Animal Nutrition 5 (2019) 217–226

Contents lists available at ScienceDirect

Animal Nutrition

journal homepage: http://www.keaipublishing.com/en/journals/aninu/

Review Article

Fermentation characteristics of resistant starch, arabinoxylan, and β-glucan and their effects on the gut microbial ecology of pigs: A review

Utsav P. Tiwari, Amit K. Singh, Rajesh Jha*

Department of Human Nutrition Food and Animal Sciences, College of Tropical Agriculture and Human Resources, University of Hawaii at Manoa, HI 96822, USA

ARTICLE INFO

Article history:
Received 25 August 2018
Received in revised form
3 March 2019
Accepted 23 April 2019
Available online 9 May 2019

Keywords:
Butyrate
Fermentation
Gut ecology
Microbiota
Short-chain fatty acids
Swine

ABSTRACT

Dietary fibers (DF) contain an abundant amount of energy, although the mammalian genome does not encode most of the enzymes required to degrade them. However, a mutual dependence is developed between the host and symbiotic microbes, which has the potential to extract the energy present in these DF. Dietary fibers escape digestion in the foregut and are fermented in the hindgut, producing short-chain fatty acids (SCFA) that alter the microbial ecology in the gastrointestinal tract (GIT) of pigs. Most of the carbohydrates are fermented in the proximal part, allowing protein fermentation in the distal part, resulting in colonic diseases. The structures of resistant starch (RS), arabinoxylan (AX), and β-glucan (βG) are complex; hence, makes their way into the hindgut where these are fermented and provide energy substrates for the colonic epithelial cells. Different microbes have different preferences of binding to different substrates. The RS, AX and βG act as a unique substrate for the microbes and modify the relative composition of the gut microbial community. The granule dimension and surface area of each substrate are different, which influences the penetration capacity of microbes. Arabinose and xylan are 2 different hemicelluloses, but arabinose is substituted on the xylan backbone and occurs in the form of AX. Fermentation of xylan produces butyrate primarily in the small intestine, whereas arabinose produces butyrate in the large intestine. Types of RS and forms of βG also exert beneficial effects by producing different metabolites and modulating the intestinal microbiota. Therefore, it is important to have information of different types of RS, AX and βG and their roles in microbial modulation to get the optimum benefits of fiber fermentation in the gut. This review provides relevant information on the similarities and differences that exist in the way RS, AX, and βG are fermented, and their positive and negative effects on SCFA production and gut microbial ecology of pigs. These insights will help nutritionists to develop dietary strategies that can modulate specific SCFA production and promote beneficial microbiota in the GIT of swine.

1. Introduction

Diet induces a change in the microbial ecology and fermentation end products in the gut, which in turn, influences the nutritional, physiological, and immunological functions of pigs (Brestoff and Artis, 2013; Jha et al., 2019). Cereal grains and different agro-industrial coproducts represent major portions of the pig diet which contains a considerable amount of fermentable carbohydrates like resistant starch (RS) and non-starch polysaccharides (NSP) such as AX and βG (Tiwari and Jha, 2016). Most parts of the RS and NSP are not digested in the small intestine and passes to the

* Corresponding author.
E-mail address: rjha@hawaii.edu (R. Jha).
Peer review under responsibility of Chinese Association of Animal Science and Veterinary Medicine.

Production and Hosting by Elsevier on behalf of KeAi

https://doi.org/10.1016/j.aninu.2019.04.003

large intestine where microbes ferment these substrates and produce short-chain fatty acids (SCFA), which in turn influence microbial ecology and overall gut health of pigs (Pieper et al., 2009). Saccharolytic fermentation predominantly takes place in the proximal colon as most microbes prefer to utilize carbohydrates over proteins (Giuberti et al., 2015). Whereas, proteolytic fermentation takes place in the distal colon producing branched-chain fatty acids and potentially harmful metabolites like ammonia (from deamination of amino acids and hydrolysis of urea), indoles, and phenols (from carboxylation of amino acids). These harmful metabolites cause several colonic diseases in the distal colon as the availability of fermentable carbohydrates in the distal colon is minimal (Jha and Berrocoso, 2016). Fermentation of carbohydrates mainly produces SCFA (acetate, propionate, and butyrate) and lactate as major metabolic end products. Production of SCFA is dependent upon the fermentation substrate available and microbial ecology in the gut (Jha and Berrocoso, 2015). Hence, the composition of SCFA produced in the gut can be manipulated by changing the substrate that reaches the colon (Bach Knudsen, 2015). Production of lactic acid bacteria as a result of carbohydrate fermentation is considered beneficial whereas protein fermentation represents a potential risk factor for disruption of the intestinal ecosystem (Jha et al., 2019). Hence, it is of utmost importance to make a dietary strategy that can increase SCFA production constantly throughout the colon by promoting beneficial gut microbiome without compromising growth performance and health of an animal. Due to the difference in fermentation characteristics of various fibrous feed ingredients, nutritionists require a thorough understanding on the inclusion of RS and NSP in the diet of pigs to get the optimum benefits of fiber fermentation in the gut. This review has attempted to critically analyze the role of different types of RS and NSP like AX and βG in swine nutrition. More specifically, this review is focused on describing the structural variation of RS, AX, and βG in different feed ingredients and the way they affect the physiology of digestion, fermentation, and modulation of microbial ecology in the gastrointestinal tract (GIT) of pigs (Table 1).

2. Structural difference of resistant starch, arabinoxylan, and β-glucan

Resistant starch is a homopolysaccharide of glucose, i.e., a linear molecule of α-1-4-D-glucan, which is resistant to digestion by endogenous enzymes of pigs. There are 5 types of RS based on their physicochemical properties. RS1: this group contains starches which are physically inaccessible, i.e., starches locate inside the fiber-protein matrix, e.g., coarsely ground or whole kernel grains), and RS1 does not break down with normal cooking. RS2: this group contains the granular type or the non-gelatinized native starch granules (e.g., raw potato, green banana, and cornstarch) and can be reduced by thermal treatment. RS3: this group contains heat-stable starches that are produced by gelatinization and retrogradation (slow recrystallization), e.g., cooked and cooled starchy foods. RS4: this group is produced by chemical modification (etherification, esterification and cross-linking), and RS4 is resistant to hydrolysis by host enzymes as well as by bacterial amylase (Birt et al., 2013).

Arabinoxylan is a heteropolysaccharide of D-xylose units joined by β-linkage and substituted by arabinose randomly along the chain, which also allows random substitution of the acetyl group and D-glucuronic acid. Arabinose residue further gets feruloylated, i.e. forms dimer or trimer with ferulic acid, hence forming a heterogenous intermolecular complex. This matrix makes it difficult for the enzymatic degradation and leads to potential encapsulation of nutrients (Pedersen et al., 2014; Tiwari and Jha, 2017). The arabinose substitution on the xylan backbone determines the digestibility and fermentability of AX (Tiwari and Jha, 2016; Tiwari et al., 2018). Arabinose substitution in wheat and rye differs significantly. In wheat, one third of arabinose are linked to the singly substituted xylan backbone, and rest two thirds are linked to the doubly substituted xylan backbone. Whereas in rye, two thirds of arabinose are linked to the singly substituted xylan backbone, and only one third are linked to the doubly substituted (Höije et al., 2008). The structure of AX differs depending upon the botanical origin as well as the specific part of the grain. There is lower arabinose substitution in the aleurone layer and higher in pericarp or testa (Bach Knudsen et al., 2017). Pericarp and testa in grain are the places where almost all lignin is located. Hence, AX from the aleurone layer is readily fermented whereas those from pericarp and testa are slowly fermented. The cell wall in the endosperm layer contains a lower amount of AX than those in bran rich fractions. Aleurone contains a higher amount of insoluble polysaccharides than remaining of other endosperm layer (Bach Knudsen et al., 2017). Aleurone and pericarp also consist of larger amount of ferulic acids than is found in any other starchy endosperm layer (Barron et al., 2007). Aleurone layer in wheat contains a large amount of AX (Bach Knudsen et al., 2017) whereas the aleurone layer in oat bran contains a higher concentration of βG (Wood, 2010). The AX present in the endosperm layer of wheat and rye are less branched with arabinose-to-xylose (A:X) ratio ranging from 0.50 to 0.70 and from 0.48 to 0.55, respectively, whereas that of rice (0.80) and sorghum (0.87) are heavily branched and contains more arabinose, galactose and glucuronic acid substituents (Zhang et al., 2015).

Most of the βG contain pure glucose as their sugar component except for seaweed (laminarin) which also contains mannose (Zhao and Cheung, 2011). Most commonly used βG from cereals in general, such as barley, consists of both β(1-3) and β(1-4) linkage on the main chain in the ratio of 1:3 (Lambo et al., 2005) and requires β-glucanases with both β(1-3) and β(1-4) cleavage activity to degrade them completely (Hughes et al., 2008). Fungal βG (e.g., mushroom) have the most complex structure with β(1-3) linked glucose on the main chain and varying ratio of β(1-6) and β(1-4) on the side chain (Wong et al., 2005). The βG in algae have β(1-3) linked linear glucan backbone with β(1-6) linked glucose on the side chain in the ratio of 3:1 (Read et al., 1996). The βG from bacteria (e.g., curdlan) are linear, unbranched, and highly insoluble whereas, βG from seaweeds (e.g., laminarin) are highly branched and soluble (Zhao and Cheung, 2011). The βG from oat and barley are similar in structure, but the ratio of β(1-3) and β(1-4) varies (Wood and Beer, 2002). Concentration of βG varies among the most commonly used cereals in the diets of pigs, i.e. highest in oat (29 to 63 g/kg) and barley (36 to 99 g/kg), intermediate in wheat and rye (7 to 17 g/kg), and lowest in corn (1 g/kg) (Bach Knudsen et al., 2017). Most brans contain a higher amount of insoluble fiber than cereal grains except oat bran which is more soluble as it contains a higher amount of βG (Wood, 2010). The βG from oat has a high molecular weight and is more insoluble than barley βG as they contain a higher proportion of β(1-4) linkage (0.7) and lower proportion of β(1-3) linkage (0.3; Duss and Nyberg, 2004). Hence, βG from barley is a more readily fermentable substrate for microbes in the GIT of pigs because of their higher solubility.

