Husbandry and Nutrition

Review

Action Mechanisms of Fibrolytic Enzymes in Ruminant Nutrition

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ABSTRACT

Background: Ruminants consume pasture and forages, but occasionally they do not have the necessary capacity for this, affecting digestibility. One of the strategies to improve quality is the utilization of exogenous enzymes that break down the structure of the cell wall, and permit better nutrient intake. **Aim.** To conduct a comprehensive study on the action mechanisms of exogenous fibrolytic enzymes in ruminant nutrition. **Development:** The plant cell wall is made of cellulose, hemicellulose, and lignin. The cellulases, hemicellulases, and lignocellulolytic enzymes are engaged in their degradation, being used satisfactorily in the diet to enhance digestibility with positive effects on other species' production. **Conclusions**: This practice favors greater nutrient availability for digestion and absorption, and it contributes to the improvement of physiological processes, and on many occasions, it is evidenced through livestock yield increases.

Key words: animal feed, cellulases, mannanases, xylanases (*Source*: *AGROVOC*)

INTRODUCTION

Ruminant rearing is one of the most relevant activities in agriculture. The meat and milk are first-need items, so their production and sales increase thanks to high consumption demands by the world population (García, 2020).

In tropical countries, ruminant nutrition is mainly based on pastures and forages; however, productivity and the nutritional value of plants depend on the existing climatic conditions, annual precipitation distribution, and other environmental and management factors (Roca-Cedeño *et al*., 2020). In these areas, the high temperatures raise plant tissue lignification, and consequently, their digestibility is reduced (Mendoza *et al*., 2014).

One of the strategies to enhance forage digestibility in tropical regions is the addition of exogenous fibrolytic enzymes (Kumar and Sridhar, 2021). Accordingly, the aim of this review

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paper is to conduct an in-depth study of the action mechanisms in the application of exogenous fibrolytic enzymes to feed ruminants.

DEVELOPMENT

Ruminant nutrition

Nutrition is one of the most relevant factors to increase the livestock potential during the different growth stages. Reaching proper animal weight requires adequate planning of available resources, so it is necessary to supply the necessary nutrients to the animals in order to meet their feeding needs and achieve higher productive development (Nunez *et al*., 2020).

In recent years, the increased prices of plant cellulosic fiber and feedstuffs led to a search for alternative sources of animal nutrition (Evan and Marcos, 2020). One of the proposals is the utilization of agro-industrial wastes for cattle nutrition in tropical areas (Escorza *et al*., 2019; Godoy *et al*., 2020)

However, the harvest residues are poorly digestible, and have low energy, mineral, and vitamin contents (Kumar and Sridhar, 2021). Nevertheless, their utilization through proper feeding systems, enables the use of locally-available agro-industrial wastes for cattle nutrition (Piracon, 2020)

The fibrolytic enzymes produced by anaerobic microorganisms are involved in the digestion of fiber, which takes place in the rumen. Therefore, the utilization of exogenous enzymes to treat low-quality feeds permits a reassessment of alternative sources of feeds for these species (Kumar and Sridhar, 2021). To better understand the mode of action of biocatalysts, it is important to know the chemical composition of the plant cellular wall.

The plant cellular wall

It is made of cellulose, hemicellulose, and lignin. In higher plants, cellulose appears in the form of microfibrillae within the primary and secondary walls, as a result of hydrogen bonds between the chains. It is an insoluble polymer made of glucose residues linked through glucoside bonds β(1,4), which are oriented in highly-arranged crystalline parallel domains with more disorganized amorphous regions (Lee *et al*., 1997).

Hemicellulose is the second most abundant structural polysaccharide in plants, which is associated with cellulose in most plant species (Bhat and Hazlewood, 2001). It is mainly composed of D-glucose, D-galactose, D-mannose, D-xylose, and L-arabinose units, which are bound in several combinations (Mendoza *et al*., 2014).

Lignin is strongly intertwined chemically, with the carbohydrate of the cell wall through ether bonds that make up an extensive grid, and it is recalcitrant to degradation (Moore and Jung, 2001). It is a complex, soluble polymer with phenylpropane unit branches, which reinforces the cellulose and hemicellulose bindings (Tarasov *et al*., 2018). It has a variable structure, and depends on the plant type, phenological stage, and the photosynthetic rate (Ortiz, 2010).

The decomposition of the plant cellular wall entails the synergistic involvement of several biocatalysts. Some of the most widely-used are cellulases, hemicellulases, and lignocellulolytic enzymes (Bajaj and Mahajan, 2019).

These enzymes are engaged in the degradation of the plant cellular wall

Cellulases

Cellulases are constituted by an enzyme complex that catalyzes the degradation of cellulose, and is formed by β-(1,4) endonucleases (E.C. 3.2.1.4), cellobiohydrolases (EC 3.2.1.91) and β-(1,4) glycosidase (E.C. 3.2.1.21). All of them work synergically and sequentially, their end product is glucose monomers (Bhardwaj *et al*., 2021).

