Review Article

Major cereal carbohydrates in relation to intestinal health of monogastric animals: A review

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ABSTRACT

Type, quality, and origin of cereals in diets of poultry and pigs could influence gut microbes and affect their diversity and function, thereby impacting the intestinal function of the monogastric animal. In this review, we focus on the major carbohydrates in cereals that interact directly with gut microbes and lead to the production of key metabolites such as short-chain fatty acids (SCFA), and discuss how cereal fiber impact intestinal health of poultry and pigs. An overview of how the cereals and cereals-derived carbohydrates such as beta-glucans, resistant starch, cellulose, and arabinoxylans could promote intestinal health and reduce the use of in-feed antibiotics in animal production are presented. The metabolic pathway utilized by microbes and the mechanism of action underlying the produced SCFA on intestinal health of monogastric animals is also discussed.

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1. Introduction

The concentration, type and source of carbohydrate fractions in the diet could potentially alter the balance of the gut microbiota, influence intestinal absorptive function and immune response in monogastric animals (Knudsen et al., 2017). Crop cereals are the source and major plant carbohydrates or fibers in poultry and pigs diets and account for more than two-thirds of the total energy intake in these animals (Bach Knudsen et al., 2012). Fibers in cereals include the non-starch polysaccharides (NSP), resistant starch (RS), fructo-oligosaccharides and non-carbohydrate polysaccharides such as lignin. Certain carbohydrate fractions in cereals appear to have beneficial influence on the intestinal health of poultry and pigs. This is due to the fermentation of the carbohydrate fractions by anaerobic bacteria under specific intestinal conditions, leading to the production of metabolites such as short-chain fatty acids (SCFA). Short-chain fatty acids are organic products mainly composed of acetate, propionate, and butyrate. Short-chain fatty acids possess functional roles in regulating host metabolism, immune system, and cell proliferation (Koh et al., 2016). Short-chain fatty acids are present at high concentrations in the cecum and proximal colon, where they act as energy sources in colonocytes (especially butyrate), but can also be transported to the peripheral circulation to act on the different body organs and peripheral tissues. They act as signaling molecules and regulate different biological processes, including the promotion of gut integrity, immune response and reduction of pathogenic bacteria population.

The presence of the cereal fibers in the intestine of the animal could lead to increased microbial diversity and strengthen the host mucins (Desai et al., 2016). Microbial metabolism of cereal grain fibers and components (especially cereal bran) could also release

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ferulic acid, which could serve in the modulation of gut physiology (Makki et al., 2018). Thus, it appears that cereal fibers (isolated or native in cereal) could favorably modulate the intestinal health of monogastric animals. An improved intestinal health is central to an increased growth performance and health status of monogastric animals. Therefore, it could be rational to suggest that the beneficial impact of functional cereal fibers on intestinal health might reduce the need for increased in-feed antibiotics in monogastric animal production.

The review would discuss the beneficial effects of the major grain carbohydrates such as starch, RS, cellulose, β-glucans, and arabinoxylans (AX) on intestinal health of pigs and poultry. A section in the review discusses various pathways engaged by the colonic bacteria to produce the SCFA, factors that affect the production of the SCFA and the important microbes responsible for the fermentation of carbohydrates to SCFA in poultry and pigs. Finally, it presents a brief overview of the mechanism of action of the produced SCFA on intestinal health of monogastric animals.

2. Cereal components and composition

The cereal grain is made up of the bran, germ, and endosperm. The bran is the hard outer layers of cereal grain containing the combination of aleurone and pericarp (outer bran layer). The cereal germ develops into a new plant and starch is stored in the endosperm. The non-digestible carbohydrates are found in each component but vary in type, level, physical and chemical characteristics (Table 1). The fibers in different grains, as well as their individual components, have different biological characteristics, which could relatively affect the functional effects of the fibers. Fibers in cereals include the non-starch polysaccharides (NSP), RS, fructo-oligosaccharides and non-carbohydrate polysaccharides such as lignin. The NSP are carbohydrate fractions predominantly linked by β-glycosidic bond including cellulose, hemicellulose, and pectic polysaccharides (arabinogalactans, pectins etc.) (Kumar et al., 2012).

However, the starch, RS, AX, mixed linkage β-glucans, cellulose, and the non-carbohydrate component lignin are the predominant polymers in cereals.