3. Normal microbial community in the gastrointestinal tract of pigs

The GIT of pigs consists of a complex and diverse group of microbes. Bacteria comprise the majority of the microbial population in the GIT of pigs, which consists of over 50 genera and more than 500 species of bacteria (Jensen and Jorgensen, 1994). Almost 90% of bacteria in the GIT of the pig are Gram-positive, and rest are Gram-

Table 1
Effects of resistant starch (RS), arabinoxylan (AX) and β-glucan (βG) on microbial community in the gastrointestinal tract of swine.

Dietary fiber	Type of dietary fiber	Microbial proliferation	Site	Reference
RS	RS2	Increased growth of *Bifidobacterium*, *Ruminococcus bromii*, *Eubacterium rectale*	Colon	Martinez et al. (2010)
		Increased growth of *Bacteroidetes* and *Actinobacteria*	Colon	Young et al. (2012)
		No effect on microbial proliferation	Feces	Martinez et al. (2010)
	RS3	Increased growth of *R. bromii*	Colon	Haenen et al. (2013)
		Increased growth of *E. rectale*	Colon	Martinez et al. (2010)
		Increased bacterial group belonging to *Clostridium* cluster IV, IX, XV, XVI, XVII	Colon	Haenen et al. (2013)
		Decreased bacterial group belonging to *Clostridium* cluster XIVa	colon	Haenen et al. (2013)
	RS3 (pattern A)	Increased growth of *Atopobium*	Colon	Lesmes et al. (2008)
	RS3 (pattern B)	Increased growth of *Bifidobacterium*	Colon	Lesmes et al. (2008)
	RS4	Increased growth of *Bacteroidetes* and *Actinobacteria*	Colon	Martinez et al. (2010)
		Increased growth of *Bifidobacterium* and *ParaBacteroides distasonis*	Colon	Martinez et al. (2010)
		No effect on microbial proliferation	Caecum	Metzler-Zebeli et al. (2015)
AX	AX (from wheat)	Increased *Lactobacilli*, no effect on *Escherichia coli*	Colon	Van Laere et al. (2000); Mirande et al. (2010)
	AX	Arabinoxylan not fermented by *Lactobacilli*, *Enterococci*, *E. coli*, *Clostridium perfringens*	*In vitro* study	Crittenden et al. (2002)
		Oligosaccharide with more than 5 units of xylan increased proliferation of *Bacteroides*	Colon	Mirande et al. (2010)
	AX	Oligosaccharide with less than 5 units of xylan increased proliferation of *Bifidobacteria*	Colon	Moura et al. (2007)
	AX	Among oligosaccharides xylotriose and xylotetraose was best utilized by *Bifidobacteria*	Colon	Ejby et al. (2013)
	AX	*B. breve* and *B. infantis* are not able to degrade AX, whereas *B. longum* and *B. ovatus* could only partially degrade AX and *B. adolescentis* and *B. vulgatus* could completely degrade AX	*In vitro* study	Van Laere et al. (2000)
βG	Mixed linked βG	Reduced *Lactobacilli*, *Enterobacteria* and *Streptococci*	Colon	Pieper et al. (2008)
	βG	Improved growth of overall microbes	Stomach	Leterme et al. (2000)
	βG (from barley)	Increased proliferation of *Lactobacilli* and *Bifidobacteria* when compared with wheat based diet	Colon	Garry et al. (2007)
	βG (from wheat)	Increased proliferation of *Bifidobacteria* and decreased the concentration of *Clostridium* species	Colon	Pieper et al. (2008)
	βG (from hulled barley)	Increased proliferation of *Lactobacilli*	Colon	Pieper et al. (2008)
	βG (from hulless barley)	Decreased proliferation of *Lactobacilli*	Colon	
	βG (from oat as well as microbial beta glucan)	Increased growth of *Bifidobacteria*	Colon	Mårtensson et al. (2005)
	βG (from barley)	Did not increase growth of *Bifidobacteria* (*B. infantis, B. adolescentis, B. longum*)	*In vitro* study	Crittenden et al. (2002)
	βG (from barley)	Increase growth of *Bifidobacteria* (*B. infantis, B. adolescentis, B. longum*)	*In vitro* study	Zhao and Cheung (2011)
	Purified βG	Increased *Lactobacilli*	Ileum	Pieper et al. (2008)
	βG (from cereal)	Decreased proliferation of *Lactobacilli*	Ileum	
	βG (from cereal)	Increase proportion of *Lactobacilli* and decreased amount of coliforms	Feces	Pieper et al. (2008)

negative (Gaskins, 2001). Species diversity of the majority of bacteria is high in the large intestine due high retention time of the digesta, and their population is in the range of 10^{10} to 10^{11} per gram of intestinal content (Jensen and Jorgensen, 1994). Due to the acidic environment in the stomach and proximal small intestine, the number of bacteria is lower (10^3 to 10^5 per gram of intestinal content) than that in the distal part. The pig gut is sterile at the time of birth. However, colonization of microbes in the GIT of pigs begins as soon as they are born. *Streptococcus* spp. and *Escherichia coli* create an anaerobic environment and start the colonization which paves the way for other microbes like *Bacteroides* and *Bifidobacteria*, to start forming a colony (Konstantinov et al., 2006). Before weaning of piglets, *Lactobacillus* predominates the whole small intestine (Petri et al., 2010). The predominant strains of *Streptococci* in the small intestine before weaning ferments lactose, whereas the predominant strains of *Streptococci* after weaning do not ferment lactose (Fouhse et al., 2016).

On the other hand, predominant anaerobes in the colon before weaning are *Bacteroides* spp. However, their number starts increasing only after weaning. Increased growth rate after weaning has been associated with an increase in the proliferation of *Provetella* as they are responsible for an increase in the concentration of immunoglobulin A (IgA) (Mach et al., 2015). Immunoglobulin A restricts pathogenic microbes from getting entry to the epithelial cells and prevents their colonization (Inman et al., 2010).

4. Resistant starch fermentation and its effect on microbial population

A diverse range of starches that are included in RS are fermented in the large intestine instead of being enzymatically digested in the small intestine of pigs (Bird et al., 2007; Jha et al., 2010a; Jha and Leterme, 2012). Starch digestion in pigs is more desirable than its fermentation because digestion products of starch are a better source of energy, whereas fermentation products of starch (SCFA) are less energy efficient (Giuberti et al., 2015). The SCFA can provide up to about 15% of the maintenance energy requirement of the growing pigs and 30% in gestating sows (Varel and Yen, 1997). However, an increase in the concentration of SCFA, more specifically of butyrate, improves the gut mucosal health as well as the immune system of pigs (Jha et al., 2019). Diet rich in RS increases butyrate production in the proximal part of the colon in pigs and modulates the microbial composition (Haenen et al., 2013). Microbes in the GIT has been well known to play a vital role in the development of the immune system and preventing the host from infection (Jha et al., 2019). The RS induced change in the gut microbiota is influenced by several factors like the initial composition of gut microbes (Walker et al., 2010), type of RS (Martinez et al., 2010), crystalline polymorphisms of same type of RS (Lesmes et al., 2008), and the location of the intestine where they are fermented. High amylose-containing starches are

effectively degraded by *Bifidobacteria* (Macfarlane and Macfarlane, 2003).

When RS1 was supplied to pigs through a long-term intake of raw potato starch, it improved the integrity of mucosa by increasing butyrate production and reducing damage to colonocytes (Nofrarías et al., 2007). Increasing dietary amylose or RS content in the diet of pigs can cause a potential physiological change, leading to a proliferation of commensal microbes in the GIT of pigs, which in turn, increase SCFA production (Giuberti et al., 2015). Effect of RS2 on the microbial population is not consistent. However, it helps in the proliferation of *Eubacterium* and *Ruminococcus* spp. The granular type RS2 which are extracted and available in pure form are found to increase butyrate production (Weaver et al., 1992). Butyrate is involved in changing the composition of intestinal microbiota by increasing the proportion of *Bifidobacterium* spp., *Ruminococcus bromii* and *Eubacterium rectale* (Martinez et al., 2010). In rats, supplementation of RS2 increased the proliferation of *Bacteroidetes* and *Actinobacteria* in colonic digesta (Young et al., 2012). However, in pigs, a significant increase in those 2 genera (*Bacteroidetes* and *Actinobacteria)* was reported in RS4, not in RS2 (Martinez et al., 2010). Supplementation of RS2 did not affect the microbial population in the feces (Martinez et al., 2010) or in the cecum and colon (Sun et al., 2016). However, the significant proliferation of *R. bromii* and *E. rectale* was seen in RS2 at the species level (Martinez et al., 2010). Raw or boiled RS2 was effectively degraded by *R. bromii* than by *Bacteroides thetaiotaomicron* (Ze et al., 2012). Increase in proliferation of *Ruminococcus* species is associated with improved butyrate production and gut health (Pryde et al., 2002).

