Food Bioscience 43 (2021) 101267

Contents lists available at ScienceDirect

Food Bioscience

journal homepage: www.elsevier.com/locate/fbio

The effects and benefits of arabinoxylans on human gut microbiota – A narrative review

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ARTICLE INFO

Keywords:
prebiotics
Functional food
Gut microbiome
Symbiosis
Dysbiosis

ABSTRACT

Prebiotics are a class of functional foods which target beneficial microbial species of the gut to benefit host health. They consist of dietary fibres which, after ingestion, are degraded and fermented by microorganisms in the colon. Arabinoxylan (AX) is an important member of the prebiotic family. This non-digestible fibre is commonly found in cereal grains such as wheat and rice. Human *in vivo* studies have demonstrated that consumption of various species of AXs has profound effects on gut microorganisms.

AX exists in different structures across cereal types. Structural differences of AXs impact their cleavage, degradation, and fermentation by gut microbiota. However, this structural diversity also makes it difficult to compare and contrast studies of different AXs. Nevertheless, common bacterial targets of prebiotics across all AX structures include *Bifidobacterium* spp. and *Lactobacillus* spp., which are both beneficial to human health. Existing research on AXs has primarily focused on wheat derived AX. As the structure of rice AXs varies significantly from that of wheat AXs, more research is needed on the effects of rice AXs on gut microbiota. This narrative review synthesises the current understandings of how prebiotic AX affects gut microbiota and its implications for human health.

1. Introduction

Microbial communities live in symbiosis with humans with the gut being the most densely populated site. Microbes that inhabit the gut can have a host relationship that is beneficial, neutral, or detrimental under certain conditions (Reid et al., 2011). Gut microbiota impact host physiology by affecting energy homeostasis, immunity, digestion, vitamin synthesis and inhibition of pathogen colonisation (De Filippo et al., 2010; Kau, Ahern, Griffin, Goodman, & Gordon, 2011). The appropriate functional association between gut microbiota, intestinal epithelial cells and the host immune system maintains the balance between tolerance and immunity to pathogenic microbes, non-pathogenic microbes, and food (Mendis, Leclerc, & Simsek, 2016). It has been established that high microbial diversity is associated with a healthy gut microbiota, and the loss of diversity correlates with increased risk of disease (Scott, Antoine, Midtverdt, & van Hemert, 2015). Microbial imbalance in the gut, described as a functional association among microbiota, intestinal epithelial cells and host immune system, is linked to a wide spectrum of health conditions including gastrointestinal diseases, liver disease, obesity, mood disorders, gynaecological conditions and other facets of human health (Scott et al., 2015).

Functional foods can be defined as foods which improve health and wellbeing (Zhurlova & Kaprelyants, 2017). Many functional foods, working with gut microbiota, offer health-promoting abilities (Zhurlova & Kaprelyants, 2017). In particular, the biotic family of functional foods focus on the proliferation, stabilisation and diversification of beneficial bacteria that are important components of human gut microbiota (Scott et al., 2015). Probiotics containing live beneficial microorganisms introduce beneficial microbes into the gastrointestinal system. Prebiotics are ingredients which are non-digestible to humans but stimulate

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https://doi.org/10.1016/j.fbio.2021.101267
Received 11 October 2020; Received in revised form 18 July 2021; Accepted 21 July 2021
Available online 22 July 2021

the growth of microbes in the gut via fermentation (Tsai et al., 2019). Interest rises in identifying and developing prebiotics that increase microbial diversity for promoting general health and aiding against dysbiosis of gut microbiota with the host (Mendis et al., 2016; Scott et al., 2015).