3. Cellulose

The main structural component of the cell walls in all cereal grains is made up of cellulose. Cellulose is an insoluble fiber and has a linear homopolymer of β-(1 → 4) linked glucose units. Several studies have examined the effects of isolated cellulose from cereals on intestinal health of poultry and pigs (Ndou et al., 2019; Zeitz et al., 2019). Many studies seem to show a relationship between the dose and particle size of dietary cellulose on the intestinal health of pigs and poultry. Cao et al. (2003) examined the effects of dietary cellulose levels on growth and gut function of 2-month-old Single Comb White Leghorn male chickens by feeding 3 purified diets that contained 0, 3.5% and 10% cellulose in equal amount of nutrients (including energy density) for 7 d. The authors found that total cecum microbial count and nutrient retention time was reduced in chickens fed diets supplemented with 3.5% cellulose, whereas chickens fed 10% dietary cellulose had significantly increased counts of uric acid-degradative bacteria such as Peptococcaceae and Eubacterium, including *Peptostreptococcus.* Increased uric-acid concentration could trigger inflammatory responses in the gut, including increased submucosal edema and release of extracellular DNA from host cells (Crane et al., 2016). Pascoal et al. (2012) included 1.5% purified cellulose, 3% soybean hull or 9% citrus pulp in diets of growing pigs, it was found that purified cellulose decreased the frequency of diarrhea as compared to other included components. Another study also showed that the intestinal morphology of chickens was improved and litter moisture content was reduced in birds supplemented with 0.5% insoluble fiber as compared to birds supplemented with 0, 0.3%, and 0.4% insoluble fibre levels (Rezaei et al., 2011). Two recent studies verified the influence of cereal-derived cellulose on nutrient absorption, SCFA production, intestinal serosa thickness and litter moisture content in monogastric animals. One noted that dietary cellulose functionalities could further be improved by using media milling to reduce the size of cellulose particles (Table 2). The authors found that milled cellulose enhanced capacity for holding water, binding bile acids and resulted in increased fermentability of cellulose into SCFA (Dubey et al., 2018). In another study, supplementation of nano-crystallised cellulose resulted in a dose-dependent increase in the weight and density of the cecum, which contributed to the overall intestinal development of birds (Han et al., 2016). A similar effect was observed in pigs (Lenis et al., 1996).

With this range of intestinal health benefits (increased nutrient digestibility, improved intestinal morphology, and modulation of gut microbiota) in pigs and poultry, cellulose appears to be effective in a reduced particle form and at a regulated inclusion rate (<10% of the diet).

The mechanism by which cellulose seems to positively influence intestinal health might be related to its fecal bulking tendencies (Topping, 2007), which is peculiar to insoluble fibers. Increased fecal bulk stimulates passage through the colon, resulting in faster transit time and thus a reduced time available for water reabsorption and surface adhesion of pathogenic bacteria. It was also suggested that dietary cellulose could also benefit the gut by stimulating the growth of beneficial bacteria, which in turn decreases the hepatic DNA binding activity of NF-κB, leading

Table 1
An overview of dietary cereal components.[1]

Component of cereals	Carbohydrate components	Description
Bran	Fructans, small amount of resistant starch	Highest in many dietary fiber levels and iron content. Digestible carbohydrate composition less than in endosperm. Presence of antinutrients (e.g. phytic acid)
Outer bran layers	Cellulose, lignin, hemicellulose (arabinoxylans)	
Aleurone	Cellulose, hemicellulose (arabinoxylans), β-glucans	
Germ	Cellulose, fructans, lignin, fat, B-vitamins, iron	Relatively low in dietary fiber level and nutrients like vitamins (vitamin B_5). Relatively high in iron content.
Endosperm	Cellulose, Hemicellulose (arabinoxylans, xyloglucans, and glucomannan), resistant starch, B-vitamins, iron	Least in dietary fiber level and highest in starch level.

[1] Adapted from Bernstein et al. (2013).

Table 2
Cereal carbohydrates and their major sources with determined intestinal health benefit.

Fiber	Major cereal source	Level of fiber, %[1]	Beneficial form (native or isolated)	Soluble or insoluble in water	Fermented end product	Intestinal health benefit
Beta-glucan	Hulled oat	28	Both	Soluble	SCFA	Immune activation, Improves the tight junction proteins and intestinal morphology
	Hulless oat	41				
	Hulled barley	43				
	Hulless barley	42				
Arabinoxylan	Wheat	81	Both	Soluble	SCFA	Improves the intestinal morphology and gut microflora
	Rye	89				
	Hulless barley	48				
Cellulose	Hulled oat	82	Isolated	Insoluble	SCFA	Improved nutrient digestibility, intestinal morphology, and modulation of the gut microbiota
	Hulled barley	39				
	Corn	17				
RS	All major cereals	Variable	Isolated	Soluble	SCFA	Modulation of the gut microbiota, Improves the tight junction proteins and intestinal morphology

SCFA = short-chain fatty acids; RS = resistant starch.
[1] Adapted from Jha and Berrocoso (2015).

to a reduction in pro-inflammatory cytokine response (Di Caro et al., 2019).

4. Starch

Starch is composed of glucose monomers, which are linked by α-glycosidic bonds. Starch digestion and absorption consist of 3 phases: the intraluminal phase, the brush border phase, and the glucose absorption phase. Starch is ingested, then enzymatically hydrolyzed, and finally absorbed as glucose for energy metabolism in the small intestine (Maggs et al., 2008). The digestibility of starch mainly depends on its physical structure (including the starch granule organization), which determines the accessibility of intestinal enzymes, and also on the ratio between amylose and amylopectin (Li et al., 2015; Olukosi et al., 2008). In addition, the contents of non-starch components such as lipids and protein, soluble NSP, which increase digesta viscosity, thereby slowing down nutrient absorption in the small intestine could impair starch digestibility (Singh et al., 2010). The amylose to amylopectin ratio, the type of dietary cereal or dietary processing method are mainly associated with poor digestibility of starch in cereals, which in-turn might affect intestinal health of animals (Choct and Annison, 2007; Högberg and Lindberg, 2004). Few studies have investigated the role of cereal's starch content on pigs and poultry intestinal health.