The retrograded type RS3 occurs in 3 different patterns. The A type pattern is generally observed in cereals and low amylose starches as they have an open structure and are highly digestible. The B type pattern is seen in potatoes and high amylose starches as they have a close-packed structure and are resistant to digestion by amylase. The C type pattern is found in legume starch and is highly resistant to enzymatic action (Biliaderis, 1991). Although *Bifidobacterium* spp. and *Clostridium butyricum* are known to have amylase activity that can utilize high amylopectin and soluble starch, but they were able to utilize RS3 retrograded in B type pattern containing a high amount of amylose (Birt et al., 2013). On the other hand, RS3 retrograded in A type pattern resulted in a proliferation of *Atopobium* spp. (Lesmes et al., 2008). The RS3 is involved in increasing the proportion of *R. bromii* (Haenen et al., 2013) and *E. rectale* (Martinez et al., 2010; Ze et al., 2012). Supplementation of RS3 increased the proliferation of bacterial group belonging to *Clostridium* cluster IV, IX, XV, XVI, XVII, whereas those belonging to *Clostridium* cluster XIVa were decreased (Haenen et al., 2013). This difference in the bacterial proliferation of *Clostridium* cluster can be because of the dependence of 2 important butyrate-producing bacteria (*Roseburia* and *E. rectale*) present in *Clostridium* cluster XIVa on residual carbohydrate as well as pH level (Louis et al., 2007). The pattern in which RS3 is retrograded affects the way they interact with microbes. The RS3 with low amylose content increases the proliferation of *Atopobium*, whereas those with high amylose content help in the proliferation of amylolytic microbes like *Bifidobacterium* spp. and *C. butyricum*. Chemically modified RS4 was developed by modifying the target starch molecules that helps to control reduction in starch digestibility. For examples, chemical modification like acetylation or butyralation of high amylose starch promotes better growth when challenged with necrotic enteritis. Chemical modification helped to increase acidity in the gut and suppress the growth of pathogenic organism. The RS4 augments the proportion of *Bifidobacterium adolescentis* and *Parabacteroides distasonis* (Martinez et al., 2010). However, cecal microbial diversity and abundance of phylum were not impacted by RS4 (Metzler-Zebeli et al., 2015).

Different microbes have a preference of binding to the different substrate. Each type of RS act as a unique substrate for the microbes and modifies the relative composition of the gut microbial community. The granule dimension and surface area of each RS are different, which influences the penetration capacity of microbes into the starch granules. Hence, microbial proliferation in the GIT of pigs is highly influenced by the type of RS being offered to the pigs. Different types of RS favor different types of microbes. The RS2 favors *Ruminococcus* and *Eubacterium*; RS3 helps to increase the proliferation of all the *Clostridium* clusters except the one that possesses the butyrogenic bacteria like *Roseburia*; and RS4 favors production of *Bifidobacteria.* Changes and variation in the microbial population in the colon of pigs are not just because dietary composition (use of different types of RS as substrate) but are also associated with host, microbes and their interaction (Jha et al., 2019).

5. Arabinoxylan and β-glucan fermentation and its effect on microbial population

The major NSP in common cereals fed to pigs are AX, cellulose and mixed linked βG (Bach Knudsen et al., 2017). The structure of cell wall is complex, and their composition and properties vary depending upon the location of tissues. Cell wall is thick and hydrophobic and consists of xylans, cellulose and a significant amount of lignin. On the other hand, endosperm (aleurone layer) is thin and hydrophilic and consists mainly of AX and βG (Izydorczyk and Dexter, 2008). The composition and structure of AX and βG are different in various cereals and coproducts. For example, the solubilities of AX and βG in corn and wheat distillers dried grain with solubles (DDGS) are different, so is the A:X ratio or the degree of substitution of arabinose on xylan backbone (Pedersen et al., 2014). Hence, AX and βG act differently when they are in extracted forms or when they exist as a part of grain matrix. The viscous property of these 2 polysaccharides is related to their molecular structure and molecular weight. Beta-glucan is more viscous than AX as the molecular weight of βG (2.1×10^6 to 2.3×10^6) is higher than that of AX (0.07×10^6 to 0.6×10^6) (Saulnier et al., 2007; Wood, 2010). The viscous property created by AX and βG in the intestinal lumen increases the digesta retention time and delays the process of digestion and absorption (Bach Knudsen, 2015; Tiwari et al., 2018). However, this viscous property of βG can be beneficial in the sense that it helps in the removal of cholesterol from the body pool by reducing the reabsorption of bile acids from the small intestine (Tiihonen et al., 2015).

Bacteroides possess the most expanded glycolytic gene that can degrade xylan (Zhang et al., 2014) by producing extracellular endoxylanase (glycoside hydrolase family 10) (Mirande et al., 2010; Ejby et al., 2013). The AX extracted from wheat is not used by *E. coli*, but increases the growth of *Lactobacilli* (Van Laere et al., 2000). However, mixed-linked βG in the diet significantly reduced the number of *lactobacilli*, *enterobacteria,* and *streptococci* (Pieper et al., 2008). The utilization of oligosaccharides of AX by gut microbes is limited to *Bifidobacteria,* and few Firmicutes like *Lactobacillus brevis* (Moura et al., 2007) as *Bacteroides* can only degrade those oligomers or polymers which have more than 5 units of xylan or which are larger than xylo-pentose (Mirande et al., 2010). Among the lower xylo-oligosaccharides, xylotriose and xylotetraose are utilized much efficiently than xylobiose by *Bifidobacteria* (Ejby et al., 2013). *Bifidobacteria* comprises about 25% of the total cultivable gut microflora (Pastell et al., 2009) and favors xylo-oligomers as a substrate over hexose sugars, but the selectivity of xylo-oligosaccharides is affected by arabinose substitution on the xylan

backbone. A substrate with high arabinose substitution is favored by *Bifidobacterium* when compared with *Bacteroides* spp., but substrate with lower arabinose substitution results in overall better fermentation (Amrein et al., 2003). Lower arabinose substitution (A:X = 0.34) significantly increased levels of cecal *Bifidobacteria* after 2-week intake of 2.5 g/kg of AX in chickens but had no effect on *Enterobacteriaceae* and *Lactobacilli* (Courtin et al., 2008). Hence, lowering the arabinose substitution will improve the overall fermentation, and AX will be utilized by *Bacteroides*. However, a higher degree of substitution favor *Bifidobacteria* proliferation over *Bacteroides*. Hence, *Bacteroides* are the primary AX degraders which degrade the larger polymers (hexose or more) of AX into smaller fragment mainly in the proximal colon. Arabinoxylan utilization by *Bifidobacteria* in the distal part depends upon how efficiently the primary AX degraders worked. *Bacteroides* are a better degrader of xylan whereas *Bifidobacteria* utilizes arabinose more efficiently. Hence, metabolic syntrophy among these dominant commensal microbes is maintained by their preference to different chain length as well as arabinose substitution on the xylan backbone, subsequently establishing microbial ecology.

Supplementation of βG has been found to selectively increase the proliferation of *Lactobacilli*, *Bifidobacterium* as well as other butyrate-producing bacteria. Most of the bacterial groups has been found to degrade βG except *Enterobacteria*ceae (Beckmann et al., 2006). Beta-glucan can promote the proliferation of bacteria in the stomach of weaned pigs. Beta-glucans are viscous, and they increase the retention time of digesta in the GIT, thereby extra time for the bacteria to proliferate (Leterme et al., 2000; Jha et al., 2010a). Also, βG produced by *Lactobacilli* increases their acid tolerant capacity by 15 times (Stack et al., 2010). This shows the positive and protective effect that βG can have on the beneficial microbes in the GIT. Beta-glucan in the barley-based diet increased the proliferation of *Lactobacilli* and *Bifidobacteria* when compared to a wheat-based diet in the colon (Garry et al., 2007). The reason behind this might be the presence of a higher concentration of βG in barley than in wheat (Jha et al., 2010a). On the other hand, βG in the wheat-based diet increased *Bifidobacteria* and decreased the concentration of *Clostridium* species (Pieper et al., 2008). Beta-glucan in hulled barley promoted the growth of *Lactobacilli* whereas βG in hulless barley decreased the growth of *Lactobacilli* and promoted the growth of xylan-degrading bacteria (Pieper et al., 2008). The isolates of βG, as well as microbial βG from oat-based products, stimulated the growth of *Bifidobacteria* spp. (Mårtensson et al., 2005). However, *in vitro* model using βG from barley as carbon substrate did not help in the proliferation of 3 *Bifidobacterium* spp (*B. infantis*, *B. adloescentis*, and *B. longum*) (Crittenden et al., 2002). Whereas all 3 *Bifidobacterium* spp. proliferated from 1 to 2.3 $\log_{10}$ cfu using purified βG substrates (Zhao and Cheung, 2011). Purified βG increased the ileal *Lactobacilli* content whereas βG in cereal matrix decreased the proportion of *Lactobacilli* (Pieper et al., 2008). This indicates that purified βG as a better substrate for the proliferation of beneficial bacteria like *Lactobacilli* and *Bifidobacteria* than βG found in grain matrix. It has been found that the *Bifidobacteria* and *Lactobacilli* can utilize βG isolated from the cereals. Beta-glucan and RS have been found to show a similar effect on fecal microbes. Both of them increase the proportion of *Lactobacilli* whereas decrease the number of coliforms (Pieper et al., 2008). Hence, it is not just the content of mixed linked βG that influences the microbial population in GIT of pigs but also their physical forms (purified or grain matrix).

