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Review Article

An update on carbohydrases: growth performance and intestinal health of poultry

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Abstract

Poultry is an imperative domesticated livestock species that provides high quality protein and micronutrients as meat and eggs. In poultry production, feed is the single major input constituting 70–75% of total production cost. Feed mainly consists of cereal grains, those provide energy to the birds. However, these grains contain different levels of anti-nutritional factors such as non-starch polysaccharides (NSP). These NSP are indigestible by poultry birds due to the lack of vital endogenous enzymes (carbohydrases) thus increase intestinal viscosity which slower the migration and absorption of nutrients. Consequently, these NSP may also increase the chances for infection by inducing competition within gut microbiota for digestible nutrients. This affects bird's health and increases the production cost. Therefore, there is a need to find efficient and effective solutions for these problems. Carbohydrases supplementation have an important role in poultry diets with high NSP contents. Feed enzymes are being used from years to enhance growth performance and digestibility but have limited activity for selective ingredients. New generation carbohydrases with a board range of activity and stability help to degrade the complex substrates and improve growth performance of poultry. Present review summarizes the updated

literature on the use of carbohydrases to improve bird's performance and intestinal health.

Keywords: Nutrition, Veterinary science, Physiology, Microbiology, Structural biology, Biotechnology

1. Introduction

Livestock plays a key role in alleviation of poverty as well as food scarcity. Among livestock, poultry is one of the significant commodities that provide high quality protein and micronutrients through meat and eggs those are more easily taken up by the human body than plant based foods. In poultry farming, feed constitutes 70–75% of total production cost. Poultry feed is based primarily on cereal grains mainly corn/maize, wheat, sorghum and vegetable protein meals which are supplied to meet most of energy and protein requirements in the poultry diet. Recently, these grains are also being used for bio-fuel production. Due to this paradigm shift of farming from the food industry to bio-fuel industry and increase in the prices of these raw ingredients in international market open the ways to find out less costly and alternative sources of energy and protein for animal feed. The more affordable ingredients including barley, oat, triticale, rye, olive cake and sunflower meal (Al-Harathi, 2017; Teymouri et al., 2018; Waititu et al., 2018), play important role in substitution of corn, wheat and soybean but have some anti-nutritional factors which may affect growth performance and intestinal health of the birds.

Non-starch polysaccharides (NSP; soluble and insoluble), one of anti-nutritional factors, which are present in large amount in feed ingredients such as wheat, barley, sunflower meal, canola meal etc., and are indigestible by birds as they lack the endogenous enzymes necessary to digest the beta type of linkages present in these ingredients. Owing to lack of endogenous enzymes, that degrade dietary fibers (structural carbohydrates or non-digestible components that make up the plant cell wall) including high molecular weight soluble NSP, intestinal viscosity increased which slows down the migration and absorption of nutrients. Consequently, this affects bird's health and increases the production cost. Another concern for poultry producers is subclinical pathogenic challenges owing to the use of such low quality ingredients. These subclinical pathogens also provide a way to other pathogenic infections such as necrotic enteritis (Kaldhusdal, 2000). Immerseel et al. (2004) proposed that such infections were associated with water soluble NSP present in rye and barley which slow down digestion and leaving undigested nutrients for pathogenic microbial propagation. Therefore, there is a need to find the solutions for these problems. Exogenous feed enzymes (EFE) supplementation in poultry with high NSP diets showed improvement in nutrients availability as well as digestibility (Saleh et al., 2018; Zhou et al., 2009). These enzymes contribute to the growth performance with

improvement in intestinal health (histo-morphology and microbiota) of birds. Numerous studies had confirmed the supplementation of EFE to improve energy utilization and performance in chickens (Ravn et al., 2018; Zhou et al., 2009).

Keeping in view the above mentioned problems of high fiber diets, this review has been written to provide updated information about the use of carbohydrases to cope with these problems in the poultry with improvement in growth performance and intestinal health.

