Review Article

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

Tolulope O. Adebowale a, b, *, Kang Yao a, b, *, Abimbola O. Oso c

a University of the Chinese Academy of Sciences, Beijing, 10008, China
b Key Laboratory of Agro-Ecological Processes in Subtropical Region, Institute of Subtropical Agriculture, Chinese Academy of Sciences, Hunan Provincial Engineering Research Center for Healthy Livestock and Poultry Production, Scientific Observing and Experimental Station of Animal Nutrition and Feed Science in South-Central, Ministry of Agriculture, Changsha, 410125, China
c Department of Animal Nutrition, Federal University of Agriculture, Abeokuta, PMB 2240, Nigeria

ARTICLE INFO

Article history:
Received 27 January 2019
Received in revised form 9 May 2019
Accepted 5 September 2019
Available online 20 September 2019

Keywords:
Arabinoxylans
Beta-glucans
Resistant starch
Cellulose
SCFA
Intestinal health

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.

© 2019, Chinese Association of Animal Science and Veterinary Medicine. Production and hosting by Elsevier B.V. on behalf of KeAi Communications Co., Ltd. This is an open access article under the CC BY-NC-ND license (http://creativecommons.org/licenses/by-nc-nd/4.0/).

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 colonicocytes (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
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).

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 | Relatively low in dietary fiber level and nutrients like vitamins (vitamin B), relatively high in iron content. Least in dietary fiber level and highest in starch level. |
| Germ                 | Cellulose, fructans, lignin, fat, B-vitamins, iron | |
| Endosperm            | Cellulose, Hemicellulose (arabinoxylans, xyloglucans, and glucomannan), resistant starch, B-vitamins, iron | |

1 Adapted from Bernstein et al. (2013).

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 (Crandall 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
et al., 2019).

...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 ideal 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 \textit{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: RS1 or type 1, RS2 or type 2, RS3 or type 3, RS4 or type 4 (chemically modified starch) and RS5 or type 5 (amylose-lipid complex) (Zhao et al., 2018b). RS1 are termed encapsulated starch because they represent starch that is resistant and in a physically inaccessible form. RS2 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 RS1 and RS2 in diets, but leads to the formation of RS3. RS4 are non-granular starch-derived materials. They are generally formed during the retrogradation (cooked and cooled) of starch granules. RS4 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 RS4. The RS5 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 RS2 and RS4 from high-amylose maize could modulate gut microbiota, improve intestinal morphology and enhance intestinal immune response to stress (Table 3). For instance, RS2 increases the fecal abundance of bacteria (\textit{Ruminococcus bromii}) that importantly produces butyrate, whereas RS3 increases \textit{Bifidobacterium adolescentis} and \textit{Parabacteroides distasonis} (Martinez 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 Bacteroidetes ratio and the relative abundance of \textit{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 occcludens-1) was recorded in their progeny (Lebois 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 (RS4), the degree of specificity in SCFA delivery to the lower intestinal tract was increased, resulting in improved gut...

### Table 2

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

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

SCFA – short-chain fatty acids; RS – resistant starch.

1 Adapted from Jha and Berrocoso (2015).
health of the broiler chickens. This additionally suggest that RS4 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 RS3 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 acetylation and deacetylation and the hypoxia-inducible factor) (Correa-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 (RS2, RS3 and RS4) 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 fiber 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-protectase 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 potential 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.

### Table 3

| Type of RS     | Description                                | Intestinal function                                      |
|---------------|--------------------------------------------|----------------------------------------------------------|
| RS1           | Physically protected starch                | Could modulate digestive disorders                       |
| RS2           | Unstabilized resistant granules of starch  | Modulate gut microbiota, improve intestinal morphology and enhance intestinal immune responses to stress |
| RS3           | Retrogradated starch                       | Reduces intestinal pH, Modulate gut-microflora           |
| RS4           | Chemically modified starches               | Modulate gut absorptive function, tight junction proteins, and the gut microbiota population |
| RS5           | Amylose-lipid complex                     | —                                                        |

RS = resistant starch.
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 coccosides—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 (Cummins 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 classified 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 distilled 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 ≥ 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.
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 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, constituting 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, Veillonellaceae, 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 Veillonellaceae with representatives of Veillonellaceae 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

---

**Fig. 1.** An overview of carbohydrates and their metabolic end products. SCFA = short-chain fatty acids.
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 Ruminococcaceae family of the Firmicutes group, *E. rectale* 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 bacteroidetes 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 *Ruminococcus 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 and protozoa by direct binding and lysis of microbial membranes was reported that butyrate induced the synthesis of endogenous butyrate (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 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 influentially 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.