Arabinoxylans (AXs) are non-starch polysaccharides (NSP) found in cereal grains and have been previously identified as prebiotics (Damen et al., 2011; Grootaert et al., 2006). They have been found to be greatly beneficial in promoting the diversity and function of gut microbiota (Mendis et al., 2016). The structure of AXs varies amongst different cereal grains and even between the bran and endosperm from the same cereal (Wang et al., 2020). These structures are classified into branched and linear, with branched AXs showing greater performance in promoting the proliferation of microorganisms and increasing production of short-chain fatty acids (SCFAs) according to *in vitro* studies (Tuncil, Thakkar, Arioglu-Tuncil, Hamaker, & Lindemann, 2018). The degrees of and mechanisms underlying the effects of commercially available AXs on gut microbiota vary significantly due to variations in the chemical substitutions and molecular weights resulting from using diverse methods of manufacturing or extracting the AXs (Tuncil et al., 2018; Wang et al., 2020).

This narrative review firstly examines the impact of the structural differences in AXs affecting their degradation and fermentation by gut microbiota. This review will then discuss the prebiotic relationship between AXs and gut microbes, and how the utilisation of AXs by these gut bacteria may potentially benefit human health.

2. Arabinoxylans

2.1. Chemical structures in cereal grains

AXs are the main non-digestible fibre of cereal grains, including wheat, rice, rye, maize, corn, sorghum, and oat (Hald et al., 2016). They have a complex structure consisting primarily of a chain of linear (1, 4)-β-D-xylose residues that is substituted at intervals with α-L-arabinose residues through α(1,2) and/or α(1,3), glycosidic linkage (Fig. 1) (Adams, Kroon, Williamson, Gilbert, & Morris, 2004; Nielsen et al., 2018; Saulnier, Sado, Branlard, Charmet, & Guillon, 2007; Wang et al., 2020). Xylose generally represents more than 50 % of the constitutive sugars with a great diversity of side chains present on the main chain (Saulnier et al., 2007).

AXs exist in diverse gross and fine structures, ranging from long-chains within cereals to short-chain fractions resulting from various types of enzymatical cleavages of the molecule (McCleary et al., 2015; Salden et al., 2018). At a gross structural level, AXs are classified as either branched or linear, although the linear structures are not strictly linear but considerably less branched. Examples of linear AXs include wheat and rye. They consist of a single side-chain of arabinose residues, monosubstituted on position O-3 or di-substituted on positions O-2 and O-3 of the xylose residue backbone (Saulnier et al., 2007; Zhurlova & Kaprelyants, 2017). Examples of branched AXs include rice, maize and sorghum. They have a large distribution of side chains and high degrees of substitutions (Saulnier et al., 2007; Schendel, Meyer, & Bunzel, 2016; Zhurlova & Kaprelyants, 2017). Another structural characteristic of AXs is the presence of ferulic acid esterified to arabinose at the O-5 position (de O Buanafina, 2009; Mendez-Encinas, Carvajal-Millan, Rascon-Chu, Astiazaran-Garcia, & Valencia-Rivera, 2018; Saulnier et al., 2007).

The structure of branched AXs is slightly more complex than linear AXs (Rosicka, Komisarczyk, Nebesny, & Makowski, 2016). The branching consists of arabinose units as well as xylopyranose, galactopyranose and α-D-glucuronic acid or 4-O-methyl-α-D-glucuronic residues (Izydorczyk & Biliaderis, 2007; Rosicka et al., 2016). Furthermore, branched AXs have higher proportions of ferulates in their side chains (Fig. 2) (Nino-Medina et al., 2010; Rao & Muralikrishna, 2006; Yuwang et al., 2018). Some of these ferulate residues undergo free radical induced oxidative coupling to form ferulate dimers and higher oligomers (Bunzel, Ralph, Marita, Hatfield, & Steinhart, 2001). This creates inter- and intramolecular cross-linking between AX chains (Ralph, Quideau, Grabber, & Hatfield, 1994). The cross-linking is important for plant protection mechanisms against pathogens as well as prebiotic capacities and antioxidative properties for potential benefits in human health (Santiago & Malvar, 2010; Yang, Maldonado-Gomez, Hutkins, & Rose, 2014). Ferulic acid oxidative coupling during digestion promotes selective AX fermentation and limits non-beneficial bacterial growth (Snelders et al., 2014).