2. Main text

2.1. Feed ingredients and their composition

Poultry feed is primarily composed of cereal grains, protein meals and minerals/vitamins to meet energy and protein requirement of birds. Carbohydrates (polysaccharides) present in these ingredients broken down into mono-saccharides (glucose, etc.) to serve as energy source and have been classified on the basis of their location (structural/cell wall and storage/cell contents), nutritional/physiological values (starch and NSP) and analytical methods. Based on the analytical methods these dietary fibers are mainly classified as crude fiber (CF), neutral detergent fiber (NDF) and acid detergent fiber (ADF). These dietary fibers have also been classified as insoluble dietary fibers and soluble dietary fibers based on their digestibility as presented in Fig. 1a. Among these fibers, NSP are non- α -glucan heterogeneous group of polysaccharides with varying degrees of structure, size and water solubility. NSP include cellulose, hemicellulose (arabinoxylans), β -glucans, fructans etc. Cellulose, arabinoxylans, and β -glucans comprise most of the fiber in cereal grains fed to the poultry (Knudsen, 1997). Cellulose, water insoluble fiber with β (1–4) linked glucose molecules, is considered to be the major structural component of cell walls. Arabinoxylans are composed of a linear backbone of β (1–4) linked xylose units with side chains of arabinose and other sugars linked to carbon 2, 3, or 5 on xylose. Beta-glucans are composed of β -D-glucose polysaccharides with β (1–3) (1–4) glycosidic linkages. Arabinonxylans and β -glucans, however, are soluble in water. β -glucans solubility is related to both molecular size and the types of bonds in the polymer. Luchsinger et al. (1965) showed that water soluble β -glucans had fewer long sequences of β (1–4) bonds before interruption with a β (1–3) bond. The longer the sequence of β (1–4) bonds, the more it behaved like cellulose. The degree of branching varies between cereals as wheat and barley have higher degree of polymerization and molecular weight than that in corn. Degradation of these fibers using various exogenous microbial enzymes has been presented in Fig. 1b.

Wheat contains larger amounts of high molecular weight arabinoxylans with 7.3% of total dry matter and showed considerable anti-nutritive properties (Choct, 2006; Knudsen, 2014), while barley contains large amounts of β -glucans with a high ratio