6. Microbial utilization of short chain fatty acids

The end products of RS, AX, and βG fermentation are SCFA like acetate, propionate and butyrate and various gasses like hydrogen, carbon dioxide and methane (Englyst et al., 1992). The most abundant end product of fermentation in the proximal GIT is acetate which accounts for more than 90% of total SCFA produced, and the concentration of propionate and butyrate is very minimal. However, the condition changes in the distal part where the concentration of SCFA increases with a ratio of approximately 60% acetate, 25% propionate, and 15% butyrate. Most of the SCFA (more than 90%) absorption occurs in the anionic dissociated form, as they are weak acids (Velázquez et al., 1997). The SCFA are absorbed from the apical membrane by 3 different processes: passive diffusion in lipid soluble form (dissociated form) (Velázquez et al., 1997), the anion exchange between bicarbonate and SCFA (Kawamata et al., 2007), and by the help of transporters like monocarboxylate transporter 1 (MCT1) and sodium-coupled monocarboxylate transporter 1 (SMCT1). The MCT1 is coupled to transmembrane hydrogen gradient, and SMCT1 mediates SCFA absorption by enterocytes (Cuff et al., 2005). Different microbes utilize deoxysugars (like rhamnose, fucose) or lactate and produce 1,2 propanediol (Saxena et al., 2010). Microbes like *Salmonella enterica* serovar Typhimurium, metabolize this 1,2 propanediol to propionate or propanol (Bobik et al., 1999). For example, *Roseburia inulinivorans* has been found to produce propanediol from fucose, which is converted to propionate in human GIT. However, the same bacteria when grown on glucose produces butyrate instead of propionate (Scott et al., 2006). Similarly, butyrate is produced by the *Megasphaera elsdenii* (*Clostridium* cluster IX) when they are grown on glucose, but the same bacteria produce propionate when grown on lactate (Hino and Kuroda, 1993). Both Firmicutes and Bacteroidetes enter the succinate pathway via methylmalonyl-CoA (decarboxylation of methylmalonyl-CoA produces propionyl-CoA). Firmicutes produces propionate from organic acids (Flint et al., 2012), whereas *Bacteroides* utilize peptides and polysaccharides for the production of propionates (Watanabe et al., 2012). *Phascolarctobacterium succinatutens* can grow only on succinates (Watanabe et al., 2012), whereas *Viellonela parvula* uses lactate as the main substrate; however, they can get additional energy from succinates (Janssen, 1992). Hence, the production of SCFA varies depending upon the microbes and the substrate available for fermentation.

6.1. Fermentation of resistant starch, arabinoxylan, and β-glucan in the small intestine

Purified and isolated βG are readily and easily fermented in the proximal GIT or small intestine of pigs, whereas the βG which occur in grain matrix are fermented in the distal parts of the GIT (Pieper et al., 2008; Jha et al., 2010a). Presence of higher amount of βG would result in increased production of SCFA, which ultimately would reduce the pH of the small intestine. A major group of bacteria with several health benefits is *Lactobacilli*, and their proliferation increase in the small intestine when barley containing a higher amount of βG is fed. *Lactobacilli* is acid tolerant and can survive in the acidic environment caused due to higher fermentation. Bach Knudsen and Canibe (2000) fed oat bran containing a higher amount of βG to cannulated pigs and found a higher concentration of lactic acid in the small intestine. Weiss et al. (2016) found a higher ratio of *Lactobacilli* to *Enterobacteriaceae* when pigs were fed barley-based diet (2.3) compared to wheat-based diets (1.3). This increased ratio suggests improved resistance against pathogenic microbes in the small intestine with the use of barley in the diet. *Lactobacilli* have shown to outcompete other bacterial groups when it comes to colonization and nutrient availability in GIT (Lawley and Walker, 2013). It might be the result of this competitive effect of *Lactobacilli* that there was a significant reduction in the number of other microbes like *Bacteroides*,

Clostridium, *Roseburia* when pigs were fed a barley-based diet (Weiss et al., 2016). It can be concluded that βG present either in oat- or barley-based diet increases the proliferation of *Lactobacilli* as well as the concentration of the lactic acid in the small intestine. This decreases the pH and leads to decrease in a number of pathogenic bacteria like *E. coli* or other members of *Enterobacteriaceae* which are sensitive to the acidic environment.

Clostridium clusters are generally involved in the production of butyrate (Duncan et al., 2004; Louis et al., 2007). *Faecalibacterium* and *Roseburia*, which are 2 bacterial genera with the ability to produce butyrate, are associated with *Clostridium* cluster IV and XIVa, respectively (Louis et al., 2007). The growth of these butyrate-producing bacteria was higher in pigs fed wheat-based diet compared to barley-based diet (Weiss et al., 2016). This might be because of the presence of a higher amount of fructans in wheat (15 g/kg) compared to barley (6 g/kg). Weiss et al. (2016) recommended that it is not the AX content, but the amount of fructans that causes an increase in butyrate production. The amount of soluble AX in wheat was similar to that of barley whereas barley has a higher amount of insoluble AX. Barley also possesses a higher amount of βG when compared to wheat. However, it was not the barley but wheat that increased butyrate production. Hence, it can be ruled out that an increase in butyrate concentration in the small intestine is due to the presence of a higher amount of βG in the diet. In the case of oat bran, Bach Knudsen et al. (1993) claimed that AX but not βG is responsible for the enhanced butyrate production. Ivarsson et al. (2014) found a strong positive correlation between butyrate production and the intake of xylose, but there was no correlation between butyrate production and AX intake. This can be an indication of xylan acting as the substrate for the production of butyrate in the small intestine, not the arabinose. Production of butyrate in the hindgut was found in a higher proportion when pigs were fed a higher amount of AX (Högberg et al., 2006), which is in accordance to the finding of Ivarsson et al. (2014) who showed a relation between butyrate production and arabinose degradation in the colon. Also, a positive correlation between intake of arabinose and production of propionate was observed in the ileum (Ivarsson et al., 2014), indicating that fermentation of arabinose results in an increased proportion of propionate in the small intestine. *Prevotella* spp. in the colon is responsible for the production of acetate. However, a positive correlation between *Prevotella* spp. and butyrate production in the small intestine was observed (Ivarsson et al., 2014), indicating that *Prevotella* spp. degrade xylans responsible for butyrate production in the small intestine. Thus, it can be concluded that fermentation of xylan results in the increased production of butyrate in the small intestine, and the bacteria responsible for this increased butyrate production is *Prevotella* spp. The fermentation of arabinose increases the production of propionate in the small intestine and butyrate in the large intestine. Also, the role of fructans and xylan in increased production of butyrate in the small intestine is much higher than that of βG.

Besides producing butyrate, AX also plays an important role in maintaining the integrity of gut by increasing proliferation of goblet cell as well as secretion of IgA. Goblet cells in the GIT produce mucin. Mucin production is increased by *Lactobacillus* (Che et al., 2014), as well as other species which can help to improve the gut barrier as pathogenic microbes cannot penetrate through the dense mucous layer (Mendis and Simsek, 2015). The AX from wheat bran has been found to increase the number of goblet cells (Dock-Nascimento et al., 2007) which secretes not only mucin but also protein barrier factors (Bergstrom et al., 2008) hence protects intestinal epithelial cells. Arabinoxylan from wheat bran increases the concentration of IgA (Chen et al., 2015), which protects mucosal epithelia by preventing pathogenic microbes from getting attached to epithelial cells.

6.2. Fermentation of resistant starch, arabinoxylan, and β-glucan in the large intestine

Microbial fermentation in the hindgut depends on the amount of RS, AX, and βG available for the microbes, i.e., substrate and microbial interaction (Choct, 1997). A significant portion of the soluble AX and βG are fermented in the proximal colon as the fragment length of soluble AX is smaller whereas the fermentation of larger fragments or insoluble AX and βG takes place in the distal colon (Choct, 1997; Tiwari et al., 2018). Fermentation of soluble AX or βG improves gut health comparatively better than insoluble ones (Wellock et al., 2007). However, RS delays the fermentation of other fiber fractions like mixed linked βG or soluble AX in the large intestine of pigs by shifting the microbial metabolism towards utilization of starch (Jonathan et al., 2012).

Source of RS affects the production of SCFA and changes the molar ratio of production of acetate, propionate, and butyrate, but most of RS are butyrogenic (Giuberti et al., 2015). Degradation of RS2 and RS3 is the highest in the proximal colon, and so is the production of lactic acid and SCFA by these RS. However, degradation decreases as there is a progressive decrease in the flow of digesta towards the distal colon leading to change in fermentation metabolite and bacterial profile (Jha and Berrocoso, 2015). However, RS4 has a modification in the structure of starch due to cross-linking, transglycosylation or esterification which prevents hydrolysis of starch both by host enzymes and by bacterial amylases (Birt et al., 2013). Production of butyrate due to fermentation of RS is 2 times higher than that produced due to the fermentation of NSP (Birt et al., 2013). The molar ratio of butyrate production is affected by the source as well as the amount of RS available for the microbes for fermentation, which ultimately influence the proliferation of butyrate-producing bacteria (Pieper et al., 2008). Energy provided by butyrate is vital to maintain the gut ecosystem as well as the health of pigs. In the absence of energy (butyrate), fermentation shifts towards amino acids, i.e., carbon skeleton from deamination of amino acids is used as energy source, and ammonia is absorbed and disposed of as urea (Jha et al., 2019). However, in the presence of energy, ammonia is removed as microbial biomass (Bach Knudsen et al., 1993), i.e., the resident microbes in the large intestine retain more nitrogen for their growth. The RS gets depolymerized quicker than AX and βG. Thus, RS are rapidly fermented in the proximal part whereas AX and βG are fermented slowly in the distal part of the large intestine. In other words, fermentation starts only after the substrate (RS, AX, or βG) gets depolymerized by microbial hydrolytic enzymes. Faster the rate of depolymerization of a substrate, faster the carbohydrates will be available for fermentation by the bacteria.