The structure of AX influences how the substrate is fermented and degraded by gut microbiota (Salden et al., 2018). An *in vitro* study by Tuncil et al. (2018) compared wheat, sorghum, rice and corn brans and their effects on gut microbiota diversity. This study showed sorghum bran and rice bran had the highest arabinose xylose ratios (1.25 and 1.19, respectively), indicative of higher levels of branching. Branching densities significantly affect arabinoxylan fermentation by gut microbiota (Rumpagaporn et al., 2015). The relative abundance of arabinose and xylose across bran types was also statistically significant, with rice bran exhibiting the lowest proportions of both, at 25.1 % and 21.2 %, respectively (Tuncil et al., 2018). These structural differences have produced varying outcomes in human clinical trials and animal studies (Chen et al., 2014; Windey et al., 2015; Zambrana et al., 2019). Zambrana et al. (2019), studied the effects of rice AX and detected microbiota changes including decreases in non-beneficial bacteria including *Campylobacter*, and increases in beneficial bacteria including *Lactobacillus*. Windey et al. (2015), studied the effects of wheat AX, with only one significant increase detected. The same increase (*Bifidobacterium* spp.) was seen in a study by Chen et al. (2014) on wheat AX.

2.2. Degradation and fermentation

As non-starch polysaccharides, AXs pass through the small intestine

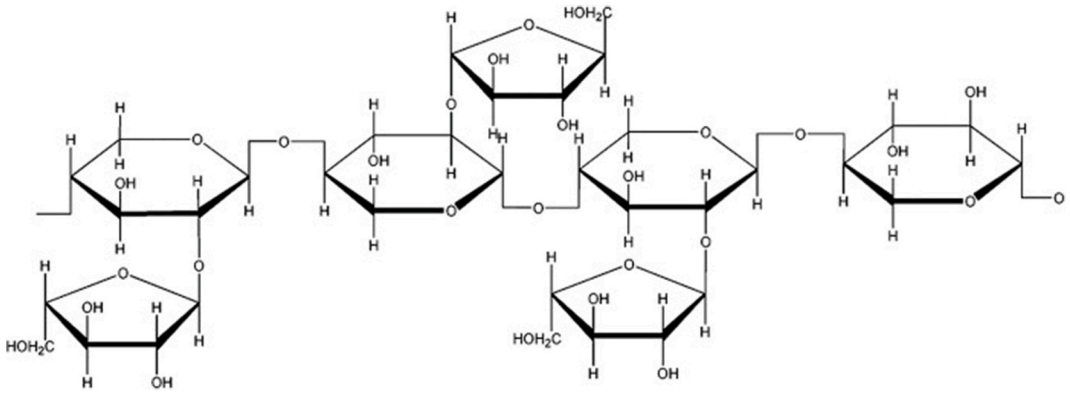

Fig. 1. The general structure of arabinoxylans (Sinha, Kumar, Makkar, De Boeck, & Becker, 2011).

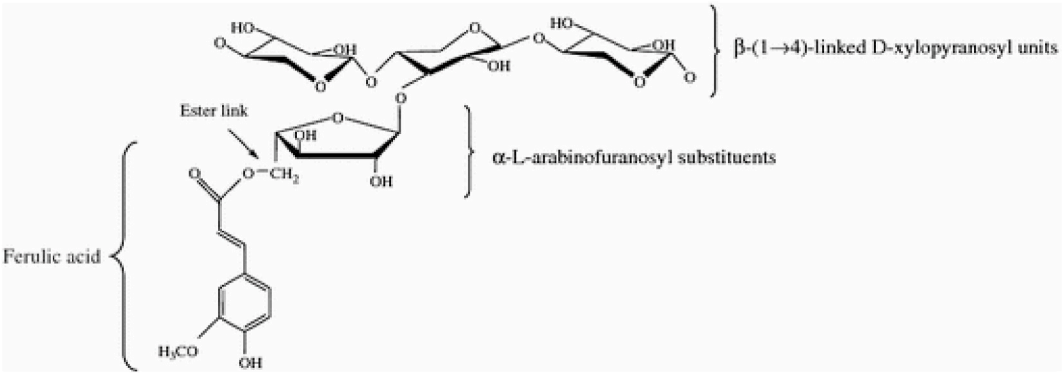

Fig. 2. Structure of feruloylated arabinoxylans (Nino-Medina et al., 2010).