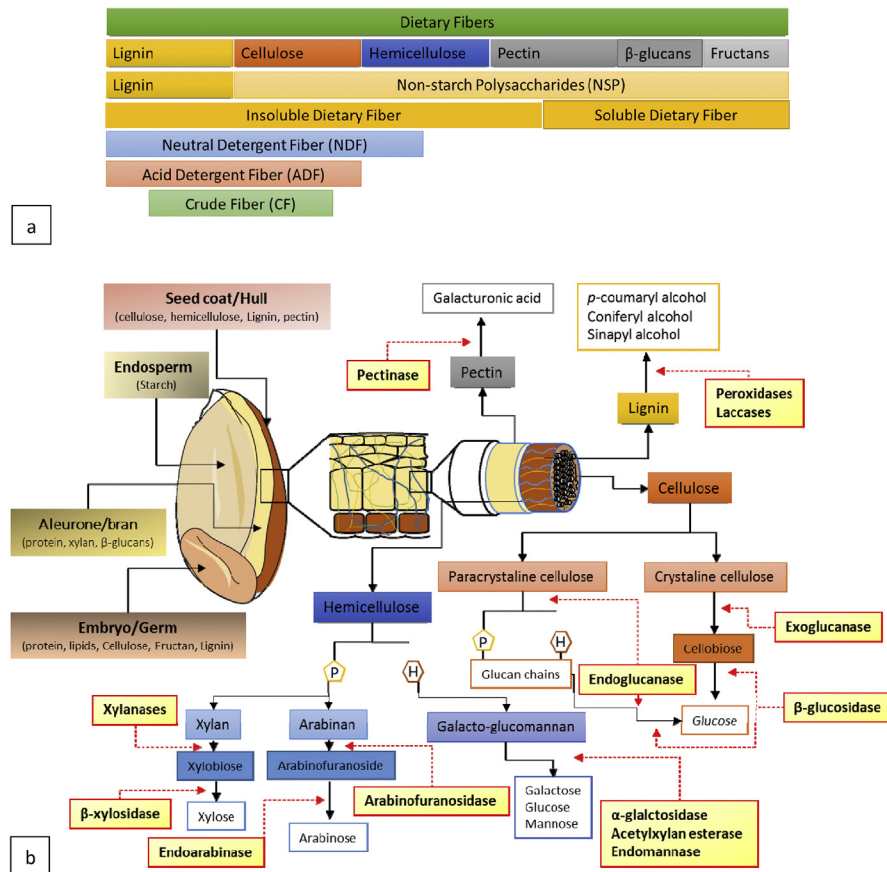


Fig. 1. An illustration presenting (a) classification of dietary fibers, (b) distribution of dietary fibers in grains and sites for enzymatic attack on these fibers.

of β (1–3) to β (1–4) bonds. The gels formed when these two grains are fed together and reduce nutrient digestibility and availability. Non-viscous grains, such as corn, have cell walls made up primarily of low molecular weight arabinoxylans and small amounts of β -glucans, which do not cause the viscosity problems. Soybean and canola meals contain arabinoglactans, galactans, xylans and β -glucans as structural components of cell walls, but their levels are relatively low (Knudsen, 1997; Slominski, 2011). They have higher levels of the oligosaccharides (stachyose and raffinose) along with pectin. The pectin found in soybean meal are composed of a backbone of galacturonic acids with side chains containing rhamnose, galactose, arabinose, xylose, and fructose (Kawamura et al., 1966; Slominski, 2011). Pectin is associated with cellulose in the cell wall and become soluble in the gastro intestinal tract (GIT). NSP have numerous mechanisms of actions in GIT.

2.2. Mechanisms of anti-nutritive effects of NSP

NSP act through various mechanisms to provoke anti-nutritive effects. When these soluble dietary fibers fed in bulk amount increase the viscosity of intestinal contents

by making viscous gels which decrease the rate of diffusion of endogenous digestive enzymes and substrates with hampered interaction at the mucosal surface (Choct et al., 1996). This increased viscosity also induces thickening of the mucous layer in the intestine (Hedemann et al., 2009) indicating that high concentrations of dietary soluble NSP in wheat which minimize the digestion and absorption of nutrients through its physicochemical effect in the intestinal tract. Consequently, slow down rate of digestion and absorption of nutrients, decrease feed intake and body weight gain. It has been estimated that 400–450 kcal of digestible energy per kg of feed remains undigested due to the NSP contents present in corn-soybean meal diets (Cowieson, 2010). On the other hand, insoluble NSP present in the cell wall entrap starch, protein and other nutrients inside called “cage effect” and hinder the access of endogenous enzymes to digestible nutrients (Bedford and Partridge, 2010).

In addition to direct effects on the gut morphology and physiology, NSP also have indirect effects (Danicke et al., 1999). Soluble NSP lower the oxygen tension in the small intestine thereby favors the development of anaerobic microflora that can lead to production of short chain fatty acids (SCFA)/volatile fatty acids (VFA) and toxins by some anaerobic organisms (Simon, 1998). This induces lymphocyte infiltration in the gut wall and apoptosis of epithelial cells (Teirlynck et al., 2009). Thus, this change in the gut ecology (from an aerobic or facultative anaerobic environment to a strictly anaerobic one) may induce gastrointestinal stress and severely afflict the normal physiological processes.