Li et al. (2015) investigated the effects of amylose to amylopectin ratio, extrusion, storage duration, and enzyme supplementation on starch digestibility of corn in cannulated pigs (13.20 ± 0.94 kg). The authors concluded that a lower amylose to amylopectin ratio resulted in greater starch digestibility in corn. In addition, the ileal digestibility of starch and energy in a low amylose to amylopectin ratio corn variety was also greater than that in a high amylose to amylopectin ratio corn variety, thus suggesting that amylose-rich grains are less digestible. Starch with high amylose content and low *in vitro* digestibility increased post-ileal nutrient flow and microbial fermentation and selectively promoted *Bifidobacterium* spp. in the distal gut of pigs (Regmi et al., 2011), which could be associated with the escaped RS to the lower gut. Apparently, a higher digestible starch content in a cereal would increase nutrient availability in the upper gut (small intestine) and could reduce the amount of escaped carbohydrate to the lower gut (Fouhse et al., 2017). However, the health benefits of the RS in the lower gut are increasingly evident.

5. Resistant starch

The escaped and undigested starch from the upper gut is termed RS. Resistant starch enters the lower gut, where it undergoes partial or total fermentation or degradation. Resistant starch could be classified into 5 subgroups: RS_1 or type 1, RS_2 or type 2, RS_3 or type 3, RS_4 or type 4 (chemically modified starch) and RS_5 or type 5 (amylose-lipid complex) (Zhao et al., 2018b). RS_1 are termed encapsulated starch because they represents starch that is resistant and in a physically inaccessible form. RS_2 are starch residues that are in a certain granular form and retains their structure and resistance to enzyme and feed processing. However, heat and moisture processing destroys most RS_1 and RS_2 in diets, but leads to the formation of RS_3. RS_3 are non-granular starch-derived materials. They are generally formed during the retrogradation (cooked and cooled) of starch granules. RS_4 describe a group of starches that have been chemically modified and include starches which have been etherised, esterified or cross-bonded with chemicals in such a manner as to decrease their intestinal digestibility. The acetylated high-amylose maize starch and the butyralated high-amylose maize starch are common forms of RS_4. The RS_5 are derived from starch that are processed to have a rearranged starch structure (molecules), in order to increase their resistant to intestinal digestive enzymes and render them a soluble polysaccharide (resistant maltodextrins) (M'sadeq et al., 2015).

Although there are limited long-term studies reporting the effect of RS on intestinal health of poultry or pigs (from 1-d-old or weaning stage to maturity), however, the available short-term evidence suggests that RS_2 and RS_4 from high-amylose maize could modulate gut microbiota, improve intestinal morphology and enhance intestinal immune response to stress (Table 3). For instance, RS_2 increases the fecal abundance of bacteria (*Ruminococcus bromii*) that importantly produces butyrate, whereas RS_4 increases *Bifidobacterium adolescentis* and *Parabacteroides distasonis* (Martínez et al., 2010). In a more recent study with sows to determine the effect of maternal diet supplemented with RS on piglet intestinal health. The authors included 33% pea starch in the diet of gestating and lactating sows, and found that the RS diet modulated the fecal microbiota of the sows during gestation, increasing the Firmicutes to Bacteriodetes ratio and the relative abundance of *Bifidobacterium* genera. However, the maternal diets supplemented with RS did not impact the colonic microbiota of their progeny, but an increased tight junction proteins (zonula occludens-1) was recorded in their progeny (Leblois et al., 2018). This provided evidence that RS could provide a better closure of the mucosa tight junctions of the progeny through maternal feeding of RS. M'sadeq et al. (2015) evaluated the role of RS in broilers challenged with necrotic enteritis. It was observed that apart from the improved absorptive function of birds fed diets supplemented with acylated starch (RS_4), the degree of specificity in SCFA delivery to the lower intestinal tract was increased, resulting in improved gut

Table 3

Type of RS	Description	Intestinal function
RS$_1$	Physically protected starch	Could modulate digestive disorders
RS$_2$	Ungelatinized resistant granules of starch	Modulate gut microbiota, improve intestinal morphology and enhance intestinal immune responses to stress
RS$_3$	Retrograded starch	Reduces intestinal pH, Modulate gut-microflora
RS$_4$	Chemically modified starches	Modulate gut absorptive function, tight junction proteins, and the gut microbiota population
RS$_5$	Amylose-lipid complex	–

RS = resistant starch.

health of the broiler chickens. This additionally suggest that RS$_4$ could increase the production of SCFA and act as an alternative for some specific functions of antibiotics in the gut. In another study, high-amylose starch was subjected to hydrothermal treatment and incorporated in the diets of young pigs, it was discovered that diets with increased RS$_3$ content promoted the production of SCFA at the distal end of the intestine, reduced intestinal pH, fecal and the proximal colonic *Lactobacilli* and *Bifidobacteria* numbers were increased, which had implications for improved gut health (Bird et al., 2007). This suggests that hydrothermal processing of cereals modified to be rich in RS might confer intestinal benefits to broiler chickens or pigs. However, the effect of hydrothermal treatment on other nutrients in the grain was not investigated. The mechanism by which RS favorably enhance intestinal health seems to be associated with its influence on intestinal microbiota, which produces the SCFA that modulates the gut immune and absorptive functions. The abundance and diversity of butyrate-producing bacteria along with decreased levels of pathogenic bacteria is associated with animals fed diets containing a high amount of RS (Haenen et al., 2013; Martínez et al., 2010). The produced SCFA from RS fermentation act as a link between the microbiota and the immune system by modulating different aspects of intestinal epithelial cells and leukocytes development, survival and function through activation of G protein-coupled receptors (free fatty acid receptor [FFAR] 2, FFAR3, G-protein-coupled receptor for nicotinate [GPR109a], and olfactory receptor 78 [Olfr78]) and by regulation of the activities of enzymes and transcription factors (histone acetyltransferase and deacetylase and the hypoxia-inducible factor) (Corrêa-Oliveira et al., 2016). Thus, it appears that modification of the RS in cereals (through processing methods, physical or chemical treatments, and transgenic approaches) or direct supplementation of isolated RS (RS$_2$, RS$_3$ and RS$_4$) might improve intestinal health of pigs and poultry.