A higher degree of substitution of arabinose or more branched AX is slowly fermented as endoxylanase enzyme produced by bacteria acts on xylan backbone and has to pass through the branch of arabinose before it can reach to xylan (Tiwari et al., 2018). This is the opposite in the case of RS. The RS which is heavily branched or the one that contains a higher amount of amylopectin provides a larger surface area for the enzymes to act on, hence are broken down in smaller fragments (monomers and dimers) and are rapidly fermented (Giuberti et al., 2015). Degradation of the more linear polymer of RS or the RS that contains a large amount of amylose and low amount of amylopectin gets slowly fermented as their degradation yields larger fragments (larger oligomers) which cannot be directly used by bacteria and further needs to be broken down to smaller fragments. Furthermore, a higher degree of substitution with arabinose impose the risk of forming dimers or trimers with ferulic acids which makes the AX structure more complex and more difficult to break through, hence delays the fermentation (Tiwari et al., 2018). Ferulic acid is the most abundant

or predominant phenolic acids present in most cereals as well as in wheat and rye brans which are esterified to AX. Physico-chemical properties are affected by the crosslinking of these diferulates with lignin. Branching increases surface area for the enzyme in solution to act on starch granules in RS (solid substrate), hence surface area accessible to enzymes is an important parameter (Tester et al., 2006). Lower branching or high amylose starch forms smaller surface area and more intramolecular bonds and delays starch degradation. However, not just the branching but the type of surface of starch in RS also affects fermentation. The RS present in tubers have a larger smooth surface, hence are more resistant to enzymatic hydrolysis than the RS present in cereals which have a granular surface (Lehmann and Robin, 2007) and a more open structure (Englyst et al., 1992; Regmi et al., 2011). Cereals high in amylose favor proliferation of *C. butyricum*, whereas cereals high in amylopectin favor *Clostridium ramosum* and *Bacteroides* (Pieper et al., 2009; Bindelle et al., 2011). Barley high in amylose content increased butyrate production both *in vivo* (Bird et al., 2007) and *in vitro* (Jha et al., 2011a). Thus, linear RS and branched AX are resistant to degradation and fermentation, whereas linear AX and branched RS are easily and rapidly degraded. According to Jha et al. (2011b), lower half-time of fermentation ($T_{1/2}$) is an indicator of fermentation taking place throughout the colon whereas higher $T_{1/2}$ means fermentation is taking place mainly in the distal part of the colon. Hence, it is very important to figure out the ingredients having lower $T_{1/2}$ values as they would minimize protein fermentation since microbes prefer carbohydrates over protein. Reducing protein fermentation would prevent the release of toxic compounds as well as prevents the proliferation of protein fermenting pathogenic microbes (Williams et al., 2005; Jha and Berrocoso, 2016). Usually, there is a shortage of fermentable carbohydrates in the distal part of the colon. Hence including more linear RS and more branched AX in the diet would help to prevent protein fermentation as they would get slowly depolymerized and therefore lately fermented. Distal fermentation is more important for a healthy colon and distal fermentation of RS is more desirable as that would contribute to the higher uptake of butyrate by the colonocytes.

Arabinoxylan and βG are not completely fermented in the colon of pigs. The βG and RS are fermented to a greater extent than AX and hence are capable of modulating the physicochemical properties of digesta. *In vitro* studies have shown that various microbes such as *Lactobacilli*, *Enterococci*, *E. coli*, *Clostridium perfringens* are not able to ferment AX (Crittenden et al., 2002). Viscous property of βG increases the retention time of digesta in small intestine and are fermented in the small intestine. Whereas, RS (from rapeseed meal) reduces the retention time of digesta and are not fermented (Vries et al., 2016). The solubility of AX also affects SCFA production as insoluble AX are less fermentable compared to soluble ones because insoluble AX contains about 100 folds more of ferulic acid as compared to soluble ones (Bunzel et al., 2001). Besides SCFA production, soluble AX also influences gut health by increasing fecal bulk, reduction in transit time, lowering pH in the intestinal lumen as well as bile acid profiles (Tungland and Meyer, 2002). Soluble AX and βG are responsible for changing the viscosity of luminal digesta (Zijlstra et al., 1999; Tiwari et al., 2018). Increase in viscosity acts as a physical barrier between nutrients and enterocytes absorption which results in immune stimulation, villus cell loss, increase proliferation of cells in crypts making it deeper and atrophy in chronic cases. Utilization of energy in supporting immune response diverts the energy utilization in promoting the growth of pigs (Jha et al., 2019). Different *Bifidobacterium* spp. produce SCFA differently when βG is used as the substrate. The higher amount of SCFA was produced by *B. infantis* than *B. longum*, and the ratio of acetate, propionate, and butyrate produced by *B. adolescentis* was 8:1:1 (Zhao and Cheung, 2011). Amount of insoluble βG is higher in oat than in barley. Thus, the presence of a more significant amount of soluble βG in barley-based diet fed to pigs would produce a higher concentration of total SCFA as well as a higher molar proportion of propionic and butyric acids in the cecum and colon. Arabinoxylan in corn resulted in a higher production of SCFA when compared with AX in wheat or rice bran when human feces was used as microbial inoculum in an *in vitro* study (Rose et al., 2010). This might be because AX in corn is comparatively less branched than rice bran; hence, are easily degraded and produces a higher amount of SCFA.

6.3. Butyrate production by resistant starch, arabinoxylan, and β-glucan in the large intestine

Butyrate-producing bacteria are widely distributed across the different clusters of *Clostridium*. The butyrogenic bacteria are gram-negative, anaerobic *Firmicutes* having low mol% of guanine-cytosine content. However, the bulk of potent butyrate-producing bacteria (*Faecalibacterium prausitzii*, *E. rectale*, and *Roseburia* spp.) belongs to *Clostridium* cluster IV and XIVa (Louis and Flint, 2009). In humans, out of 3 butyrate-producing bacteria, *Faecalibacterium* is present in the largest amount which comprises almost 5% to15% of the total microbial population (Eckburg et al., 2005), whereas the other 2 butyrate producers (*Eubacterium* and *Roseburia*) comprises 5% to 10% of the total microbial species (Aminov et al., 2006). These butyrate-producing bacteria are lactate utilizing bacteria which produces acetyl CoA from lactate and condensation of acetyl CoA with subsequent reduction to butyryl CoA results in the formation of butyrate (Pryde et al., 2002). In the absence of acetate, 75% of the supplied glucose is converted to lactate; however, the presence of acetate results in the production of butyrate (Diez-Gonzalez et al., 1999). Both the proportion of butyrate-producing bacteria as well as the concentration of butyrate were higher at pH 5.5 whereas *Bacteroidetes* dominated at pH 6.5. This indicates that mild acidic pH allows butyrate-producing bacteria to grow well and be able to compete against gram-negative xylan degrading bacteria (*Bacteroides* spp). The *R. inulinivorans* has been found to produce propanediol from fucose, which gets converted to propionate in human GIT. However, the same bacteria when grown on glucose produces butyrate instead of propionate (Scott et al., 2006). Similarly, butyrate is produced by the *M. elsdenii* when they are grown on glucose, but the same bacteria produce propionate when grown on lactate (Hino and Kuroda, 1993).

Both RS and AX produce butyrate differently. Most of the studies done with pigs either *in vitro* (Weaver et al., 1992) or *in vivo* (Marsono et al., 1993) or with humans (Topping et al., 1993) claim RS to be superior to AX, βG, or any other NSP in butyrate production (Bird et al., 2000). This is because the amount of butyrate produced by RS is 20 to 28 mmol% whereas NSP fermentation results in 10 to 15 mmol% of butyrate (Brouns et al., 2002). Though RS have been suggested to produce more butyrate than NSP, Ingerslev et al. (2014) and Nielsen et al. (2014) found the opposite. They observed AX derived from whole grain rye to be superior to RS2 in butyrate and acetate production in pigs. Also, a positive correlation was found between digested AX and net butyrate absorption in catheterized pigs fed a cereal-based diet (Bach Knudsen and Lærke, 2010). Arabinoxylan from rye flakes stimulates butyrate-producing bacteria thereby amount of butyrate more efficiently than RS from raw potato as well as high amylose corn starch (RS2) in the proximal and mid colon (Bach Knudsen and Lærke, 2010). However, AX derived from wheat did not affect colonic or cecal butyrate concentration (Belobrajdic et al., 2012). Among the different types of RS, RS3 is considered as the most powerful butyrogenic substrate (Brouns et al., 2002). Length of the 1,4-α-D-glucan chain and the

degree of polymerization of glucose affect the butyrogenic properties of RS3. However, 20 to 25 units of glucose polymerization on the chain of RS3 produce a higher amount of butyrate (Jacobasch et al., 2006). Fermentation of AX concentrate derived from wheat was rapid with the decrease of pH only in the cecum whereas fermentation of AX from whole grain matrix was slower with the decrease in pH both in the proximal colon and cecum (Bach Knudsen, 2015). Hence, it can be concluded that parent grain (rye, wheat, or any other cereals) from which AX is derived as well as pH in the intestinal lumen affects butyrate production. Arabinoxylan is a relatively better butyrate producer when compared to RS2. However, RS3 is the most potent butyrogenic substrate not only among different types of RS but also better than AX, βG or any other NSP.

Increase in production of butyrate not only results from the increased proliferation of butyrate-producing bacteria but can also be as a result of increased acetate produced by *Prevotella* (Ivarsson et al., 2014) and lactate produced by *Bifidobacterium*. This is because about 90% of butyrate is derived from acetate (Duncan et al., 2004) and in ruminants (sheep), 60% of the butyrate has been found to be synthesized directly from extracellular acetate (Leng and Leonard, 1965). Acetate and lactate are produced as a result of fermentation by *Prevotella* and *Bifidobacterium*, and those acetates can be consumed by butyrate-producing bacteria in the gut to produce butyrate (Belenguer et al., 2006; Rios-Covian et al., 2015). Hence, it is not just RS, AX, βG or any other substrate passing through the colon that affects proliferation of butyrate-producing bacteria and subsequently the butyrate production but also the metabolites like lactate or acetate produced by other microbes like *Prevotella* and *Bifidobacterium* contribute as precursors of butyrate production. The *in vitro* study with different barley and oat cultivars confirmed that βG increased the molar ratio of butyrate (Pieper et al., 2009; Jha et al., 2010b). However, feeding high level of βG increased production of lactate and propionate in the colon with no effect on the production of butyrate (Pieper et al., 2012). Despite lactate and propionate being precursors of butyrate production through the cross-feeding mechanism, it has no effect in increasing the production of butyrate.