and reach the transverse and descending colon where they are fermented by microbes (Mendis et al., 2016). Cleavage of AXs occurs when the first bonds in the structure are broken and degradation occurs to break down the remaining structures. Fermentation then occurs as the further breakdown and utilisation of the degraded substances by gut microbes (Mendis et al., 2016). The extent of fermentation of AXs depends on their structures, with unbranched AXs showing greater affiliation for fermentation than branched AXs (Mendis et al., 2016). Conversely, the increased surface area of branched AXs makes them resistant to fermentation and degradation (Tiwari, Singh, & Jha, 2019). The mechanisms of cleavage of branched AXs also differ from that of linear AXs, as the cleavage point differs between these structures and different classes of enzymes are needed for their cleavage (Beily, Vrsanska, Tenkanen, & Kluepfel, 1997). Major metabolites of degradation and fermentation are the residual SCFAs, including acetate, propionate and butyrate. These SCFAs serve as energy sources to tissue cells and have a multitude of health benefits, such as reducing inflammation, promoting intestinal epithelial barrier integrity, and suppressing tumour growth (Mendis et al., 2016).

Full understanding of the degradation and fermentation of AXs by gut microbiota is difficult due to the variations in AX structures, extraction processes, effects on degradation and fermentation locations, as well as cleavage ability. Processes of degradation and fermentation are reliant on the symbiotic relationships between the host and their unique compositions of gut microbiota (Van Soest, 2004). It should be noted that the majority of human (Francois et al., 2012; Salden et al., 2018; Walton, Lu, Trogh, Arnaut, & Gibson, 2012; Windey et al., 2015) and animal (Chen et al., 2014; Geraylou et al., 2013; Neyrinck et al., 2011; Van Graeyveld et al., 2008; Van Hees et al., 2019) *in vivo* studies have investigated the effects of wheat based AXs on their degradation and fermentation. This trend is also seen in *in vitro* studies, however, to a lesser extent (Arcila, Weier, & Rose, 2015; Nielsen et al., 2018; Tuncil et al., 2018; Vardakou et al., 2008; Vardakou, Palop, Gasson, Narbad, & Christakopoulos, 2007; Yacoubi et al., 2016).

2.3. Pre-treatments

Since most of the AX content in cereal grains is water-unextractable, pre-treatment of cereal grains has been shown to increase fermentability and digestibility of AX, and thus its utilisation by gut microbiota (Arcila et al., 2015; Vardakou et al., 2008). Extrusion and extraction as pre-treatment methods are highly individual and often not disclosed by manufacturers due to, at least, the difficulty associated with the process (Arcila et al., 2015). During extrusion a substance is ground down to finer working particles. During extraction the substance is removed and broken down. An *in vitro* study by Arcila et al. (2015) investigated different extrusion methods to determine whether this process affects the availability of NSPs as a primary source of dietary fibre. The results showed that all extrusion methods increased the availability of NSPs compared to non-pre-treated wheat bran. A study by Yacoubi et al. (2016) investigated the effects of multicomponent enzyme preparation on wheat grain. This pre-treatment increased the content of water-soluble AX and decreased the degree of polymerisation of the xylan-backbone of resultant processed grain products (Yacoubi et al., 2016). These studies further showed that low substituted AX with reduced molecular weight yields higher concentrations of bacterial fermentation enzymes and thus greater degradation and fermentation abilities. It is clear that identity and diversity of gut microbiota play an important role in the degradation and fermentation of particular prebiotics.