6. Beta-glucans

Beta-glucans are water soluble fibers existing in high concentrations in oats and barley. Interestingly, the relative proportion of the fibre in the 2 cereals is relatively comparable (Talati et al., 2009). Beta-glucans can also be found in various bacteria, yeast, mushrooms, fungi and seaweed. The tertiary conformation of mushroom β-(1 → 3)-glucans, yeast and fungi (1 → 3) (1 → 6)-β-glucans is known to be important for immune stimulating activity, macrophage nitrogen oxide synthesis, and the limulus factor G activation (Ishimoto et al., 2017). However, the β-glucans in cereals mainly exist as (1 → 6) linkages in the main chain. The isolated β-glucans from mushrooms and fungi exerts high intestinal health effects because of their chemical linkage (Jacob and Pescatore, 2014). This indicates that the functionality of β-glucans on the intestinal health of poultry or pigs would largely vary according to the native sources and the inherent chemical linkages. Shao et al. (2013) showed that 100 mg/kg of β (1 → 3) (1 → 6) extracted from

Saccharomyces cerevisiae increased mRNA expressions of tight junction proteins, improved nutrient digestibility and villus to crypt ratio of broiler chickens. Broiler chickens fed dietary supplemented yeast-derived β-glucan and experimentally challenged with *Eimeria* spp. also showed favorably modulated intestinal mucosal immune response and reduced tissue lesion severity (Cox et al., 2010). Similarly in pigs, dietary inclusion of β(1–3) (1–6)-D-glucan from yeast stimulated growth and enhance immune parameters (Vetvicka and Oliveira, 2014). These studies suggest an increased beneficial effect of β-glucans from fungi on intestinal health of pigs and poultry. However, studies comparing the effect of cereal-derived and fungi-derived β-glucans on intestinal function of monogastric animals are rare. Also, limited studies have examined the role of cereal-derived β-glucans on poultry or pig intestinal health, probably because of its limited intestinal functionality as compared to the fungi-derived glucans. However, one recent study demonstrated that native β-glucan in barley was enhanced through improved agronomical conditions and it was offered to growing pigs. The dietary treatments were as follows: low quality barley diet, low quality barley diet containing β-glucanase and β-xylanase enzyme supplement, high quality barley diet, high quality barley diet containing β-glucanase and β-xylanase enzyme supplement. It was reported that the production of SCFA was increased and the population of beneficial bacteria such as the *Lactobacillus* spp. was positively influenced in pigs fed high quality barley based diet. Strikingly, enzyme supplementation had no effect on both types of barley. The authors attributed the beneficial effect of the high quality barley diet to the higher β-glucan content in the diet (Clarke et al., 2018). Broiler chickens were also fed enzyme supplemented (glucanase-xylanase-protease complex) oats and barley based diets (finely grounded) from d 1 to 35, and the authors reported increased SCFA concentrations, reduced intestinal viscosity and higher weights of gut organs in the birds fed the enzyme supplemented oat or barley based diets (Jozefiak et al., 2006). This suggests that an improved agronomical or crop genetic manipulations with or without exogenous enzyme supplementation could release the enormous potentials of the stored β-glucan in oats and barley for improved gut health of pigs or poultry. It could be additionally suggested that isolated β-glucan from fungi or mushroom could be incorporated in cereals through physical or biological means to increase their inherent potentials for improved gut health in animals.

In human nutrition, the potentials of carbohydrate fractions, especially the β-glucans in cereals have been well adapted to reduce many cardiovascular disease and intestinal related complications (Jenkins et al., 2002). One of the suggested modes of action of β-glucans is through its potentials in wound healing. Vascular injury may contribute to the pathogenesis of cardiovascular disease and β-glucans such as zymosan seems to have increased beneficial effect on wound healing (Browder et al., 1988; Kibos et al., 2007). Therefore, cereals could be considered as both an energy and functional ingredient.

The metabolic effects of β-glucans is associated with its fermentation in the hind gut to yield larger amounts of propionate and butyrate (Queenan et al., 2007). In stressful or pathogenic situations, it directs cellular pathways to act as a pro-inflammatory immune stimulator or simply act as an anti-inflammatory modulator in a normal health situations (Teng and Kim, 2018). The potentials of β-glucan that resides in cereals are yet to be clearly elucidated under immune challenging situations in poultry or pigs.

7. Arabinoxylans

Arabinoxylans, also called pentosans, are mainly composed of xylose and arabinose chains. They are localized in the cell walls of starchy endosperm, aleurone, in the bran tissues, as well as in the husk of some cereals. They account for approximately 70% of the non-starch polysaccharides in wheat bran and 90% in the wheat endosperm, whereas in barley, the aleurone cell wall is composed primarily of AX with smaller amounts of AX in the endosperm (Bacic and Stone, 1981; Lu et al., 2000).