According to the mechanisms suggested for cellulose degradation, enzymes β-(1,4) endonucleases catalyze the hydrolysis of internal bonds β-(1,4) glycoside of the amorphous region of cellulose, at random, with new ends that facilitate the action of cellobiohydrolases (CBH), and release units of cellobiose at the terminal ends. Among the CBH are the CBH-I forms that act from the reducing end of the cellulose chain, and the CBH II, which release cellobiose from the nonreducing end (Kumar and Verma, 2020). When the amorphous cellulose areas are degraded, the hydrolysis of the crystalline region takes place thanks to the synergistic action of endo and exocellulases. The β-glucosidases hydrolysis the cellobiose into glucose (Jørgensen *et al*., 2007).

Hemicellulases

Hemicellulases constitute a group of enzymes that catalyze the hemicellulose degradation reactions. Because of the variability of the hydrolyzing substrates, they can be classified depending on the type of hemicellulose or bond broken. Among them are xylanases, β-mannanases, xylosidases, arabinases, and galactosidases (Iráizoz, 2011)**.** Some of the most commonly used for animal nutrition are the xylanases, cellulases, and β- mannanases (Craig *et al.*, 2019; Saeed *et al.*, 2019).

- **Xylanases**

The xylanases (EC 3.2.1.8) catalyze the hydrolysis of bonds β-(1,4) glycosides of xylane, at random, to produce xylo-oligomers (Malhotra and Chapadgaonkar, 2018). Xylane is the most abundant polymer in the hemicellulose of the plant cellular walls. It comprises between 20 and 40% of the biomass, so its degradation is fundamental to make proper use of the products of lignocellulosic materials, as a source of useful energy (Polizeli *et al*., 2005). This enzyme is used to treat diets with a high content of insoluble fibers for monogastric animal nutrition (Matos *et al*., 2018).

- **β-Mannanases**

The enzymes involved in the hydrolysis of mannane linear polymers are β-mannanases (EC 3.2.1.78), β-mannosidases (EC 3.2.1.25) and β-glucosidases (EC 3.2.1.21). Other enzymes like αgalactosidases and the acetyl-mannan esterases, are required to remove the substitutes of the lateral chain (Moreira and Filho, 2008).

The most outstanding enzyme of this complex is β-mannanase, which produces short β-(1,4) mannane oligomers, and then turn into mannose molecules due to the action of β-mannosidases (Chauhan, Puri, Sharma, & Gupta, 2012). These proteins catalyze the hydrolysis of β-(1,4)-D-mannanoside bonds of mannanes, galactomannanes, and glucomannanes, at random (Yamabhai *et al*., 2016).

Lignocellulolytic enzymes

These enzymes modify the lignin structure through oxidizing-reduction mechanisms. They are part of the lignin-peroxidase, manganese-peroxidase, versatile peroxygenase, and lacase complex. The utilization of these catalysts to pre-treat biomass is critical to access the polysaccharide matrix, an essential stage in efficient fiber degradation.

The covalent bonds of the lignin molecule are mostly aryl-ether, aryl-aryl, and carbon-carbon, and they are not hydrolyzed through typical mechanisms (Brink *et al*., 2019). The catalytic mechanism is based on the generation of intermediate free radicals with a high reactivity, which are capable of accepting or ceding an electron, and therefore, may generate the oxidation or reduction of these compounds. The lignocellulolytic enzymes act synergistically with the rest of the enzymatic complexes (Tarasov *et al*., 2018).

Mode of action of exogenous enzymes in ruminants

The mode of action of biocatalysts used in the nutrition of these species is a complex and significant issue tackled in current research. According to Velázquez-De Lucio *et al.* (2021), the action of every enzyme is different and interdependent; its inclusion in feedstuffs should be rational and careful to achieve the best possible effect. Besides, the enzymes act directly and indirectly on the substrates; for instance, on the lignocellulolytic complex, they degrade the lignin as the main effect. However, they also provide access to the nutrients bound to that structure, especially carbohydrates and proteins, as a secondary effect (Beauchemin *et al*., 2004).

Biocatalysts may change the food quality before consumption, through certain stimuli during rumen digestion, and/or the post-rumen digestive tract. Although the pH, temperature, and substrate type conditions outside the rumen not always favor the action of enzymes (Mcgrath *et al*., 2018). In the rumen, they act directly in the digestion of the food, or stimulate the digestive activity indirectly, in synergy with the microorganisms in the rumen (López-Ordaz *et al*., 2020). Likewise, the enzymes might stay alive in the back digestive tract, and contribute indirectly to nutrient absorption due to laccase reduction of the viscosity of the intestinal ingesta (Ojha *et al*., 2019).

Moreover, the conditions of the substrate affect the action of enzymes, which are more effective in the humid feeds than in the dry feeds, so the presence of water facilitates their solubility, and it is essential to reduce the polymers into monomers. According to Nsereko *et al*. (2000), the application of solid enzyme preparations does not favor the pre-ingestive interaction between the enzymes and the feeds.