3. Gut microbiota in humans

3.1. Current understanding of microbiota ecology

Various species of human gut microbiota have been identified using metagenomic sequencing studies (Qin et al., 2010). The genera *Faecalibacterium*, *Clostridium*, *Bacteroides*, *Ruminococcus*, and *Roseburia* are among the 25 most abundant lineages of human gut microbiota (Walker et al., 2011). Composition of gut microbiota has been shown to change with age, with stability reached during adulthood, and are affected by other factors including ethnicity, socioeconomic status, and disease states (Bowyer et al., 2019; Carson et al., 2018; Nagpal et al., 2017). Recent findings indicate that among healthy individuals there is a shared minimal gut genome, with variations seen at a species level across age, race and socioeconomic status (Bowyer et al., 2019; Carson et al., 2018; Nagpal et al., 2017; Qin et al., 2010). Substantial variations in gut microbial species have been shown to occur across health status, especially between healthy individuals and those with gastrointestinal diseases (Qin et al., 2010). Furthermore, these variations occur across beneficial microbes or pathogenic microbes exhibiting different host health repercussions. The relationship between host genetic variation and the diversity of gut microbiota is largely unknown, although, a recent twin study demonstrated that there are heritable microbial taxa that impact host health and metabolism (Goodrich et al., 2014). Gut environment plays a critical role in determining what microorganisms can survive and proliferate in the gut (Walter & Ley, 2011). Due to a low pH and rapid luminal flow in the stomach and small intestine, microbial growth is limited in these parts of the digestive tract (Walter & Ley, 2011). Less acidic pH, larger volume, lower concentration of bile salts and longer retention time in the colon make it an ideal place for microbial proliferation (Walter & Ley, 2011).

3.2. Microbiota and their utilisation of carbohydrates

Bacteria possess enzymes to cleave, ferment and digest carbohydrates. AXs are degraded by many microbial and plant enzymes including xylanases, arabinofuranosidases, acetyl esterases, ferulic acid

esterases and methyl glucuronidases (Vardakou et al., 2008). For example, ferulic acid esterases and xylanases work together to release ferulic acid from the AX molecule (Vardakou et al., 2008). The action of xylanases has the greatest influence on the degradation of the AX backbone. At the same time, ferulic acid esterases release ferulic acid from short-chain feruloylated xylooligosaccharides (Vardakou et al., 2007). These enzymes have been reported in human models (Hopkins et al., 2003), and it was confirmed *in vitro* that their production by gut microbiota was induced by the addition of AX to human faecal fermentation vessels (Vardakou et al., 2008). These findings imply that when the required bacteria are present in the gut, they will degrade and ferment AX and in turn, release enzymes to aid this process further.

3.3. Important bacteria to host health

The *Bifidobacterium* spp. are estimated to make up only 2 % of total gut microbiota, however, they play a significant role in host health (Ventura, Turroni, Lugli, & Van Sindersen, 2014). These species have the ability to breakdown complex carbohydrates, including AX, and are frequently used for measuring the effects of AX on gut microbiota populations (Hald et al., 2016). Further to this role, *Bifidobacterium* spp. protect the host against pathogens by competitive exclusion, modulation of the immune system, and provision of vitamins and other nutrients to the host (O'Callaghan & van Sinderen, 2016).

Another key genus in host health is *Lactobacillus* (Rossi et al., 2016). This genus includes 217 recognised species, which live in a variety of habitats where carbohydrate-based substrates are available (Rossi et al., 2016). The role of *Lactobacillus* spp. in the ecology of gut microbiota is difficult to determine using *in vivo* research methods due to its presence in many functional foods commonly consumed (Rossi et al., 2016). Its presence as either a true inhabitant or a transient species does not deter from its benefit to host health (Rossi et al., 2016). Other bacteria of importance to human health include *Roseburia*, *Faecalibacterium*, *Ruminococcus* and *Bacteroides* (Francois et al., 2012; Sheflin et al., 2017). The presence of pathogenic microbes and their interactions between the host and other microbes that inhabit the gut can lead to various outcomes for host health and furthermore impact the diversity of gut microbiota.

