex until it reaches a state of dynamic equilibrium. This is a state for which the ecosystem is able to self-regulate to maintain its functions by constantly adjusting microbial populations, an ecosystem which cannot be stable [4].

A single food is usually insufficient to cover the nutritional needs of the animal; hence, there is a need to combine several foods within a ration. The lambs are fed with green fodder or preserved fodder: hay, straw and corn silage. Their complementary food is, in most cases, cereals, with dehydrated soybean seed called soybean meal, a food that is very rich in protein. All foods consist of water, minerals, carbohydrates, fat and nitrogen. Livestock rations contain approximately 70–80% carbohydrates [5], mainly in the form of starch, cellulose and hemicellulose. As a result, carbohydrates provide on average nearly three-quarters of the food energy of farm animals. Two broad categories of carbohydrates are distinguished according to their location in the plant cell: cytoplasmic (or intracellular) and parietal.

2. Anatomy of the digestive tract of the sheep

Sheep have a digestive tract similar to that of other ruminants; its length of 22–43 m is comparable to that of the goats [6]. The stomach of sheep consists of four digestive organs: the rumen, the reticulum, the omasum and the abomasum (**Figure 1**). The rumen is the first digestive organ. It occupies the left part of the abdomen and is the largest of the gastric reservoirs [7]. It contains 70–75% of the total contents of the digestive tract, representing 50–60% of its volume [8]. The wall of the rumen consists of a muscular tunic which constitutes the bulk of its mass. Its inner surface consists of a horny epithelium, bristled with papillae of varying shapes and dimensions that play an important role in the absorption of products resulting from the metabolism of rumen microorganisms: volatile fatty acids (VFA) and ammonia. Rumen is an excellent reservoir for fermentation; it has anaerobic conditions where most food components are degraded by an extremely abundant and diversified microflora [9]. The reticulum can be compared to junction where the particles that enter and leave the rumen are sorted. It is composed of a reticulated mucosa containing also absorbent papillae. Its main function is to ensure the circulation of particles: it is from the reticulum that the contractions start, which ensure the motor skills of all gastric containers. Food remains in the rumen until it is small enough ($\leq$1 mm) to pass through the reticulo-omasal orifice [10]. This is why the rumen and the reticulum are considered as a single organ, called reticulo-rumen. The partially fermented food then passes into the omasum which is a smaller organ than the rumen and larger than the reticulum. The omasum is a spherical organ made up of many mucous lamellae, similar to the leaves of a book, hence its name. These strips, arranged parallel to the passage of food, ensure the filtration of food particles and absorb water and minerals from the digestive content, before their arrival in the abomasum [11]. The abomasum is the only secretory reservoir. It is lined with a glandular mucosa

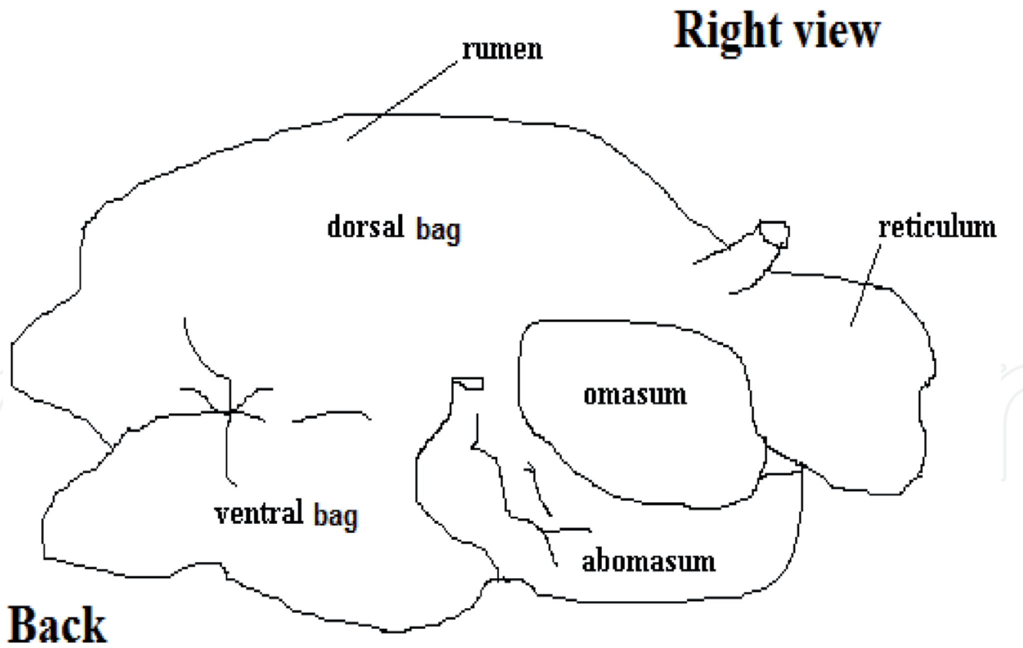

Figure 1.
Diagram of part of the ruminant digestive tract [7].

similar to that of the monogastric stomach. It consists of secreting cells that produce mucus, hydrochloric acid (pH: 2–3) and pepsin.