7. Conclusion

Structural variation, degree of polymerization, and branching of RS, AX, βG, and types of RS being offered to interact with the digestive process throughout the GIT, leading to change in the fermentation characteristics and modulation of the microbial community. Degradation of RS on the proximal or distal part of GIT depends on the type of RS. The solubility of AX and βG also affects SCFA production as insoluble AX and βG are less fermentable compared to soluble ones. Branching in RS increases the surface area for the enzymes to act on. However, branching in AX decreases area for xylanase to act on the xylan backbone. Though arabinose and xylan occur in the form of AX, arabinose has been found as a butyrogenic substrate in the large intestine. However, in the small intestine, the role of xylan as a butyrogenic substrate is more pronounced. Most of the bacterial group except *Enterobacteriaceae* can degrade βG, and a larger polymer of AX is degraded by *Bacteroides* while smaller oligomers of AX is degraded by *Bifidobacteria*. It is not just the content of RS, AX or βG but also their physical forms (purified or grain matrix) influence the microbial population in the GIT of pigs. The pH reduction in the hindgut as a result of fermentation suppresses the growth of pathogenic organism, whereas beneficial microbes flourish. Though several studies have started to take into consideration the levels of RS, AX, and βG and its fraction, further information is needed to identify an appropriate source and the amount of RS, AX, and βG that can improve gut health while maintaining or improving the performance of pigs.

Conflict of interest

None.

Acknowledgment

Graduate student Utsav P. Tiwari was supported by USDA National Institute for Food and Agriculture, Hatch/Smith-Lever Project HAW02030-H, managed by the College of Tropical Agriculture and Human Resources, University of Hawaii at Manoa, Honolulu, HI USA.

References

Aminov RI, Walker AW, Duncan SH, Harmsen HJM, Welling GW, Flint HJ. Molecular diversity, cultivation, and improved detection by fluorescent in situ hybridization of a dominant group of human gut bacteria related to Roseburia spp. or Eubacterium rectale. Appl Environ Microbiol 2006;72:6371–6.
Amrein TM, Gränicher P, Arrigoni E, Amadò R. In vitro digestibility and colonic fermentability of aleurone isolated from wheat bran. Food Sci Technol 2003;36:451–60.
Bach Knudsen KE. Microbial degradation of whole-grain complex carbohydrates and impact on short-chain fatty acids and health. Adv Nutr Int Rev J 2015;6:206–13.
Bach Knudsen KE, Canibe N. Breakdown of plant carbohydrates in the digestive tract of pigs fed on wheat- or oat-based rolls. J Sci Food Agric 2000;80:1253–61.
Bach Knudsen KE, Lærke HN. Review: rye arabinoxylans: molecular structure, physicochemical properties and physiological effects in the gastrointestinal tract. Cereal Chem 2010;87:353–62.
Bach Knudsen KE, Jensen BB, Hansen I. Digestion of polysaccharides and other major components in the small and large intestine of pigs fed on diets consisting of oat fractions rich in beta -D-glucan. Br J Nutr 1993;70:537–56.
Bach Knudsen KE, Nørskov NP, Bolvig AK, Hedemann MS, Lærke HN. Dietary fibers and associated phytochemicals in cereals. Mol Nutr Food Res 2017;61:1–15.
Barron C, Surget A, Rouau X. Relative amounts of tissues in mature wheat (Triticum aestivum L.) grain and their carbohydrate and phenolic acid composition. J Cereal Sci 2007;45:88–96.
Beckmann L, Simon O, Vahjen W. Isolation and identification of mixed linked β-glucan degrading bacteria in the intestine of broiler chickens and partial characterization of respective β-glucanase activities. J Basic Microbiol 2006;46:175–85.
Belenguer A, Duncan SH, Calder AG, Holtrop G, Louis P, Lobley GE, Flint HJ. Two routes of metabolic cross-feeding between Bifidobacterium adolescentis and butyrate-producing anaerobes from the human gut. Appl Environ Microbiol 2006;72:3593–9.
Belobrajdic DP, Bird AR, Conlon M, Williams B, Kang S, McSweeney CS, Zhang D, Bryden WL, Gidley MJ, Topping DL. An arabinoxylan-rich fraction from wheat enhances caecal fermentation and protects colonocyte DNA against diet-induced damage in pigs. Br J Nutr 2012;107:1274–82.
Bergstrom KSB, Guttman JA, Rumi M, Ma C, Bouzari S, Khan MA, Gibson DL, Vogl AW, Vallance BA. Modulation of intestinal goblet cell function during infection by an attaching and effacing bacterial pathogen. Infect Immun 2008;76:796–811.
Biliaderis CG. The structure and interactions of starch with food constituents. Can J Physiol Pharmacol 1991;69:60–78.
Bindelle J, Pieper R, Montoya C, Van Kessel AG, Leterme P. Nonstarch polysaccharide-degrading enzymes alter the microbial community and the fermentation patterns of barley cultivars and wheat products in an in vitro model of the porcine gastrointestinal tract. FEMS Microbiol Ecol 2011;76:553–63.
Bird AR, Brown IL, Topping DL. Starches, resistant starches, the gut microflora and human health. Curr Issues Intest Microbiol 2000;1:25–37.
Bird AR, Vuaran M, Brown I, Topping DL. Two high-amylose 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;97:134–44.
Birt DF, Boylston T, Hendrich S, Jane J-L, Hollis J, Li L, McClelland J, Moore S, Phillips GJ, Rowling M, Schalinske K, Scott MP, Whitley EM. Resistant starch: promise for improving human health. Adv Nutr Int Rev J 2013;4:587–601.
Bobik TA, Havemann GD, Busch RJ, Williams DS, Aldrich HC. The propanediol utilization (pdu) operon of Salmonella enterica serovar LT2 includes genes necessary for formation of polyhedral organelles involved in coenzyme B(12)-dependent 1, 2-propanediol degradation. J Bacteriol 1999;181:5967–75.
Brestoff JR, Artis D. Commensal bacteria at the interface of host metabolism and the immune system. Nat Immunol 2013;14:676–84.
Brouns F, Kettlitz B, Arrigoni E. Resistant starch and "the butyrate revolution. Trends Food Sci Technol 2002;13:251–61.