2.3. Carbohydrases and growth performance

Commercial use of carbohydrases/feed enzymes in poultry diet started in late 1980's and early 1990's due to their ability to correct wet litter conditions, digestion and apparent metabolizable energy problems owing to high fiber diets. The enzymes are being used to balance the adverse effects of NSP on gut health/performance of poultry (Aftab and Bedford, 2018). Previous studies demonstrated that fungal and bacterial enzymes effectively degrade β -glucans and arabinoxylans present in wheat, barley, rye and oats based diets (Odetallah et al., 2002; Silva and Smithard, 2002). Selection of EFE is an important task which mainly depends on the feed ingredients. Abdel-Hafeez et al. (2018) suggested that enzyme supplementation with potato peels and sugar beet pulp in broiler diets improved body weight, feed intake and feed conversion compared to control group. Cardoso et al. (2018) reported exogenous enzyme supplementation improved the nutritive value of wheat based diet with high extract viscosity and low endogenous endoxylanase activity in poultry. Yildiz et al. (2018) proved that xylanase based enzyme supplementation improved egg production and decrease intestinal viscosity regardless of the inclusion rate of distillers dried grains with solubles (DDGS). Some other recent studies on the use

Table 1. Carbohydrases, inclusion rates and their effects using various feed ingredients.

Enzyme	Substrate	Enzyme inclusion rate	Response	Reference
β-glucanase, xylanase, cellulases	Hull-Less Barley	0.5 g/kg	Supplementation of Enzyme Cocktail in the finisher diet can decrease the adverse effects of high level of Hull-Less Barley on performance of broiler chickens.	Teymouri et al. (2018)
Glucanase, Xylanase, Cellulase-complex	Raw faba bean	250 mg/kg	Enzyme supplementation with faba bean less than at 50% inclusion rate improve egg production performance.	El-Hack et al. (2017)
Glucanases	Barley	52.5 U/kg of barley	Improve the nutritive value of barley based diets.	Fernandes et al. (2016)
Xylanase	Corn-soybean meal	50–200 U/Kg	Energy utilization and digestibility of crude protein and dry matter increased with xylanase.	Stefanello et al. (2016)
Xylanase, amylase, protease	Corn/soy/wheat	2,000 U/kg, 200 U/kg 4,000 U/kg	Enzymes with direct fed microbial improved caloric efficiency by reducing the amount of energy needed to produce one kg of body weight gain.	Flores et al. (2016)
Glucanase, Amylase, Protease	Corn/soybean meal	250 g/ton	Improve nutrient digestibility.	Allouche et al. (2015)
Multi-glycanase	Wheat and barley	180 unit/g	Improve growth rate and carcass traits, blood parameters and gut physicochemical properties of broiler chickens.	Kalantar et al. (2015)
Xylanase	De-oiled rice bran	10 g/100 kg feed	Breast muscle, thigh muscle and giblet weight (percentage) was significantly increased.	Anuradha and Roy (2015)
Xylanase, cellulase and β-galactosidase	Rice bran	4520 U, 4060 U, and 2700 U	Enhance cell wall hydrolysis of rice bran with increased nutrient digestibility.	Liu et al. (2015)
Xylanase, glucanase, mannanase	Wheat-soybean meal	500 mg/kg diet	Enzyme supplementation increase body weight, decrease digesta viscosity, lowered ileal <i>C. perfringens</i> and <i>Lactobacillus</i> colonization.	Sun et al. (2015)
Xylanase, glucanase, cellulase	Wheat	0.5 g/kg	Improve growth performance, histomorphology and gut microbiota.	Agboola et al. (2015)
Glucanase, Xylanase	Wheat/corn	2500 U/kg, 250 U/kg	Enzymes stimulate performance in young birds and significantly improve ileal and cecal microbial profile.	Munyaka et al. (2015)
Glucanase	Barley	1500 U/kg	Improve the nutritive value of barley-based diets.	Costa et al. (2014)
Xylanase, Cellulase, Glucanase	Wheat offal	20% inclusion level	Reduced <i>Coliform</i> and <i>E. coli</i> counts while enhanced <i>Lactobacillus</i> counts.	Ohimain and Ofongo (2014)

of EFE, inclusion rate and their effects against various feed ingredients have also been presented in [Table 1](#).