Acknowledgements

This study was jointly supported by the National Science Foundation for Distinguished Young Scholars of Hunan Province (2016JJ0105), the Open Foundation of Key Laboratory of Agro-ecological Processes in Subtropical Region, Institute of Subtropical Agriculture, Chinese Academy of Sciences (ISA2016101), the Chinese Academy of Sciences “Hundred Talent” award (Y451022111) and the National Natural Science Foundation of China Project (31472107). The CAS-TWAS presidential scholarship awarded to Tolulope Adebowale is appreciated.

References

Bach Knudsen KE, Hedemann MS, Larke HN. The role of carbohydrates in intestinal health of pigs. Anim Feed Sci Technol 2012;173(1):41–53.
Bacic A, Stone BA. Chemistry and organization of aleurone cell-wall components from wheat and barley. Aust J Plant Physiol 1981;8(4–5):475–95.
Bernstein AM, Tiggesmeier B, Kirkpatrick K, Golubic M, Rozen MF. Major cereal grain fibers and puyllin in relation to cardiovascular health. Nutrients 2013;5(5): 1454–67.
Bird AR, Vuuran M, Brown I, Topping DL. Two high-amylase maize starches with different amounts of resistant starch vary in their effects on fermentation, tissue and digesta mass accretion, and bacterial populations in the large bowel of pigs. Br J Nutr 2007;97(1):134–44.
Browder W, Williams D, Lucore P, Pretus H, Jones E, Mcnamee R. Effect of enhanced macrophage function on early wound healing. Surgery 1988;104(2):224–30.
Cao BH, Zhang XP, Guo YM, Karasawa Y, Kumao T. Effects of dietary cellulose levels on growth, nitrogen utilization, retention time of digesta, and caecal microflora of chickens. Asian-Australas J Anim Sci 2003;16(6):863–6.
Choc M, Annison G. The inhibition of nutrient digestion by wheat pentosans. Br J Nutr 2007;97(1):123–32.
Clarke LF, Sweeney T, Curley E, Duffy SK, Rajauria G, O’doherty JV. The variation in chemical composition of barley feed with or without enzyme supplementation influences nutrient digestibility and subsequently affects performance in pigs 2018;102(3):799–809.
Consortium P. Similarities and specificities of gut-microbiota of pigs and chickens. 2017.
Corrêa-Oliveira R, Fachi JL, Vieira A, Sato FT, Vinolo MAR. Regulation of immune cell function by short-chain fatty acids. Clin Transl Immunol 2016;5(4):et3.
Cousin PJ, Foligne B, Deutsch S-M, Massart S, Parayre S, Le Loi Y, et al. Assessment of the probiotic potential of a dairy product fermented by propionibacterium freudenreichii in piglets. J Agric Food Chem 2012;60(32):7917–27.
Cox CM, Summers LH, Kim S, McIeroy AF, Bedford MR, Dalloul RA. Immune responses to dietary betaglucan in broiler chicks during an Eimeria challenge. Poult Sci 2010;89(12):2597–607.
Crane JK, Broome JE, Liu S. Biological activities of uric acid in Infection due to enteropathogenic and Shiga-Toxigenic Escherichia coli. Infect Immun 2016;84(4):976–88.
Cummings J, Blackburn M, Pogson D, Murzin MJ, et al. Dietary cellulose supplementation modulates the immune response in a Murine endotoxemia model. Shock 2019 [Published Ahead of Print].
Dubrej R, Toh Y-R, Yeh A-L. Enhancing cellulose functionalizes by size reduction using media-mill. Sci Rep 2018;8(1):11343.
Englyst KN, Englyst HN. Carbohydrate bioavailability. Br J Nutr 2007;94(1):1–7.
Firman HC, Sweeney T, Curley E, Duffy SK, Rajaouria G, O’doherty JV. The variation in chemical composition of barley feed with or without enzyme supplementation influences nutrient digestibility and subsequently affects performance in pigs 2018;102(3):799–809.
Firman HC, Sweeney T, Curley E, Duffy SK, Rajaouria G, O’doherty JV. The variation in chemical composition of barley feed with or without enzyme supplementation influences nutrient digestibility and subsequently affects performance in pigs 2018;102(3):799–809.
Firman HC, Sweeney T, Curley E, Duffy SK, Rajaouria G, O’doherty JV. The variation in chemical composition of barley feed with or without enzyme supplementation influences nutrient digestibility and subsequently affects performance in pigs 2018;102(3):799–809.
Firm H, Sweeney T, Curley E, Duffy SK, Rajaouria G, O’doherty JV. The variation in chemical composition of barley feed with or without enzyme supplementation influences nutrient digestibility and subsequently affects performance in pigs 2018;102(3):799–809.
Firm H, Sweeney T, Curley E, Duffy SK, Rajaouria G, O’doherty JV. The variation in chemical composition of barley feed with or without enzyme supplementation influences nutrient digestibility and subsequently affects performance in pigs 2018;102(3):799–809.
Firm H, Sweeney T, Curley E, Duffy SK, Rajaouria G, O’doherty JV. The variation in chemical composition of barley feed with or without enzyme supplementation influences nutrient digestibility and subsequently affects performance in pigs 2018;102(3):799–809.
Firm H, Sweeney T, Curley E, Duffy SK, Rajaouria G, O’doherty JV. The variation in chemical composition of barley feed with or without enzyme supplementation influences nutrient digestibility and subsequently affects performance in pigs 2018;102(3):799–809.
Firm H, Sweeney T, Curley E, Duffy SK, Rajaouria G, O’doherty J
Jozeika D, Rutzkowski A, Jensen BB, Engberg RM. The effect of beta-glucan supplementation of barley- and oat-based diets on growth performance and fermentation in broiler chicken gastrointestinal tract. Br Poult Sci 2006;47(1): 57–64.