3. Digestive tract physiology

3.1 Physico-chemical conditions in the rumen

The most favorable conditions for microbial fermentations are found in the rumen and reticulum. It presents itself as the richest and the most complex microbial ecosystem. Rumen is considered to be analogous to a reactor operating continuously with anaerobic microorganisms. It is characterized by the following physico-chemical conditions: the average temperature of the digests in the rumen is constant; it oscillates between 39 and 40°C, and it can reach 41°C during intense fermentations [12]. It is estimated that the average pH during a day ranges from approximately 6.25 to 6.8 [13]. But a rapid fermentation can lower the pH to less than 5, after consuming a rapidly fermentable carbohydrate-rich diet. The pH is generally regulated by saliva, which contains sodium bicarbonate and phosphate salts that buffer the acidity of the rumen at a near-neutral value. The amount of ammonia in the rumen must exceed a critical threshold for a significant portion of the day to ensure a high rate of microbial growth and digestion and hence a significant feed intake. The amount of ammonia needed to optimize the population of microorganisms in the rumen requires an advantageous protein/energy ratio in the absorbed nutrients and is variable according to the diet. In general, for feed-based diets, the ammonia content must be greater than 200 mg of nitrogen per litre [14]. During ruminal fermentation, the population of microorganisms (especially bacteria) ferments carbohydrates and produces energy, gases (CH_4, CO_2, H_2), heat and organic acids. The authors reported concentrations of 74.7, 9.4, 6.5, 5.3, 3.4 and 1.3 (m.mol/l), respectively, for acetate, propionate, butyrate, isobutyrate, valerate and isovalerate [15]. The concentrations of VFA in the rumen change differently depending on the experiment. These different developments could be explained by the essential role of the mucosa in the absorption of VFAs and by the rate at which the rumen is emptied. The degradation in the rumen of the various substrates and in particular of soluble sugars by the ruminal microflora is accompanied by a strong gas production. The average composition of the gas pool is 60–65% CO_2, 25–30% CH_4, 6–9% N_2, 0.3–0.6% O_2, 0.1–0.3% H_2 and 0.001% H_2S [16]. Gases thus produced in the rumen are largely eliminated by eructation, ensured by the contractions of the rumen, the frequency of which increases with the pressure exerted on the wall.