The AX from rye and wheat are to a large extent soluble, whereas the solubility of AX found in corn and sorghum is comparatively lower (Knudsen, 2014). Interestingly, the AX in each component of a cereal (bran, aleurone or endosperm) also varies in intestinal solubility and functionality (Glitso et al., 1998). However, isolated AX from the aleurone cell wall shows the highest degree of functionality on the intestine (Glitso et al., 1998). Studies incorporating isolated AX from cereals and native AX in cereals have reported beneficial effects on the intestinal health of pigs and poultry. The degree and profile of substitution, molecular weight as well as the xylose to arabinose ratio of AX in cereals seems to primarily influence the increased potential of AX for intestinal and immunomodulatory function in piglet and poultry.

Several studies have tested the effect of isolated or cereal-derived AX on pig or poultry intestinal health. In one study, 5 groups of 6 pigs were each fed one diet based on wheat starch only, or treatment diets in which some wheat starch was replaced by 10% AX, or 10% oat-derived glucans, a combination of AX and glucan (1:1), or completely replaced with ground whole wheat (Gorham et al., 2017). The authors concluded that the presence of whole-wheat grain and/or isolated carbohydrate fractions, such as AX, could increase caecum bacteria diversity and improve gut health. The study further showed that cereals-derived AX and β-glucans could have an increased synergistic effect on the intestinal health of pigs. Similarly, in poultry, a synergistic effect of wheat bran with inulin was reported. Increased villus height in the jejunum and ileum, and increased villus height to crypt depth ratio, SCFA and diverse microbial profile were found in chicks fed diets supplemented with 10% wheat bran and 2% inulin (Li et al., 2018). The authors attributed the improved intestinal morphology, diverse microbial profile and increased colonic butyrate levels of the birds to a synergistic effect of the native AX and the supplemented inulin. This implies that cereals carbohydrate fractions might exhibit synergistic effects on gut health.

Nielsen et al. (2014) fed diets rich in AX (rye flakes and wheat bran) to pigs for 3 wk. The authors found that the AX rich diets significantly increased the butyrogenic microbial species (beneficial gut microbes) such as *Faecalibacterium prausnitzii, Roseburia intestinalis, Blautia coccoides–Eubacterium rectale, Bifidobacterium* spp. *and Lactobacillus* spp. and the concentration of SCFA in the piglets. This shows that utilization of 2 natural sources of AX could also enormously benefit the gut of animals. However, wheat and rye cultivars are the primary sources of AX in single stomach animal diet, but are faced with the challenge of wide variation in chemical composition, energy contents, and amino acid digestibility (Zhao et al., 2018a). This limits the potentials that wheat and rye cultivars could provide in animal feed and nutrition. However, the promising prospect of applied genomic selection and enzyme supplementation might increase the availability of the cereal bioactive carbohydrate to the animals (Juliana et al., 2018).

Gallardo et al. (2018) suggested that the combination of a multicarbohydrase containing 700 U α-galactosidase, 2,200 U galactomannanase, 3,000 U xylanase, and 22,000 U β-glucanase per kg of diet and phytase (Phy, 500 FTU per kg of diet) could improve the nutritive value of cereals and cereal byproduct (wheat bran) in poultry bird, whereas Tiwari et al. (2018) suggested that only xylanase, mannase or their combination is sufficient to improve the nutritive and functional values of AX and other bioactive carbohydrates in cereals and co-products for growing pigs and broiler chickens. These authors supposed that either a multi- or single enzyme supplementation could enhance the cereals bioactive carbohydrates for improved intestinal function in animals.

8. Classification and digestion of the cereal carbohydrates

Carbohydrates could be classified according to their chemical, nutritional, or physiological effects (Cummings et al., 1997; Englyst and Englyst, 2007). The linkages, units, degrees of polymerization (DP), and functional groups of carbohydrates are considered under the chemical classification, whereas the nutritional classification classed carbohydrates according to the degree of their digestion, absorption or fermentation in the upper or lower digestive tract. The health effects of carbohydrates are considered under the physiological classifications.

All carbohydrates with at least 2 units of carbon chains must be enzymatically broken into monosaccharides before they could be absorbed in the small intestine and utilized by the animals for body needs. However, monosaccharides such as glucose, fructose, and galactose are absorbed in the small intestine. Disaccharides (such as lactose and sucrose) and polysaccharides (such as starch) are the digestible carbohydrates. They are digested in the mouth and in the small intestine by specific endogenous enzymes that specializes in carbohydrate hydrolyzation (e.g the disaccharidases). Other polysaccharides that are not digested in the mouth and small intestine, such as the RS and non-starch polysaccharides are classed under the fermentable carbohydrates (Fig. 1). The fermentable carbohydrates are not digested and absorbed in the small intestine but are metabolized by the commensal bacteria in the large intestine. The non-fermentable or poorly fermented carbohydrates are mostly excreted in the feces without passing through digestion in the small and large intestine of the monogastric animals. Bacteriolytic fermentation of some of the poorly fermented carbohydrates could occur at the distal end of the large intestine.