Xylanases (hemicellulase) and β -glucanases (cellulase) are commonly used enzymes for degradation of NSP including arabinoxylans and β -glucans in poultry feed. It has been studied that use of xylanases and β -glucanases in wheat and barley diets reduced the viscosity of the digesta by 30–50% and 300%, respectively ([Juanpere et al., 2005](#); [Mathlouthi et al., 2002](#); [Wu et al., 2004](#)). Reduced viscosity leads to improvements in protein digestibility, apparent metabolizable energy, feed consumption, body weight gain, and feed conversion. Xylanases in commercial preparations are derived from both bacterial and fungal sources such as *Bacillus* spp., *Trichoderma reesei*, etc. ([Bedford and Partridge, 2010](#); [Raza et al., 2019](#)). Xylanases randomly breaks the arabinoxylan backbone resulting in production branched xylo-oligosaccharides ([Collins et al., 2005](#)). Those are then hydrolyzed by beneficial bacteria including *Lactobacillus* and *Bifidobacterium* species resulting in an increase in their population and a decrease in pathogenic bacteria such as *Clostridium perfringens* ([Sun et al., 2015](#); [Thammarutwasik et al., 2009](#)). Xylanases additionally restrain the expansion of the fermentative microorganisms in the small intestine by increasing the passage rate of digesta and nutrient digestion ([Choct et al., 1999](#); [Ohimain and Ofongo, 2014](#)). Thus, nutrient utilization is enhanced by decreasing the competition between the host and enteric microflora. Xylanases were also found to increase the overall apparent ileal digestibility of amino acids by 15% in a corn based diet while this improvement for wheat and rye based diets were 16% and 30%, respectively ([Cowieson and Bedford, 2009](#)). Addition of EFE also increased the apparent ileal digestibility of amino acids for broiler chickens fed corn soybean meal diets ([Cowieson et al., 2010](#); [Cowieson and Ravindran, 2008](#)). On the other hand, cellulases are produced by a wide spectrum of microorganisms in nature including bacteria, some fungi, and actinomycetes. Cellulases consists of various enzymes activities such as endo-glucanase (EC 3.2.1.4), exo-glucanase (EC 3.2.1.74), and β -glucosidase (EC 3.2.1.21) ([Morana et al., 2011](#)). The end-glucanase acts on the ends of the cellulose chain and releases β -cellobiose as the end product; exo-glucanase randomly attacks the internal O-glycosidic bonds, resulting in glucan chains of different lengths; and the β -glycosidases, act specifically on the β -cellobiose disaccharides and produce glucose ([Bayer et al., 1994](#)) as presented in [Fig. 1b](#).

Besides positive effects of EFE it has also been reported that in some cases enzyme supplementation did not show improvement in bird's performance. [Mohammed et al. \(2017\)](#) proved that the performance parameters (growth performance, carcass characteristics and meat quality) were not affected by the enzyme supplementation with diets fed to broiler. [Olgun et al. \(2018\)](#) also proved that enzyme supplementation was not effective in preventing the negative effects of wheat on performance and eggshell quality. Similarly, [Walters et al. \(2018\)](#) showed that enzyme

supplementation with corn screenings did not influence the final performance. These effects might be due to the variation in the chemical structure of NSP present in these ingredients or futility of enzymes. As NSP are not chemically uniform in composition, their profile varies from feedstuff to feedstuff (Van Soest, 1967). Thus, an enzyme that can achieve a good digestibility in a feedstuff may not be able to achieve the same level in another feedstuff. So, there is a need to new enzymes that can act on a broad range of substrates.