Bunzel M, Ralph J, Marita JM, Hatfield RD, Steinhart H. Diferulates as structural components in soluble and insoluble cereal dietary fibre. J Sci Food Agric 2001;81:653–60.
Che L, Chen H, Yu B, He J, Zheng P, Mao X, Yu J, Huang Z, Chen D. Long-term intake of pea fiber affects colonic barrier function, bacterial and transcriptional profile in pig model. Nutr Canc 2014;66:388–99.
Chen H, Wang W, Degroote J, Possemiers S, Chen D, De Smet S, Michiels J. Arabinoxylan in wheat is more responsible than cellulose for promoting intestinal barrier function in weaned male piglets. J Nutr 2015;145:51–8.
Choct M. Feed non-starch polysaccharides: chemical structures and nutritional significance. Feed Milling Int 1997:13–26.
Courtin CM, Swennen K, Broekaert WF, Swennen Q, Buyse J, Decuypere E, Michiels CW, De Ketelaere B, Delcour JA. Effects of dietary inclusion of xylooligo- saccharides, arabinoxylooligosaccha- rides and soluble arabinoxylan on the microbial composition of caecal contents of chickens. J Sci Food Agric 2008;88:2517–22.
Crittenden R, Karppinen S, Ojanen S, Tenkanen M, Fagerström R, Mättö J, Saarela M, Mattila-Sandholm T, Poutanen K. In vitro fermentation of cereal dietary fibre carbohydrates by probiotic and intestinal bacteria. J Sci Food Agric 2002;82:781–9.
Cuff M, Dyer J, Jones M, Shirazi-Beechey S. The human colonic monocarboxylate transporter Isoform 1: its potential importance to colonic tissue homeostasis. Gastroenterol 2005;128:676–86.
Diez-Gonzalez F, Bond DR, Jennings E, Russell JB. Alternative schemes of butyrate production in Butyrivibrio fibrisolvens and their relationship to acetate utilization, lactate production, and phylogeny. Arch Microbiol 1999;171:324–30.
Dock-Nascimento DB, Junqueira K, de Aguilar-Nascimento JE. Rapid restoration of colonic goblet cells induced by a hydrolyzed diet containing probiotics in experimental malnutrition. Acta Cir Bras 2007;22:72–6.
Duncan SH, Holtrop G, Lobley GE, Calder AG, Stewart CS, Flint HJ. Contribution of acetate to butyrate formation by human faecal bacteria. Br J Nutr 2004;91:915–23.
Duss R, Nyberg L. Oat soluble fibers (β-glucans) as a source for healthy snack and breakfast foods. Cereal Foods World 2004;49:320–5.
Eckburg PB, Bik EM, Bernstein CN, Purdom E, Dethlefsen L, Sargent M, Gill SR, Nelson KE, Relman DA. Diversity of the human intestinal microbial flora. Science 2005;308:1635–8.
Ejby M, Fredslund F, Vujicic-Zagar A, Svensson B, Slotboom DJ, Abou Hachem M. Structural basis for arabinoxylo-oligosaccharide capture by the probiotic Bifidobacterium animalis subsp. lactisBl-04. Mol Microbiol 2013;90:1100–12.
Englyst HN, Kingman SM, Cummings JH. Classification and measurement of nutritionally important starch fractions. Eur J Clin Nutr 1992;46(Suppl 2):S33–50.
Flint HJ, Scott KP, Duncan SH, Louis P, Forano E. Microbial degradation of complex carbohydrates in the gut. Gut Microb 2012;3:289–306.
Fouhse JM, Zijlstra RT, Willing BP. The role of gut microbiota in the health and disease of pigs. Anim Front Rev Mag Anim Agric 2016;6:30–6.
Garry BP, Fogarty M, Curran TP, O'Connell MJ, O'Doherty JV. The effect of cereal type and enzyme addition on pig performance, intestinal microflora, and ammonia and odour emissions. Animal 2007;1:751–7.
Gaskins HR. In: Lewis AJ, Southern LL, editors. Intestinal bacteria and their influence on swine growth. Boca Raton, FL, USA: CRC Press; 2001.
Giuberti G, Gallo A, Moschini M, Masoero F. New insight into the role of resistant starch in pig nutrition. Anim Feed Sci Technol 2015;201:1–13.
Haenen D, Zhang J, Souza C, Bosch G, Van Der Meer IM, Van Arkel J, Van Den Borne JJGC, Odette P, Smidt H, Kemp B, Hooiveld GJEJ. A Diet high in resistant starch modulates microbiota composition, SCFA concentrations, and gene expression in pig intestine. J Nutr 2013;143:274–83.
Hino T, Kuroda S. Presence of lactate dehydrogenase and lactate racemase in Megasphaera elsdenii grown on glucose or lactate. Appl Environ Microbiol 1993;59:255–9.
Högberg A, Lindberg JE, Westerlund E, Andersson R, Pettersson D, Gibson GR, Isolauri E, Moreau M-C, Roberfroid M, Rowland I. The effect of level and type of cereal non-starch polysaccharides on the performance, nutrient utilization and gut environment of pigs around weaning. Anim Feed Sci Technol 2006;127:200–19.
Höije A, Sternemalm E, Heikkinen S, Tenkanen M, Gatenholm P. Material properties of films from enzymatically tailored arabinoxylans. Biomacromolecules 2008;9:2042–7.
Hughes SA, Shewry PR, Gibson GR, McCleary BV, Rastall RA. In vitro fermentation of oat and barley derived β-glucans by human faecal microbiota. FEMS Microbiol Ecol 2008;64:482–93.
Ingerslev AK, Theil PK, Hedemann MS, Lærke HN. Resistant starch and arabinoxylan augment SCFA absorption but affect postprandial glucose and insulin responses differently. Br J Nutr 2014;111:1564–76.
Inman CF, Haverson K, Konstantinov SR, Jones PH, Harris C, Smidt H, Miller B, Bailey M, Stokes C. Rearing environment affects development of the immune system in neonates. Clin Exp Immunol 2010;160:431–9.
Ivarsson E, Roos S, Liu HY, Lindberg JE. Fermentable non-starch polysaccharides increases the abundance of Bacteroides–Prevotella–Porphyromonas in ileal microbial community of growing pigs. Animal 2014;8:1777–87.
Izydorczyk MS, Dexter JE. Barley b -glucans and arabinoxylans: molecular structure, physicochemical properties, and uses in food products – a Review. Food Res Int 2008;41:850–68.
Jacobasch G, Dongowski G, Schmiedl D, Müller-Schmehl K. Hydrothermal treatment of Novelose results in high yield of resistant starch type 3 with beneficial prebiotic properties and decreased secondary bile acid formation in rats. Br J Nutr 2006;95:1063–74.
Janssen PH. Growth yield increase and ATP formation linked to succinate decarboxylation in Veillonella parvula. Arch Microbiol 1992;157:442–5.
Jensen BB, Jorgensen H. Effect of dietary fiber on microbial activity and microbial gas production in various regions of the gastrointestinal tract of pigs. Appl Environ Microbiol 1994;60:1897–904.
Jha R, Berrocoso JD. Review: dietary fiber utilization and its effects on physiological functions and gut health of swine. Animal 2015;9:1441–52.
Jha R, Berrocoso JFD. Dietary fiber and protein fermentation in the intestine of swine and their interactive effects on gut health and on the environment: a review. Anim Feed Sci Technol 2016;212:18–26.
Jha R, Leterme P. Feed ingredients differing in fermentable fiber and indigestible protein content affect fermentation metabolites and faecal nitrogen excretion in growing pigs. Animal 2012;6:603–11.
Jha R, Rossnagel B, Pieper R, Van Kessel A, Leterme P. Barley and oat cultivars with diverse carbohydrate composition alter ileal and total tract nutrient digestibility and fermentation metabolites in weaned piglets. Animal 2010a;4:724–31.
Jha R, Bindelle J, Rossnagel B, Van Kessel A, Leterme P. In vitro fermentation characteristics for pigs of hulless barleys differing in β-glucan content. Livest Sci 2010b;133:141–3.
Jha R, Bindelle J, Rossnagel B, Van Kessel A, Leterme P. In vitro evaluation of the fermentation characteristics of the carbohydrate fractions of hulless barley and other cereals in the gastrointestinal tract of pigs. Anim Feed Sci Technol 2011a;163:185–93.
Jha R, Bindelle J, Van Kessel A, Leterme P. In vitro fiber fermentation of feed ingredients with varying fermentable carbohydrate and protein levels and protein synthesis by colonic bacteria isolated from pigs. Anim Feed Sci Technol 2011b;165:191–200.
Jha R, Fouhse JM, Tiwari UP, Li L, Willing BP. Dietary fiber and intestinal health of monogastric animals. In: Kim SW, Jha R, editors. Nutritional intervention for the intestinal health of young monogastric animals. Frontiers in Veterinary Science; 2019. 6:48.
Jonathan MC, Van Den Borne JJGC, Van Wiechen P, Souza C, Schols HA, Gruppen H. In vitro fermentation of 12 dietary fibres by faecal inoculum from pigs and humans. Food Chem 2012;133:889–97.
Kawamata K, Hayashi H, Suzuki Y. Propionate absorption associated with bicarbonate secretion in vitro in the mouse cecum. Pflügers Archiv – Eur J Physiol 2007;454:253–62.
Konstantinov SR, Awati AA, Williams BA, Miller BG, Jones P, Stokes CR, Akkermans ADL, Smidt H, de Vos WM. Post-natal development of the porcine microbiota composition and activities. Environ Microbiol 2006;8:1191–9.
Lambo AM, Öste R, Nyman MEG-L. Dietary fibre in fermented oat and barley β-glucan rich concentrates. Food Chem 2005;89:283–93.
Lawley TD, Walker AW. Intestinal colonization resistance. Immunology 2013;138:1–11.
Lehmann U, Robin F. Slowly digestible starch – its structure and health implications: a review. Trends Food Sci Technol 2007;18:346–55.
Leng RA, Leonard GJ. Measurement of the rates of production of acetic, propionic and butyric acids in the rumen of sheep. Br J Nutr 1965;19:469–84.
Lesmes U, Beards EJ, Gibson GR, Tuohy KM, Shimoni E. Effects of resistant starch type III polymorphs on human colon microbiota and short chain fatty acids in human gut models. J Agric Food Chem 2008;56:5415–21.
Leterme P, Souffrant W-B, Théwis A. Effect of barley fibres and barley intake on the ileal endogenous nitrogen losses in piglets. J Cereal Sci 2000;31:229–39.
Louis P, Flint HJ. Diversity, metabolism and microbial ecology of butyrate-producing bacteria from the human large intestine. FEMS Microbiol Lett 2009;294:1–8.
Louis P, Scott KP, Duncan SH, Flint HJ. Understanding the effects of diet on bacterial metabolism in the large intestine. J Appl Microbiol 2007;102:1197–208.
Macfarlane S, Macfarlane GT. Regulation of short-chain fatty acid production. Proc Nutr Soc 2003;62:67–72.
Mach N, Berri M, Estellé J, Levenez F, Lemonnier G, Denis C, Leplat J-J, Chevaleyre C, Billon Y, Doré J, Rogel-Gaillard C, Lepage P. Early-life establishment of the swine gut microbiome and impact on host phenotypes. Environ Microbiol Rep 2015;7:554–69.
Marsono Y, Illman RJ, Clarke JM, Trimble RP, Topping DL. Plasma lipids and large bowel volatile fatty acids in pigs fed on white rice, brown rice and rice bran. Br J Nutr 1993;70:503–13.
Mårtensson O, Biörklund M, Lambo AM, Dueñas-Chasco M, Irastorza A, Holst O, Norin E, Welling G, Öste R, Önning G. Fermented, ropy, oat-based products reduce cholesterol levels and stimulate the bifidobacteria flora in humans. Nutr Res 2005;25:429–42.
Martinez I, Kim J, Duffy PR, Schlegel VL, Walter J. Resistant starches types 2 and 4 have differential effects on the composition of the fecal microbiota in human subjects. PLoS One 2010;5:1–11.
Mendis M, Simsek S. Production of structurally diverse wheat arabinoxylan hydrolyzates using combinations of xylanase and arabinofuranosidase. Carbohydr Polym 2015;132:452–9.
Metzler-Zebeli BU, Schmitz-Esser S, Mann E, Grüll D, Molnar T. Adaptation of the cecal bacterial microbiome of growing pigs in response to resistant starch Type 4. Appl Environ Microbiol 2015;81:8489–99.
Mirande C, Kadlecikova E, Matulova M, Capek P, Bernalier-Donadille A, Forano E, Béra-Maillet C. Dietary fibre degradation and fermentation by two xylanolytic bacteria Bacteroides xylanisolvens XB1AT and Roseburia intestinalis XB6B4 from the human intestine. J Appl Microbiol 2010;109:451–60.