3.4. Symbiosis and dysbiosis with host

Humans live in symbiosis with a diverse community of microorganisms. These micro-symbionts can be pathogenic (benefiting themselves by harming the host), commensals (benefiting themselves but not the host) or mutualists (benefiting themselves and the host). Human gut microbiota makes up a large proportion of symbiotic microorganisms of the entire body. The balance of mutualists, commensals, and pathogens is a determining factor as to whether the host is in symbiosis or dysbiosis (Reid et al., 2011). Dysbiosis occurs as an alteration in the structure and composition of the gut microbiota, resulting in an imbalance between beneficial and pathogenic microbes (Fjeldheim Dale & Arslan Lied, 2020).

In addition to those intrinsic factors outlined in the previous section, the composition of gut microbiota can be affected by several extrinsic factors, including drug intake and disease, with diet being the most influential factor (De Filippo et al., 2010; Kau et al., 2011). Due to their anti-microbial properties, antibiotics have a significant effect on gut microbiota, causing a loss of beneficial strains and the development of antibiotic-resistant ones (Goodrich et al., 2014). This effect is exacerbated during the first five years of life as the gut microbiome is still being established (Goodrich et al., 2014). Past studies have reported significant geographic and seasonal variations in gut microbiota that are related to changes in dietary patterns (Davenport et al., 2014). Obesity, a disease closely related to diet, is an important factor influencing gut microbiota which reciprocally affects body weight (Castaner et al., 2018). For example, a recent study has shown that the gut microbiota in overweight and obese participants is significantly different from that of average weighted participants (Castaner et al., 2018; Salden et al., 2018).

Dysbiosis is also prevalent in individuals with gastrointestinal disorders such as Crohn's disease and colitis as their gut microbiome have shown distinct differences compared with healthy participants (Forbes, Van Domselaar, & Bernstein, 2016). In the same study, analysis of gut bacterial species from patients with Crohn's disease and colitis demonstrated a high degree of dissimilarity in bacteria populations found between these disease states. Furthermore, when compared to studies with healthy participants, there was very little overlap in the predominant bacterial species found (Forbes et al., 2016).

Research has been conducted to determine whether the consumption of dietary fibres, including AXs, can have a beneficial and possibly protective effect against dietary-related dysbiosis. Sheflin et al. (2017) investigated the impact of AX on gut microbiota in overweight and obese participants with a prior history of colorectal cancer. The study recruited 21 subjects who consumed an AX supplement over 28 days with time points at 0, 14 and 28 days. Richness and diversity in gut microbiota did not alter at day 14; however, they were vastly increased at day 28 (Sheflin et al., 2017). This difference may lead to a better balance or symbiosis with gut microbiota.

Diversity richness in gut microbiota is theorised to reduce inflammation and prevent associated diseases (Forbes et al., 2016). Preliminary studies have shown that diversity can stimulate the differentiation and activity of regulatory T cells (differentiated immune cells) in the gut (Forbes et al., 2016). These regulatory T cells contribute to the maintenance of a tolerant environment and thus, in turn, reduce opportunities and occurrence of inflammation (Forbes et al., 2016).

Dysbiosis research is in its infancy. Therefore, research focusing on healthy gut microbiota is necessary before determining the conclusive effects of AXs on unhealthy gut microbiota.