2.4. New generation feed enzymes

Cozannet et al. (2017), first use the term new generation feed enzymes (carbohydrases). These have an ability to improve the digestibility of all nutrients with unique heat stability, a broad pH range and high level of activity. Cozannet et al. (2017) also suggested use of next-generation or new generation carbohydrases rich in xylanase and arabinofuranosidase improve overall feed digestibility in broilers. Indeed, endo-xylanases help to degrade arabinoxylan chains by hydrolyzing the xylan backbone. However, multiple arabinose substitutions reduce the efficiency of xylanases, especially in corn and associated byproducts (Knudsen, 2014). Arabinofuranosidases can cleave arabinose from the xylose backbone and offer access to endo-xylanase activity (De La Mare et al., 2013). Consequently, enriching a preparation with debranching enzymes represents an efficient way to increase the overall enzyme effect. Recently, Cowieson & Klueenter (2018) also reported the role of new generation carbohydrases to remove the antibiotic growth promoters in poultry production. This might be due to the shifting of digestion to the interior intestinal segment thereby ‘starving’ the microbiome of the posterior gut, produce fermentable oligosaccharides from the fibrous material with a beneficial effect on the intestinal pH and enterocyte proliferation (Bedford, 2000). Similarly, Askelson et al. (2017) also proved that direct-fed microorganisms and exogenous enzymes improve growth performance in poultry and are potentially important alternatives to antibiotic growth promoters.

New generation carbohydrases production still needs a wide knowledge of poultry nutrition, biotechnology, rapid analysis of raw materials, dosage optimization for better performance under *in vitro* as well as *in vivo* situations.

2.5. Carbohydrases and intestinal health

Intestinal health concept is much comprehensive and dependent on knowledge about the diet, intestinal morphology and microflora (Fig. 2a). All of these components interact with one another in order to maintain proper functioning and dynamic equilibrium of GIT. Now a days much attention is given to formulate a least cost balanced poultry diets. Intestinal morphology has an important role in well-functioning GIT for the transport of nutrients from the lumen into systemic

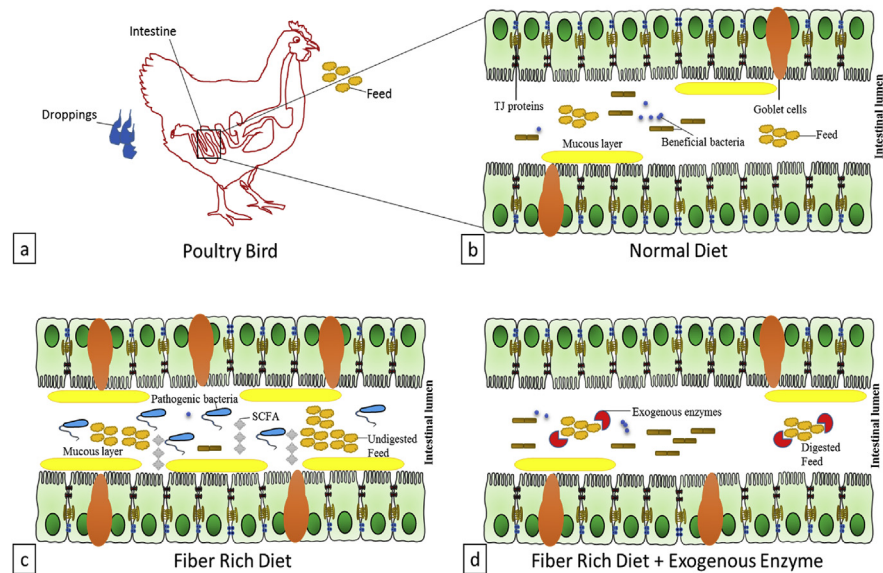


Fig. 2. Fibers, EFE and intestinal health. (a) poultry bird, (b) intestinal lumen presenting normal goblet cells, TJ proteins, mucous layer, feed, beneficial cells and enterocytes, (c) intestinal lumen presenting highly viscous environment with increased mucous, undigested feed, competition of host and microbiota for SCFA in small intestine, (d) intestinal lumen presenting carbohydrases, normal mucous, beneficial bacteria and digested feed.