3.2 The ruminal microbiome

Rumen is a strictly anaerobic ecosystem, where most of the components of lignocellulosic foods are degraded and fermented by an extremely abundant and diverse microflora and microfauna. This microbial population represents more than 350 species of bacteria, fungi and protozoa. The rumen contains a high density of bacteria (10^{11}/ml); this bacterial flora is the most effective for digesting cellulose. Almost all ruminal cellulolysis is based on the activity of cellulolytic bacteria [17]. The main bacterial cellulolytic species of the rumen are *Fibrobacter succinogenes*, *Ruminococcus flavefaciens* and *Ruminococcus albus* [18]. Cellulolytic bacteria appear in the rumen 3 to 4 days after the birth of the animal, while this organ is not yet functional. Their implantation is therefore not conditioned by the consumption of solid foods. Hemicellulolytic flora in the rumen is more widely distributed among bacterial flora than cellulolytic one [19]. A distinction must be made between three categories of hemicellulolytic bacteria: the first is composed of species with depolymerase activity and glycosidic activity, able to hydrolyse the main chain and cut the lateral chains of hemicelluloses, while using oligosaccharides and released monosaccharides. In the second category, species such as *Fibrobacter succinogenes*, for example, have depolymerase activity but are unable to use hemicellulose hydrolysis products. The third category has different glycosidic activities and can use hydrolysis products but has no depolymerase activity. Rumen contains 10^6/m of ciliated protozoa [20]. These are microscopic unicellular eukaryotic organisms, usually asexual. However, examples of conjugation with exchange of nuclear material between protozoan cells have been reported [21]. The contribution of the ciliated protozoa to the digestion of cellulose in the rumen is uncertain, due to the impossibility of obtaining them in axenic cultures. But ciliates also contribute to digestion in the rumen by degrading cellulose and vegetable starch [20]. Other ciliated species are also known as cellulolytic, but they have no indication of the extent of their activity. Highly cellulolytic ciliated protozoa include *Eudiplodinium maggii*, *Epidinium ecaudatum*, *Ostracodinium bovis*, *Orphryscolex caudatus* and *Polyplastron multivisiculatum*. *Diplodinium pentacanthum* is considered to be weakly cellulolytic. Defaunated sheep shows that the presence of protozoa in the rumen usually leads to better degradation of hemicelluloses and cellulose, when animals receive a feed-based diet, whereas with soluble carbohydrate-rich diets, the presence of these microorganisms is considered rather harmful to the animal [22]. Physiological studies show that the availability of microbial proteins for digestion is higher in defoliated ruminants than in protozoan-bearing ruminants [22]. Some species of fungus have been isolated from the rumen, but their function in the digestive ecosystem is little known and has been the subject of only rare studies. In adult ruminants, they are much more numerous in animals receiving a feed ration. In pure culture, fungi are able to solubilize a large part of plant walls, fodder, wheat straw and even more lignified fabrics such as wood [23]. With the exception of some strains of *Caecomyces communis*, all anaerobic fungi in the rumen are cellulolytic, and their cellulases are among the most active ones described so far. In addition, fungi appear to be able to solubilize in vitro a small part of the lignin of lignocellulose parietals but do not use this compound as a source of energy [24].

Bacteriophages are parasitic agents of bacteria. They are widespread in the rumen where they can eventually cause lysis of host bacteria. But their role in the food cycle and their presence in the rumen are not well known. However, the size of this population of microorganisms suggests that they are responsible for large bacterial lyses which can be a factor reducing the efficiency of food use [25].

3.3 Digestion and metabolism in the rumen

All rumen microbes are involved in the degradation of plant cell walls. These are degraded by the combined action of bacteria, fungi and protozoa. It is estimated that bacteria and fungi contribute approximately 80% of degradation activity and protozoa 20% [26]. Fibrolytic bacteria such as *Fibrobacter succinogenes*, *Ruminococcus flavefaciens* and *Ruminococcus albus* are generally considered to be the primary microorganisms responsible for the degradation of plant cell walls in the rumen. Digestion in the rumen requires microorganisms to break through resistant wall barriers and must first adhere to food particles. Plant fragments that enter the rumen at meals are quickly colonized by bacteria, fungi and protozoa. Their adhesion capacity increases their time of presence in the rumen and makes their action more effective by concentrating hydrolytic enzymes on the target tissues [27]. Attachment of rumen microorganisms to substrates is a prerequisite for digestion of food particles. Colonization and mode of attack are specific for each microbial species. Bacteria often colonize digestible tissues through stomata, lenticels or