Generally, the cereal polysaccharides (starch, NSP) have a DP $\geq$ 10. Fiber (including NSP and RS) and sugar alcohols are famously regarded as the fermentable carbohydrates (Bach Knudsen et al., 2012). Fibers are present in high concentrations, while sugar alcohols are present in low concentrations in major cereal grains used in monogastric diets. The fermentation of fibers in the colon yields SCFA and gases (carbon dioxide, hydrogen, and methane). The nutritional consequences of the produced SCFA are the primary factor responsible for the majority of the health benefits associated with the major cereal carbohydrate fractions.
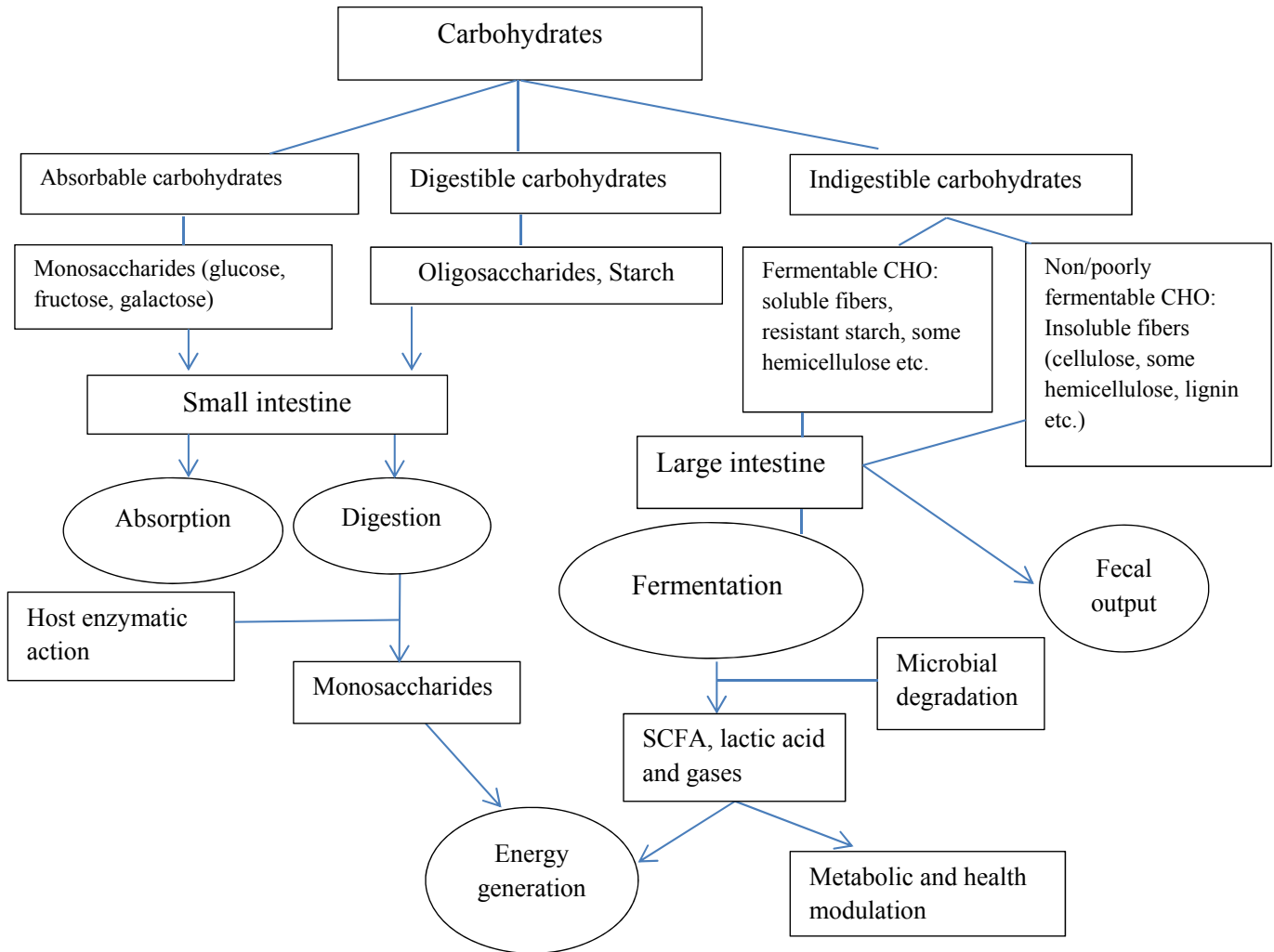
Fig. 1. An overview of carbohydrates and their metabolic end products. SCFA = short-chain fatty acids.

9. Colonic carbohydrate, short-chain fatty acids, and intestinal health

This section briefly discusses various pathways engaged by the colonic bacteria to produce the SCFA, factors that affect the production of the SCFA and the important microbes responsible for the SCFA production in poultry and pigs. The escaped carbohydrate and fiber from the upper gut are important energy sources for cecum and the colon-residing microbiota. The anaerobic bacteria activate several metabolic pathways, constituted of key enzymes to metabolize the dietary fibers for the production of metabolites such as SCFA.