circulation. The major barriers of the intestinal tract are mucus layer and tight junctions (TJ) of the epithelium as illustrated in Fig. 2b. Intestinal morphology (villus height, crypt depth and epithelial turnover rate) changes in response to exogenous agents, for example, presence or absence of food and pathological conditions (Gomide Junior et al., 2004). Deeper crypts indicate faster tissue turnover as they contain stem cells and considered villus factories (Awad et al., 2009). Intestinal mucins/mucous are high molecular weight glycoproteins secreted by goblet cells. In chickens, mucin2 are observed to be extensively expressed in goblet cells of colon and small intestine (Smirnov et al., 2005). NSP have been shown to increase mucin secretion (Tanabe et al., 2006) as illustrated in Fig. 2c. Therefore, NSP lessen the digestion and absorption of nutrients through its physicochemical effect in the intestinal tract. The GIT microflora predominantly consists of bacteria with lesser populations of fungi and protozoa. The chemical composition of digesta can alter the compositions of microflora in GIT because of different growth requirements and substrate preferences by bacterial species (Apajalahti, 2005). Langhout (2000) observed that dietary NSP considerably decrease beneficial bacteria while increases intestinal populations of pathogenic bacteria. As a result of high fiber diets, undigested/unabsorbed nutrients change in microbial populations in the gut (Bird et al., 2007; Choct et al., 1999; Mathlouthi et al., 2002).

EFE improve digestion in the small intestine and reduce the amount of substrate availability for putrefactive and starch utilizing bacteria in the large intestine. These

EFE help in the disease prevention by to reducing digesta viscosity (Pluske et al., 1997) as illustrated in Fig. 2d. Xylanase and glucanase supplementation in barley, wheat, oats, and rye based diets significantly raised caecal butyrate and acetate concentrations, but such effect was absent in hull-less varieties of barley and oats (Józefiak et al., 2006). Degradation and solubilisation of NSP by EFE increases available substrates (oligosaccharides or mono-saccharides) for microbial fermentation in the cecum (Cadogan & Choct, 2015) results in decreased VFA/SCFA production in the ileum suggesting decreased fermentation whereas caecal fermentation markedly increased. The increment in cecal fermentation resulted an influx of xylo-oligosaccharides which produces VFA/SCFA and energy from indigestible substrates and often leads to a healthier microflora (lactic acid bacteria, LAB) (Choct et al., 1999; Jia et al., 2009). Therefore, the NSP fraction supplemented with EFE represents another potential energy reservoir to increase the performance of broilers if rendered fermentable. While number of LAB adhering to the mucosa significantly dropped in 7 day old birds fed a wheat or rye based diet in combination with xylanase but such results were not observed in older birds possibly due to more starch digestion with age (Hübener et al., 2002). Similarly, arabinoxylooligosaccharides with a degree of polymerization <10 also recognized as prebiotic compounds, which pass undigested through the small intestine (Broekaert et al., 2011). They are fermented in the large intestine and promote growth of beneficial bacteria, such as butyrate-producing bacteria (Ravn et al., 2018).

In summary, the new generation carbohydrases with a suitable substrate activity, efficacy, thermostability and pH tolerance are necessary to improve the growth of birds.

3. Conclusions

Poultry diets with high soluble NSP increase intestinal viscosity hampered the nutrient digestibility and have deleterious effects on the bird's health and performance. New generation carbohydrases help in digestion of a broad range of dietary fibers with reduction of intestinal viscosity and competition between host and microbiota for SCFA in the small intestine and improve digestibility of nutrients. This also reduces the load of pathogenic microbes and improves intestinal health.

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