Moura P, Barata R, Carvalheiro F, Gírio F, Loureiro-Dias MC, Esteves MP. In vitro fermentation of xylo-oligosaccharides from corn cobs autohydrolysis by Bifidobacterium and Lactobacillus strains. LWT - Food Sci Technol 2007;40:963–72.
Nielsen TS, Lærke HN, Theil PK, Sørensen JF, Saarinen M, Forssten S, Bach Knudsen KE. Diets high in resistant starch and arabinoxylan modulate digestion processes and SCFA pool size in the large intestine and faecal microbial composition in pigs. Br J Nutr 2014;112:1837–49.
Nofrarías M, Martínez-puig D, Pujols J, Majó N, Pérez JF. Long-term intake of resistant starch improves colonic mucosal integrity and reduces gut apoptosis and blood immune cells. Nutrition 2007;23:861–70.
Pastell H, Westermann P, Meyer AS, Tuomainen P, Tenkanen M. In vitro fermentation of arabinoxylan-derived carbohydrates by bifidobacteria and mixed fecal microbiota. J Agric Food Chem 2009;57:8598–606.
Pedersen MB, Dalsgaard S, Bach Knudsen KE, Yu S, Lærke HN. Compositional profile and variation of distillers dried grains with solubles from various origins with focus on non-starch polysaccharides. Anim Feed Sci Technol 2014;197:130–41.
Petri D, Hill JE, Van Kessel AG. Microbial succession in the gastrointestinal tract (GIT) of the preweaned pig. Livest Sci 2010;133:107–9.
Pieper R, Jha R, Rossnagel B, Van Kessel AG, Souffrant WB, Leterme P. Effect of barley and oat cultivars with different carbohydrate compositions on the intestinal bacterial communities in weaned piglets. FEMS Microbiol Ecol 2008;66:556–66.
Pieper R, Bindelle J, Rossnagel B, Van Kessel A, Leterme P. Effect of carbohydrate composition in barley and oat cultivars on microbial ecophysiology and proliferation of Salmonella enterica in an in vitro model of the porcine gastrointestinal tract. Appl Environ Microbiol 2009;75:7006–16.
Pieper R, Bindelle J, Malik G, Marshall J, Rossnagel BG, Leterme P, Van Kessel AG. Influence of different carbohydrate composition in barley varieties on Salmonella Typhimurium var. Copenhagen colonisation in a challenge model in pigs. Arch Anim Nutr 2012;66:163–79.
Pryde SE, Duncan SH, Hold GL, Stewart CS, Flint HJ. The microbiology of butyrate formation in the human colon. FEMS Microbiol Lett 2002;217:133–9.
Read SM, Currie G, Bacic A. Analysis of the structural heterogeneity of laminarin by electrospray-ionisation-mass spectrometry. Carbohydr Res 1996;281:187–201.
Regmi PR, Van Kempen TATG, Matte JJ, Zijlstra RT. Starch with high amylose and low in vitro digestibility increases short-chain fatty acid absorption, reduces peak insulin secretion, and modulates incretin secretion in pigs. J Nutr 2011;141:398–405.
Rios-Covian D, Gueimonde M, Duncan SH, Flint HJ, De Los Reyes-Gavilan CG. Enhanced butyrate formation by cross-feeding between Faecalibacterium prausnitzii and Bifidobacterium adolescentis. FEMS Microbiol Lett 2015;362:1–7.
Rose DJ, Patterson JA, Hamaker BR. Structural differences among alkali-soluble arabinoxylans from maize (Zea mays), rice (Oryza sativa), and wheat (Triticum aestivum) brans influence human fecal fermentation profiles. J Agric Food Chem 2010;58:493–9.
Saulnier L, Sado P-E, Branlard G, Charmet G, Guillon F. Wheat arabinoxylans: exploiting variation in amount and composition to develop enhanced varieties. J Cereal Sci 2007;46:261–81.
Saxena RK, Anand P, Saran S, Isar J, Agarwal L. Microbial production and applications of 1,2-propanediol. Indian J Microbiol 2010;50:2–11.
Scott KP, Martin JC, Campbell G, Mayer CD, Flint HJ. Whole-genome transcription profiling reveals genes up-regulated by growth on fucose in the human gut bacterium "Roseburia inulinivorans". J Bacteriol 2006;188:4340–9.
Stack HM, Kearney N, Stanton C, Fitzgerald GF, Ross RP. Association of beta-glucan endogenous production with increased stress tolerance of intestinal lactobacilli. Appl Environ Microbiol 2010;76:500–7.
Sun Y, Su Y, Zhu W. Microbiome-metabolome responses in the cecum and colon of pig to a high resistant starch diet. Front Microbiol 2016;7:1–10.
Tester RF, Qi X, Karkalas J. Hydrolysis of native starches with amylases. Anim Feed Sci Technol 2006;130:39–54.
Tiihonen K, Rautonen N, Alhoniemi E, Ahotupa M, Stowell J, Vasankari T. Postprandial triglyceride response in normolipidemic, hyperlipidemic and obese subjects – the influence of polydextrose, a non-digestible carbohydrate. Nutr J 2015;14:1–9.
Tiwari UP, Jha R. Nutrient profile and digestibility of tubers and agro-industrial coproducts determined using an in vitro model of swine. Anim Nutr 2016;2:1–4.
Tiwari UP, Jha R. Nutrients, amino acid, fatty acid and non-starch polysaccharide profile and in vitro digestibility of macadamia nut cake in swine. Anim Sci J 2017;88:1093–9.
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 DL, Illman RJ, Clarke JM, Trimble RP, Jackson KA, Marsono Y. Dietary fat and fiber alter large bowel and portal venous volatile fatty acids and plasma cholesterol but not biliary steroids in pigs. J Nutr 1993;123:133–43.
Tungland BC, Meyer D. Nondigestible oligo- and polysaccharides (dietary fiber): their physiology and role in human health and food. Compr Rev Food Sci Food Saf 2002;1:90–109.
Van Laere KM, Hartemink R, Bosveld M, Schols HA, Voragen AG. Fermentation of plant cell wall derived polysaccharides and their corresponding oligosaccharides by intestinal bacteria. J Agric Food Chem 2000;48:1644–52.
Varel VH, Yen. Microbial perspective on fiber utilization by swine. J Anim Sci 1997;75:2715–22.
Velázquez OC, Lederer HM, Rombeau JL. Butyrate and the colonocyte. Production, absorption, metabolism, and therapeutic implications. Adv Exp Med Biol 1997;427:123–34.
Vries S De, Gerrits WJJ, Kabel MA, Vasanthan T, Zijlstra T. β -glucans and resistant starch alter the fermentation of recalcitrant fibers in growing pigs. PLoS One 2016:1–18.
Walker AW, Ince J, Duncan SH, Webster LM, Holtrop G, Ze X, Brown D, Stares MD, Scott P, Bergerat A, Louis P, Mcintosh F, Johnstone AM, Lobley GE, Parkhill J, Flint HJ. Dominant and diet-responsive groups of bacteria within the human colonic microbiota. ISME J 2010;5:220–30.
Watanabe Y, Nagai F, Morotomi M. Characterization of Phascolarctobacterium succinatutens sp. an asaccharolytic, succinate-utilizing bacterium isolated from human feces. Appl Environ Microbiol 2012;78:511–8.
Weaver AG, Krause A, Miller T, Wolin J. Cornstarch fermentation by the colonic microbial community yields more butyrate than does cabbage fiber fermentation; cornstarch fermentation rates correlate negatively. Am J Clin Nutr 1992;55:70–7.
Weiss E, Aumiller T, Spindler HK, Rosenfelder P, Eklund M, Witzig M, Jørgensen H, Bach E, Mosenthin R. Wheat and barley differently affect porcine intestinal microbiota. J Sci Food Agric 2016;96:2230–9.
Wellock IJ, Houdijk JGM, Kyriazakis I. Effect of dietary non-starch polysaccharide solubility and inclusion level on gut health and the risk of post weaning enteric disorders in newly weaned piglets. Livest Sci 2007;108:186–9.
Williams BA, Bosch MW, Boer H, Verstegen MWA, Tamminga S. An in vitro batch culture method to assess potential fermentability of feed ingredients for monogastric diets. Anim Feed Sci Technol 2005;124:445–62.
Wong K, Wong King-Yee, Kwan A Hoi-Shan, Cheung PCK. Dietary Fibers from Mushroom Sclerotia: 3. In vitro fermentability using human fecal microflora. J Agric Food Chem 2005;53:9407–12.
Wood PJ. REVIEW: oat and Rye β-Glucan: properties and function. Cereal Chem J 2010;87:315–30.
Wood P, Beer MU. Functional foods: biochemical and processing spects. Carbohydr Polym 2002;50:95–6.
Young W, Roy NC, Lee J, Lawley B, Otter D, Henderson G, Mccann MJ. Changes in bowel microbiota induced by feeding weanlings resistant starch stimulate transcriptomic and physiological responses. Appl Environ Microbiol 2012;78:6656–64.
Ze X, Duncan SH, Louis P, Flint HJ. Ruminococcus bromii is a keystone species for the degradation of resistant starch in the human colon. ISME J 2012;6:1535–43.
Zhang M, Chekan JR, Dodd D, Hong P-Y, Radlinski L, Revindran V, Nair SK, Mackie RI, Cann I. Xylan utilization in human gut commensal bacteria is orchestrated by unique modular organization of polysaccharide-degrading enzymes. Proc Natl Acad Sci U S A 2014;111:E3708–17.
Zhang S, Li W, Smith CJ, Musa H. Cereal-derived arabinoxylans as biological response modifiers: extraction, molecular features, and immune-stimulating properties. Crit Rev Food Sci Nutr 2015;55:1035–52.
Zhao J, Cheung PCK. Fermentation of beta glucans derived from different sources by bifidobacteria: evaluation of their bifidogenic effect. J Agric Food Chem 2011;59:5986–92.
Zijlstra RT, De Lange CFM, Patience JF. Nutritional value of wheat for growing pigs: chemical composition and digestible energy content. Can J Anim Sci 1999;79:187–94.