4. Arabinoxylan and gut microbiota

4.1. Prebiotic capacity of arabinoxylan

Prebiotics can selectively stimulate the growth and activity of certain gut microbes (Salden et al., 2018). As a novel class of prebiotics, AX relies on a spectrum of microbial enzymes for its degradation due to its structural variation (Salden et al., 2018). A distinctive characteristic of AX as prebiotics is that they are gradually fermented along the colon, with marked fermentation towards the distal colon (Salden et al., 2018). Therefore, AXs are not limited to rapid fermentation in the proximal colon, a major limiting factor of most other prebiotics (Grootaert et al., 2006; Salden et al., 2018). Common targets of prebiotics include *Bifidobacteria* spp. and *Lactobacillus* spp. due to their long-term use as probiotics and the general acceptance of being beneficial for host health (Saman, Tuohy, Vazquez, Gibson, & Pandiella, 2016). *In vitro* studies have confirmed that AX in batch fermentation vessels increased *Bifidobacteria* spp. and *Lactobacillus* spp. populations (Harris et al., 2019; Reis et al., 2014; Saman et al., 2016; Vardakou et al., 2007).

4.2. Effects of arabinoxylan on gut microbiota

Increased SCFA production has been used in many studies as an important indicator for fermentation of AX by bacterial species (Van Graeyveld et al., 2008). Among SCFAs, butyrate is the preferred energy source for colonocytes (epithelial cells lining the colon), and therefore, important for gut wall health (Van Graeyveld et al., 2008). SCFAs can lower intestinal pH (conducive to the growth of many beneficial microorganisms), increase the bioavailability of calcium and magnesium, and inhibit the growth of potentially harmful bacteria (Van Graeyveld et al., 2008). As the gut bacterial environment *in vivo* is under environmental stress/strain and its inhabitants subject to competitive inhibition, it is vastly different from the controlled environment *in vitro* (Oso et al., 2013; Van Graeyveld et al., 2008). A lack of SCFA production

and/or no change in *Bifidobacteria* spp. and *Lactobacillus* spp. across *in vivo* studies may be explained by competing bacterial populations when compared to results of *in vitro* studies (Oso et al., 2013; Van Graeyveld et al., 2008).

Francois et al. (2012) investigated the effects of a wheat bran based AX on gut microbiota in a double-blind, randomised, placebo-controlled, cross-over trial. The study recruited 63 healthy adults to consume 0, 3, and 10g of wheat bran extract per day (equal to 0g, 2.4g, and 8g of AX, respectively) for 3 weeks. The study showed supplementation at 10 g/d significantly increased average *Bifidobacterium* levels compared to the placebo ($p < 0.001$). An increase in the levels of *Bifidobacterium* was also identified at 3 g/d but not statistically significant ($p = 0.065$). It involved the largest number of participants of any *in vivo* study to date that investigated microbiota changes associated with AX in healthy adult participants.

A smaller study of 20 healthy adults consuming 10 g/d of wheat AX for 21 days also found an increase in *Bifidobacterium adolescentis* in comparison with a placebo (Walton et al., 2012). This study investigated the effects of a wheat AX added to bread on the gut microbiota of 40 healthy adults over 21 days. The findings showed an increase in *Lactobacillus* spp. when the participants consumed wheat AX bread. Such change was statistically significant ($p = 0.025$) when compared to the control bread even when the control bread was established to have naturally occurring fructans which were largely available for microbial fermentation in the colon.

A more recent study on 96 infants (6–12-months-old) by Zambrana et al. (2019) indicated a rise in *Lactobacillus* spp. in faecal samples after AX consumption. This study comprises one of only two *in vivo* experiments on rice based AX, the other being Sheflin et al. (2017) in which 30 g/d of rice bran was consumed by 29 adults for 28 days. This short-term study showed a rise in total bacteria at day 28 and increases in *Bacteroides* spp. levels. Due to the structural differences between wheat-based AX and rice-based AX, a long-term, rice-based AX research study in healthy adults is necessary.