Different species of animals exhibit variable population of the gut microbes that produce the SCFA. However, there seem to be more similarities than differences in the gut microbial composition of chickens and pigs. The relative abundance of the commencing intestinal colonizer (*Escherichia coli.*) is the highest in the first 2 wk of life in both chickens and piglets. However, in the pigs, coming after the *E.coli* are major representatives of Gram-positive Firmicutes and Gram-negative Bacteroidetes phylum. The major families from phylum Firmicutes include Ruminococcaceae, Lachnospiraceae, Veilonellaceae, and Lactobacillaceae. The major families from phylum Bacteroidetes include Bacteroidaceae dominating in suckling piglets and Prevotellaceae dominating in postweaning

piglets and adult pigs. Porphyromonadaceae is the last common family present in pig gut microbiota (Cousin et al., 2012; Guevarra et al., 2019). In chickens in commercial production, a different Gram-positive Firmicutes dominate in the caecum. However, family composition is the same as in pigs and includes Ruminococcaceae, Lachnospiraceae, Lactobacillaceae, and Veilonellaceae with representatives of Veilonellaceae appearing among the last ones (Zhang et al., 2018). Gram negatives from phylum Bacteroidetes at about 4-wk-old chickens. Unlike pigs, the first colonizers originate from the family Rikenellaceae, followed by Barnesiellaceae, Bacteroidaceae, Prevotellaceae and Porphyromonadaceae (Consortium, 2017). Generally, in the growing pigs, the main lower gut bacteria composition includes: *Bacteroides* spp.*, Butyrivibrio* spp.*, Clostridium* spp.*, Escherichia* spp.*, Eubacterium* spp.*, Fusobacterium* spp.*, Lactobacillus* spp.*, Peptostreptococcus* spp.*, Prevotella* spp.*, Ruminococcus* spp.*, Selenomonas and Streptococcus* spp. (Leser et al., 2002).

There is a direct relationship between the escaped carbohydrate and the existing bacteria population or proportion in the colon, thus influencing the produced SCFA in pigs and poultry (Macfarlane and Gibson, 1995). The primary SCFA present in the colon are acetate, propionate and butyrate existing in less than 6 carbon atoms, with straight and branched-chain conformation. Lactic acid (a non-SCFA) is also produced as a result of fermentation of undigested carbohydrates in the colon but the presence of some bacteria

species such as *Eubacterium hallii* prevents its accumulation in the colon (Flint et al., 2015).

Among the SCFA, acetate is the most abundantly produced. It accounts for over 50% of the total SCFA detected in the feces of monogastric animals (Louis et al., 2007). Over 70% of the produced acetate is from enteric bacteria fermentation of the undigested carbohydrates. The remaining percentage appears to be contributed by the acetogens (some particular bacteria and archaea) through the Wood−Ljungdahl pathway (Miller and Wolin, 1996). The pathway involves the reduction of carbon dioxide to carbon monoxide and formic acid or directly into a formyl group. The formyl group is reduced to methyl group which later forms the acetyl-coenzyme A (CoA) through a union with CoA and carbon monoxide (Ragsdale, 2006).

Butyrate is formed primarily from the butyryl-CoA/acetate-CoA transferase pathway by the butyrate-producing bacteria. Bacteria in the order Clostridiales (Firmicutes) are suspected to possess an increased butyryl-CoA:acetate CoA transferase activity (Levine et al., 2013). In the Lachnospiraceae and Rumincoccaceae family of the Firmicutes group, *E. rectalel Roseburia* spp. and *F. prausnitzii* that are well recognized for increased butyrate producing capability (Kien and Blauwiekel, 2008).

The succinate pathway seems to be the dominant route of propionate formation by the bacteria in the *Firmicutes* and *bacteriodetes* group (Salonen et al., 2014). Although, the acrylate pathway (propionate production from lactate) could be secondarily employed by the Veillonellaceae and Lachnospiraceae bacteria, while the propanediol pathway involves the conversion of deoxy-sugars to propionate and it is utilized by the Proteobacteria and members of Lachnospiraceae to form propionate (Reichardt et al., 2014). The specificity of different bacteria groups for the production of SCFA further relates to the substrate type. The *Ruminoccocus bromii* and diverse Lachnospiraceae seems to be in association with resistant starch and the AX fermentation (Salonen et al., 2014; Walker et al., 2011).

Ivarsson et al. (2014) fed 4 different fiber sources rich in either AX or pectins to pigs, and found differential response of the ileal and fecal microbiota composition to varied dietary non-starch polysaccharide compositions. In the study of Walugembe et al. (2015), it was observed that the metagenomics of broiler and layer chickens respond differently to dietary levels of fiber. *Helicobacter pullorum* and *Megamonas hypermegale* were increased in broiler chicks fed dietary high fiber and the opposite was found in the laying chicks group, while an increased *Faecalibacterium* population was observed in broiler chicks fed dietary low fiber and a decreased population of the same bacteria was found in laying chicks fed the same diet. This suggests that the diversity of SCFA producing bacteria might be under not only the influence of type and amount of available carbohydrate in the colon, but also the different types of animals. In addition to the above-mentioned factors, high bile salts concentrations, high or low pH, and low concentrations of trace minerals (e.g. Fe) could also influence SCFA-producing microbial population in the gut (Flint et al., 2015). Therefore, the role of cereal fiber in relation to some of these factors may be important for the overall intestinal health of the animal.