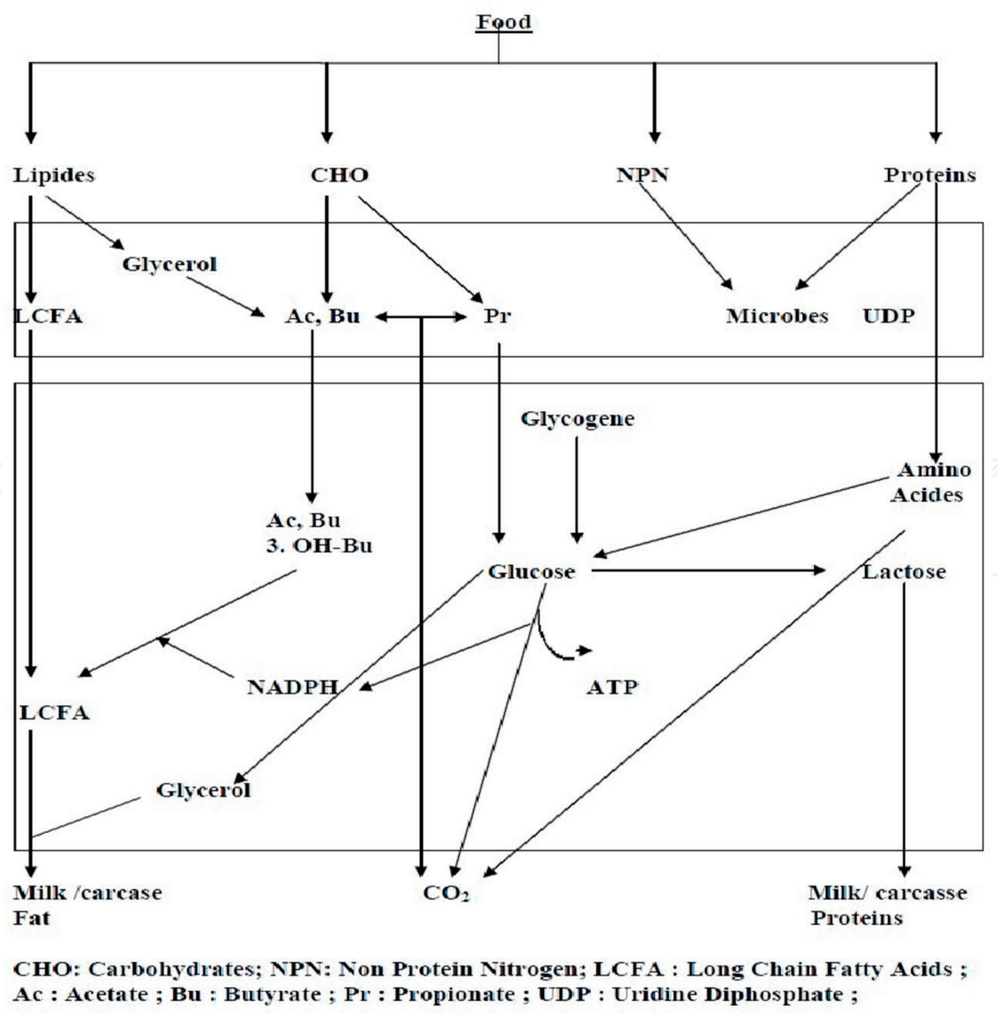

Figure 2.
Summary of digestion and metabolism of nutrient compounds (1). CHO, carbohydrates; NPN, non-protein nitrogen; LCFA, long-chain fatty acids; Ac, acetate; Bu, butyrate; Pr, propionate; UDP, uridine diphosphate.

damaged surfaces, and digestion takes place mainly from the inside to the outside of the colonized tissues. Rumen fungi also degrade the vulnerable surfaces of the plant and have, in addition, the ability to penetrate the cuticle of plants [28]. The association of protozoa with food particles is essential for their maintenance in the rumen, since their duration of division (25–35 hours) is on average higher than that of the small particles and the liquid phase in the rumen. This behaviour would explain the active role of ciliates in food degradation [29]. The integration of ruminal and tissue metabolism in feed degradation by ruminants is illustrated in **Figure 2**.

4. Sheep feed

The feeding of sheep is largely based on the use of natural or cultivated fodder, which is cultivated in green by grazing during the growing season of the grass, and in the form of fodder preserved during the winter period. Sheep feeding stuffs are mainly of plant origin, and their constituents belong to two types of structure: intracellular components and cell wall constituents.

4.1 Intracellular components

Cellular carbohydrates act as metabolites or energy reserves; soluble carbohydrates account for less than 10% of dry matter (DM) in foods, with the exception of some young grasses, beets (about 2/3 DM) and molasses (about 45% DM). Starches are present in the form of granules of varying size, mainly in seeds and their by-products as well as in tubers. Nitrogenous materials account for 5–60% of the DM of food and are mainly proteins but also polypeptides of reduced size, free amino acids and amides. Fats represent only 2–5% (apart from oilseeds and certain by-products, brewing grains, tomatoes, etc.), of which about half is in the form of fatty acids. These fatty acids are generally much unsaturated, with in particular high proportions of linoleic and linolenic acids [30].

4.2 Cell walls

Cell walls account for 15–90% of DM in food (15–45% for concentrated food, 30–80% for fodder and 60–90% for straw and certain seed husks) [31]. The plant cell wall consists of primary wall and secondary wall. Basically, the walls are deposited at an early stage of growth. A central blade forms the common boundary layer between two adjacent cells and occupies the location of the cell plate. The contiguous cells are linked together by deposition of lignin in the central blade. Most of the plant cell walls consist of polysaccharides (cellulose, hemicelluloses and pectic substances) and lignin, these constituents being strongly polymerized, as well as proteins and tannins. Typically, the polysaccharides of the plant cell wall are grouped into three fractions: (a) cellulose, the compound most resistant to chemical rupture; (b) hemicelluloses, extracted by relatively strong alkaline solution or by mild acid hydrolysis; and (c) pectic polysaccharides, extracted by hot water [32].