Juliana P, Singh RP, Poland J, Mondal S, Crossa J, Montesinos-Lopez OA, et al. Prospects and challenges of applied genomic selection—A new paradigm in breeding for good grain yield in bread wheat. Plant Genome 2018;11(3).

Kibos A, Campeanu A, Tintoiu I. Pathophysiology of coronary artery in-stent restenosis. Acute Card Care 2007;9(2):111–9.

Kien CL, Blauwielke R. Cecal infusion of butyrate does not alter cecal concentration of butyrate in pigs fed ileal JPEN - J Parenter Enter Nutr 2008;32(4): 439–42.

Knudsen KE. Fiber and nonstarch polysaccharide content and variation in common crops used in broiler diets. Poult Sci 2014;93(9):2380–93.

Knudsen KE, Norskov NP, Bolvig AK, Hedemann MS, Lærke HN. Dietary fibers and associated phytochemicals in cereals. Mol Nutr Food Res 2017;61(7).

Koh A, De Vadder F, Kovatcheva-Datchary P, Backhed F. From dietary fiber to host physiology: short-chain fatty acids as key bacterial metabolites. Cell 2016;165(6):1322–45.

Kumar V, Sinha AK, Makkak HPS, De Boeck G, Becker K. Dietary roles of non-starch polysaccharides in human nutrition: a review. Crit Rev Food Sci Nutr 2012;52(10):899–935.

Leblois J, Massart S, Soyeurt H, Grelet C, Dehareng F, Schroyen M, et al. Feeding sows the effect of inulin on ileal digestibility of feedstuffs and the pig gastrointestinal tract microbiota. The pig gastrointestinal tract microbiota. Poult Sci 2013;92(7):2077–89.

Leser TD, Amenuvor JZ, Jensen TK, Lindecrona RH, Boye M, Møller K. Culture-independent analysis of gut bacteria: the pig gastrointestinal tract microbiota. Appl Environ Microbiol 2002;68(2):873–90.

Levine LJ, Looff T, Allen HK, Stanton TB. Butyrate-producing bacteria, including mucin degraders, from the swine intestinal tract. Appl Environ Microbiol 2013;79(12):3879–81.