10. Short-chain fatty acids and the intestinal health

The intestinal health includes a balanced gut microbiota, effective immune regulation, and optimal nutrient utilization or absorption. Short-chain fatty acids act as a signaling molecule and regulate biological processes that protect the intestinal health of the host (Koh et al., 2016). Increased goblet cell differentiation and the expression of mucin-related genes are associated with increased acetate and propionate producers (Vital et al., 2013). However, overproduction of these SCFA could be harmful to the intestinal cells. To prevent the over-production of intestinal mucus which could contradict its beneficial effect, an increased acetate consumers and butyrate producers reduces the effect of acetate on mucus, thereby maintains an appropriate structure and composition of the gut epithelium (Wrzosek et al., 2013). Mcrorie and Mckeown (2017) further reported a mechanical stimulation of the gut epithelial to secrete mucus, which is associated with the effect of the SCFA on mucus thickening (Fig. 2). The SCFA also interacts with the enterocytes and dendritic, type 1 T helper, type 2 T helper, and Treg cells to modulate the adaptive immunity into pro- and/or anti-inflammatory action. Extracellular activity via SCFA-specific G-protein coupled receptors and intracellular inhibition of histone deacetylases by
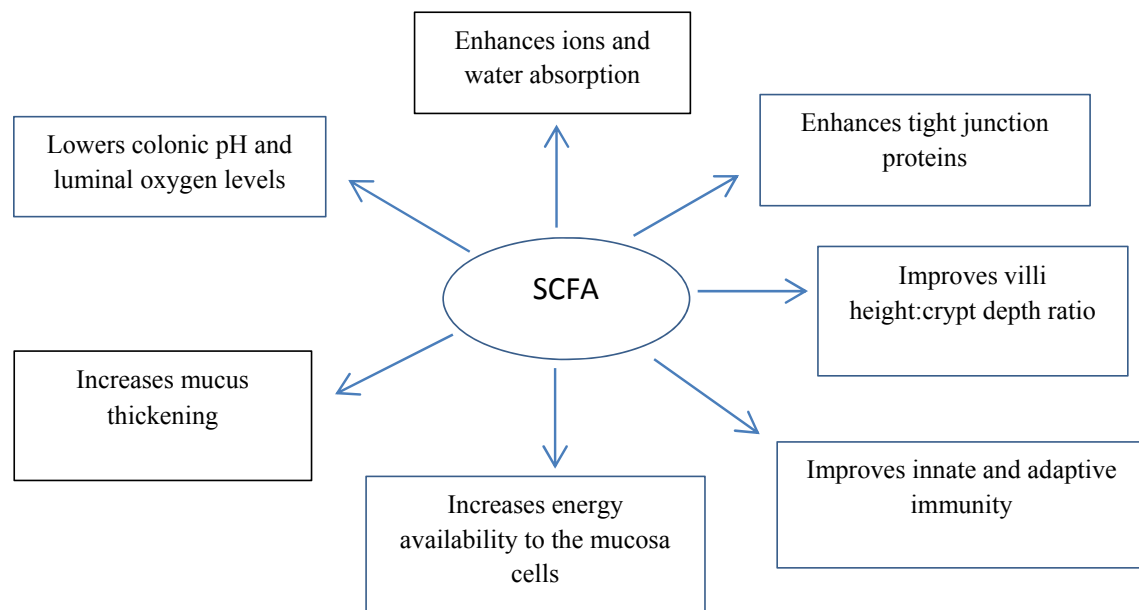

Fig. 2. Summary of beneficial effects of short-chain fatty acids (SCFA).

SCFA was also reported (Gill et al., 2018). Sunkara et al. (2011) reported that butyrate induced the synthesis of endogenous host defense peptides (HDP) gene expression, inflammatory cytokine production, phagocytosis, and oxidative burst capacities in broiler chicken cells. The HDP exhibit a broad spectrum anti-microbials potentials against bacteria, enveloped viruses, fungi, and protozoa by direct binding and lysis of microbial membranes (Sunkara et al., 2011), which prevents the development of resistance to HDP in pathogens. Moreover, porcine β-defensin (pBD) 2, pBD3, epididymis protein 2 splicing variant C (pEP2C), and protegrins were induced markedly in response to increased colonic butyrate concentration (Zeng et al., 2013). Taken together, these observations highlight the principal role of SCFA, in particular butyrate, in the regulation and maintenance of immune and intestinal health of poultry and pigs.

11. Perspectives

Cereal carbohydrates possess enormous functional qualities that could exert intestinal health benefits. Improved intestinal health would increase animal performance and could maintain optimum health function. The significant variation in the functional carbohydrate content of major cereals used in different regions for animal production seems to affect their functionality and relationship with the intestinal health. Thus, it appears that increased effort to improve cereal composition (fibers or carbohydrates) for increased energy and intestinal health benefits is warranted. Improved agronomical conditions and technologies (genetic manipulations) could increase the functional carbohydrates in both the major and minor cereals that are available for animal nutrition. This could be carried out in harmony with the principles of regulatory authorities under feed and food production to conform to the requirements of different phases (chicks, breeders, weaners, gestating etc) of animal production. The combination of 2 cereal-derived carbohydrates, regardless of enzyme supplementation in the diet could further increase the potency of functional cereal carbohydrates on intestinal health of monogastric animals.

Conflicts of interest

We declare that we have no financial and personal relationships with other people or organizations that can inappropriately influence our work, there is no professional or other personal interest of any nature or kind in any product, service and/or company that could be construed as influencing the content of this paper.

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