4.2.1 Cellulose

Cellulose is the most abundant polysaccharide in nature, accounting for 20–40% of the DM of all higher plants. It consists of glucose units bound in β-(1–4) based on the replication of cellobiose units arranged in parallel (**Figure 3**). The microfibrils of celluloses are linked to each other and to hemicellulose polymers by hydrogen bonds, but there is no evidence of covalent bonds between cellulose and other plant wall components [33].

4.2.2 Hemicelluloses

The term hemicelluloses is applied to polysaccharides of the plant cell wall which are in close association with cellulose, especially in lignified tissues. The structure of hemicelluloses is more complex since it contains both pentoses (arabinose, xylose), hexoses (glucose, mannose, galactose) and uronic acids (127) (**Figure 4**). The digestibility of hemicelluloses is strongly related to that of cellulose and negatively correlated with lignification, since hemicelluloses are strongly associated with lignin [34].

4.2.3 The pectic components

The pectic polysaccharides represent approximately 35% of the plant cell wall; they are located in particular in the central blade. In dicotyledons they are formed mainly of galactosyluronic acid, while monocotyledons appear to contain a minor portion of these polysaccharides. Other major polysaccharides are also among the components of pectins such as rhamnose, arabinose and galactose [32] (**Figure 5**).

4.2.4 Lignin

Lignin, another compound of the plant cell wall, is generally a limiting factor in the degradation of plant walls in the rumen. It is formed by the polymerization of three aromatic monomers. Lignin is not hydrolysed by bacterial enzymes. But it can be degraded by oxidation by nitrobenzene or by acidolysis in dioxane with hydrochloric acid or permanganate. It permeates the cellulosic net, prevents the adhesion of microbes to membranes and is a real physical barrier for the enzymes involved in the degradation of carbohydrate polymers [35]. The bonds between lignin compounds and hemicelluloses and arabinose units also inhibit the degradation of some of the cellulose and hemicelluloses. Lignin composition, structure and content

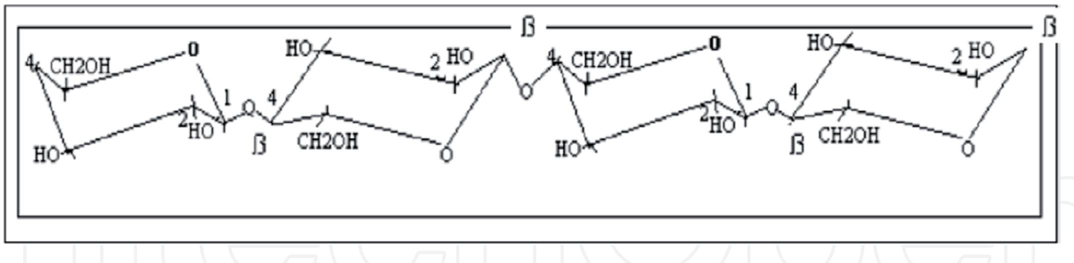

Figure 3.
Structure of cellulose (1).

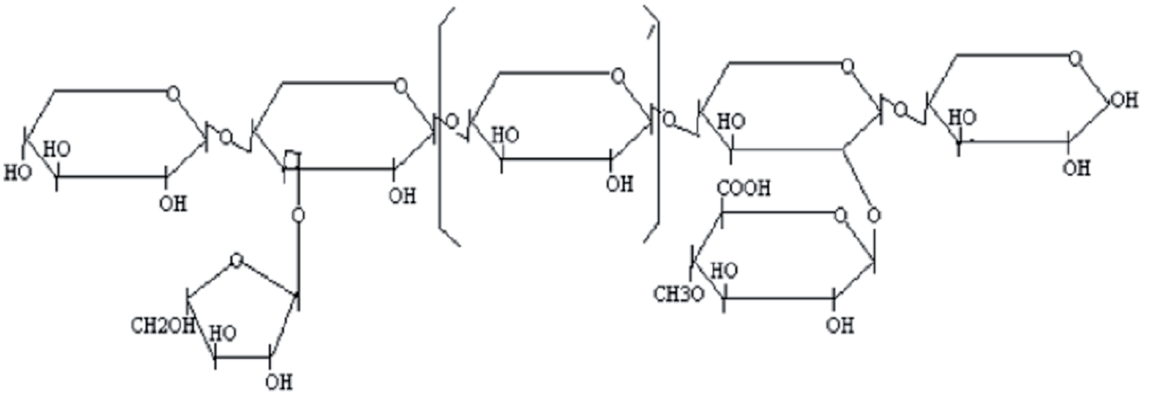

Figure 4.
Structure of hemicellulose (1).