Li B, Leblois J, Tamimiau B, Schroyen M, Beckers Y, Bindelle J, et al. Feeding sows resistant starch during gestation and lactation impacts their faecal microbiota and milk composition but shows limited effects on their progeny. PLoS One 2018;13(7):e0199588.

Lenis NP, Bikker P, Van Der Meulen J, Van Diepen JT, Bakker JK, Jonghoed AW. Effect of dietary neutral detergent fiber on ileal digestibility and portal flux of nitrogen and amino acids and on nitrogen utilization in growing pigs. J Anim Sci 1996;74(11):2687–99.

Lester TD, Amenuvor JZ, Jensen TK, Lindcrona RH, Boye M, Møller K. Culture-independent analysis of gut bacteria: the pig gastrointestinal tract microbiota revisited. Appl Environ Microbiol 2002;68(2):873–90.

Levina LV, Looft T, Allen HK, Stanton TB. Butyrate-producing bacteria, including mucin degraders, from the swine intestinal tract. Appl Environ Microbiol 2013;79(12):3879–81.

Li, B, Leblois J, Tamimiau B, Schroyen M, Beckers Y, Bindelle J, et al. The effect of inulin and wheat bran on intestinal health and microbiota in the early life of broiler chickens. Poult Sci 2018;97(9):3156–65.

Li Y, Zhang AR, Wei H, Zhou Z, Peng J, et al. In vivo and in vitro digestibility of corn starch for weaned pigs: effects of amylose:amylopectin ratio, extrusion, and the effect of dietary butyrate on serum lipids. Ann Fam Med 2009;7(2):157–63.

Teng P-Y, Kim WK, Review: roles of prebiotics in intestinal ecosystem of broilers. Front Vet Sci 2018;5:245.

Tiwari UP, Chen H, Kim SW, Jha R. Supplemental effect of xylanase and mannanase on nutrient digestibility and gut health of nursery pigs studied using both in vivo and in vitro models. Anim Feed Sci Technol 2018;245:77–90.

Topping D. Cereal complex carbohydrates and their contribution to human health. J Cereal Sci 2007;46(3):220–9.

Vetvicka V, Oliveira C. [1-3]-(1-6)-D-glucans modulate immune status in pigs: potential importance for efficiency of commercial farming. Ann Trans Med 2014;2(2):16.

Vital M, Penton CR, Wang Q, Young VB, Antonopoulos DA, Sogin ML, et al. A gene-targeted approach to investigate the intestinal butyrate-producing bacterial community. Microbiome 2013;1(1):8.

Walker AW, Ince J, Duncan SH, Webster LM, Holtop G, Z et al. Dominant and diet-responsive groups of bacteria within the human colonic microbiota. ISME J 2011;5(2):220–30.

Walugembe M, Hsieh JCF, Koszewski NJ, Lamont SJ, Persia ME, Rothschild MF. Effects of dietary fiber on cecal short-chain fatty acid and cecal microbiota of broiler and laying-hen chicks. Poult Sci 2015;94(10):2351–9.

Weszles K, Miquel S, Nooden L-M, Boyet S, Chevalier-Curt MJ, Robert V, et al. Bacteroides thetaiotaomicron and Faecalibacterium prausnitziiin the epithelium of a gnotobiotic model rodent. BMC Biol 2013;11(1):61.

Wrzosek L, Miquel S, Noordine M-L, Bouet S, Chevalier-Curt MJ, Robert V, et al. Starch with high amylose content and low in vitro digestibility increases intestinal nutrient pool size in the large intestine and faecal microbial composition in pigs. Br J Nutr 2014;112(1):1837–49.

Xu Z, Wu W, Lee Y-K, Xie J, Zhang H. Spatial heterogeneity and Co-occurrence of mucosal and luminal microbiome across swine intestinal tract. Front Microbiol 2018;9(48).

Xu Z, Zhao J, Jiang XD, Yang X, Zhang S, Huang CF. Determination of wheat composition, energy content and amino acid digestibility in different wheat cultivars fed to growing pigs. J Anim Sci 2019;51(4):256–34.

Xia Z, Anderson M, Andersen R. Resistant starch and other dietary fiber components in tubers from a high-amylose potato. Food Chem 2018b;251:58–63.