The response to supplementation with fibrolytic enzymes is variable (Bedford, 2018). Among the factors that mediate the effectiveness of these additives are the type of enzyme, its stability and specificity of the action, the animals (species, age, and morpho physiology of the gastrointestinal tract), and the characteristics of the diets (Valdivia *et al.*, 2019). In that sense, the effect may be affected by the dose, the preparation of the product, the method of administration, and the enzymatic action mechanism (Tirado-González *et al.*, 2018).

Results of the application of exogenous enzymes in ruminants

The fibrolytic enzymes were not used in ruminant nutrition due to the hypothesis of their possible immediate hydrolysis by the rumen proteases. Besides, the rumen microorganisms were known to degrade the fibrous substrates (Beauchemin *et al*., 2004). However, studies conducted later, demonstrated the advantages of this practice in polygastric animals.

Research done in recent decades found that the enzymatic treatment of forages led to increases in fiber digestibility in *in vitro* and *in vivo* experiments (Iannaccone *et al*., 2022). Most authors coincide that exogenous enzymes enhance fiber digestion (Pech-Cervantes *et al*., 2021), even when it is only 15% of rumen activity (Rosser *et al*., 2022). The effects of fibrolytic enzymes on forage degradation are significant, though the changes in the molar portion of these compounds may be inconsistent, since they depend on the fibrous source, the doses administered, and their impact on rumen fermentation (Kumar and Sridhar, 2021).

The international literature reports the utilization of several enzymatic systems in ruminant production. Selzer *et al*. (2021) demonstrated that the digestibility of the neutral detergent fiber (NDF) and the acid detergent fiber (ADF) improved following the treatment using cellulases and xylanases. Da Costa *et al*. (2019) noted that xylanases are particularly important in ruminant nutrition, as they increase disease resistance, and reduce the environmental impact by reducing animal methane production. Likewise, research studies done by Santana *et al*. (2018) and Miranda-Romero *et al*. (2022), corroborated that the digestibility of the fibrous portion depends on the combination of enzymes, the dose, and the type of substrate used.

Another advantage of enzymatic treatment is the improvements in the quality of non-conventional feeds (Jimoh, 2018). Authors like Abid *et al*. (2019) used xylanases, exo and endonucleases to enhance the nutritional value of grape spirit, whereas Cornejo-Cornejo *et al*. (2020) used xylanases to improve *in vitro* digestibility of *Musa paradisiacal* L. pod husks, and Alberto (2020) reported improvements in the nutritional quality of wheat stalks and sugarcane bagasse digestibility after treatment with laccase isolated from mushrooms.

The exogenous enzymes also have a positive impact on milk production. For instance, Refat *et al*. (2018) reported increases in milk production and digestibility of dry matter by cows fed on silage (34$ barley), and treated with fibrolytic enzymes. Furthermore, Golder *et al*. (2019) found increases in milk yields in field experiments, as a response to the application of enzymes in cows, and associated it with the elevated digestibility of feeds after treatment.

Likewise, dairy yields, mean daily weight, and feed consumption improved in goats, with the inclusion of the enzymatic extract of *Pleorutus ostreatus* in the diet (Trejo *et al*., 2017). Mendoza *et al*., (2014) highlighted that the increase of dairy and meat yields after the treatment with exogenous enzymes responds to greater digestibility of NDF and ADF.

In turn, Bortoluzzi *et al*. (2019) and Qiao *et al*. (2018), demonstrated that the treatment using β-mannanases promoted the production of neutrophils, leukocytes, and macrophages involved in the reduction of somatic cell counts in the milk, which is a potential indicator of mastitis (López-Ordaz *et al*., 2020). This disease causes inflammation of the mammary gland, and it is associated with infectious factors leading to enormous economic losses in the dairy industry (Benić *et al*., 2018).

The addition of β-mannanase in Holstein-Friesen cows under advanced lactation could reduce the consumption of dry matter in 1.8 kg per cow, compared to the control (Tewoldebrhan *et al*., 2017). This reduction in consumption was attributed to a seemingly greater digestibility of dry matter, organic matter, and protein. Moreover, Kebreab, (2016) found that the addition of β-mannanases to the diet (0.10%) raised the nitrogen conversion efficiency, milk protein, weight gain, and udder hygiene of lactating cows, without affecting methane and fecal nitrogen depositions.

According to López-Ordaz *et al.*(2020), health improvements due to enzymatic supplementation occurs because the nitrogen requirements in animals are supplemented with the consumption of dry matter and the protein in the diet. That way, high energy costs due to the deposition of excess nitrogen may be prevented, with ensuing environmental and economic benefits.

Overall, the effect of exogenous enzymes on the degradation of dry matter, fiber hydrolysis, gas production, and milk yields, largely depend on the species, forage proportion and quality, and the number of ingredients included in the diet (Tirado-González *et al*., 2021).

CONCLUSIONS

This practice offers greater nutrient availability for digestion and absorption, and it contributes to better physiological processes, and on many occasions, it can be evidenced through cattle yield increases.

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AUTHOR CONTRIBUTION STATEMENT

Research conception and design: MMT, AVA, LCS; data analysis and interpretation: MMT, AVA, LCS; redaction of the manuscript: MMT, AVA, LCS.

CONFLICT OF INTEREST STATEMENT

The author declares the existence of no conflicts of interests.