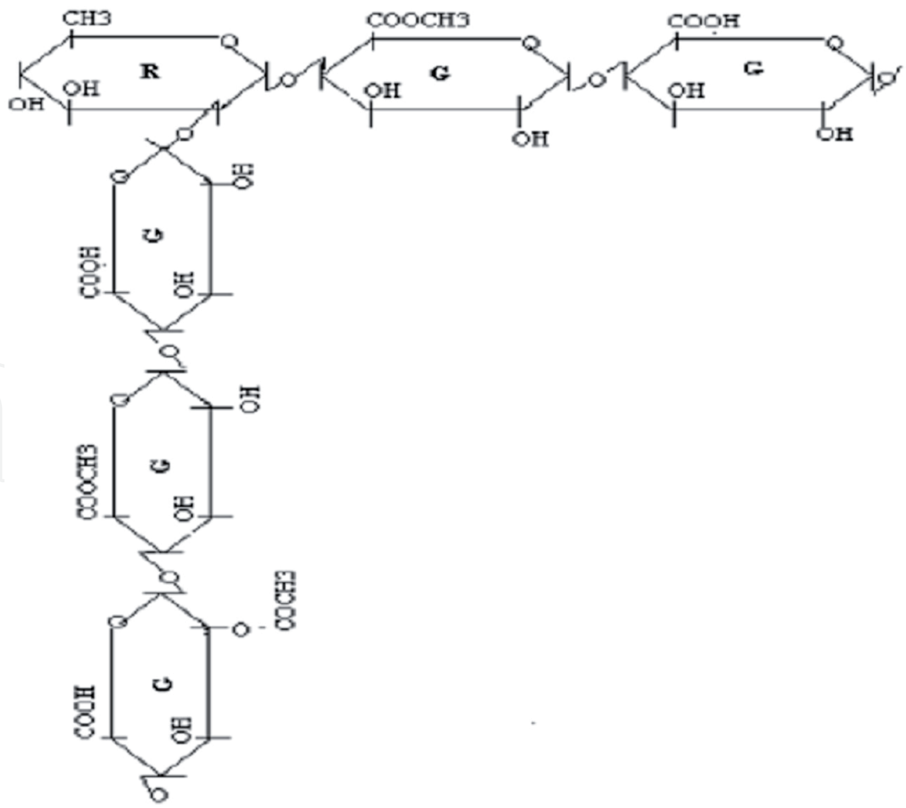

Figure 5.
Structure of pectin (1).

vary with tissues, organs, botanical origin, plant growth stage and environmental factors. The maturity of fodder plants is a determining factor in their lignin content. But for the same stage of maturity, vegetables are richer in lignin than herbs [34].

4.2.5 Proteins

Proteins are minor compounds of the plant cell wall. Three main classes of parietal proteins are distinguished: glycerin-rich proteins, proline-rich proteins and hydroxyproline-rich glycoproteins (exp: extensins). Peptide chains can be networked by ether bonds between two tyrosine molecules [36].

4.2.6 Tannins

Tannins are concentrated in the vacuoles of the plant cell [37]. They are composed of high molecular weight polyphenols (MM 500–3000). Their presence in trees, wooded shrubs and food products gives a bitter taste that can affect the animal's appetite and voluntary intake. Tannins can be divided into condensed tannins and water-soluble tannins. Condensed tannins (proanthocyanidins) are distributed in the broadest vesicles of the plant, while water-soluble tannins are restricted to dicotyledonous angiosperms which usually contain glucose as the central nucleus. Tannins affect grazing behaviour and therefore depress forage uptake in sheep [38].

5. Conclusion

Sheep have a gastrointestinal tract similar to that of other ruminants. The rumen plays a role in storing ingested foods, which are fermented by a complex anaerobic rumen microbiota population with different types of interactions. Sheep feeding is largely based on the use of natural or cultivated fodder, which is exploited in green by grazing during the growth period of the grass and in the form of fodder preserved during the winter period. Cellular carbohydrates play a role of metabolites or energy reserves; soluble carbohydrates account for less than 10% dry matter of foods, and the plant cell wall consists of primary wall and secondary wall.

Conflict of interest

The authors declare no conflict of interest.

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