AX has been shown to increase other bacterial groups including *Bacteroides*, *Prevotella*, *Roseburia* and *Streptococcaceae* (Geraylou et al., 2013; Neyrinck et al., 2011; Reis et al., 2014; Saman et al., 2016). These bacterial groups have not been considered as prebiotic targets but are beneficial in the cross-feeding chain for the breakdown of nutrients (Umu, Rudi, & Diep, 2017). Table 1 shows a summary list of human gut microbiota species known to be affected by AX and AX oligosaccharides.

Table 1
AX and arabinoxylan oligosaccharide's (AXOS) effect on the growth of known human gut microbiota species.

Microorganism	Saccharide		Reference
	AX	AXOS	
Anaerostipes hadrus		+	Li et al. (2017)
Anaerotruncus colihominis		+	Li et al. (2017)
Bacteroides Genus		+	Walton et al. (2012)
Bacteroides cellulosilyticus		+	Li et al. (2017)
Bacteroides dorei		+	Li et al. (2017)
Bacteroides fragilis	+		Crittenden et al. (2002)
Bacteroides intestinalis		+	Li et al. (2017)
Bacteroides ovatus	+		Yafei et al. (2020)
Bacterioides thetaiotaomicron	+	+	Crittenden et al., 2002; Li et al., 2017
Bacteroides uniformis	+		Crittenden et al. (2002)
Bacterioides vulgatus	+	+	Crittenden et al., 2002; Li et al., 2017
Bifidobacterium Genus	+	+	Francois et al., 2012; Hald et al., 2016; Walton et al., 2012; Windey et al., 2015
Bifidobacterium adolescentis	+	+	Crittenden et al., 2002; Van Laere, Hartemink, Bosveld, Schols, & Voragen, 2000; Li et al., 2017; Windey et al., 2015
Bifidobacterium angulatum		+	Kjolbaek et al. (2020)
Bifidobacterium bifidum	–	+	Crittenden et al., 2002; Li et al., 2017
Bifidobacterium catenulatum		+	Kjolbaek et al., 2020; Li et al., 2017
Bifidobacterium longum	+	+	Crittenden et al., 2002; Yafei et al., 2020; Kjolbaek et al., 2020
Bifidobacterium merycicum		+	Kjolbaek et al. (2020)
Bifidobacterium pseudocatenulatum	+	+	Crittenden et al., 2002; Kjolbaek et al., 2020
Blautia Genus			
Blautia luti		+	Kjolbaek et al. (2020)
Blautia wexlerae		+	Kjolbaek et al. (2020)
Clostridium Genus			
Clostridium asparagiforme		+	Li et al. (2017)
Clostridium beijerinckii	+		Crittenden et al. (2002)
Dorea Genus			
Dorea formicigenerans		+	Li et al. (2017)
Dorea longicatena		+	Kjolbaek et al. (2020)
Eubacterium Genus			
Eubacterium eligens		+	Li et al. (2017)
Eubacterium hallii		+	Kjolbaek et al., 2020; Li et al., 2017
Eubacterium rectale		+	Kjolbaek et al., 2020; Walton et al., 2012
Faecalibacterium Genus			
Faecalibacterium prausnitzii		+	Kjolbaek et al. (2020)
Fusicatenibacter saccharivorans		+	Kjolbaek et al. (2020)
Lactobacillus Genus		+	Walton et al., 2012; Zambrana et al., 2019
Lactobacillus fermentum		+	Kontula, Suihko, Tenkanen, Mattila-Sandholm, and vonWright (2000)
Lactobacillus paracasei	–	+	Crittenden et al. (2002)
Odoribacter splanchnicus		+	Li et al. (2017)
Roseburia Genus		+	Walton et al. (2012)
Roseburia hominis		+	Li et al. (2017)
Roseburia inulinivorans		+	Li et al. (2017)
Ruminococcus Genus			
Ruminococcus bromii		+	Li et al. (2017)
Ruminococcus obeum		+	Kjolbaek et al. (2020)
Ruminococcus torques		+	Li et al. (2017)

5. Discussion

5.1. Methodological considerations of existing studies

Long-term studies are generally lacking on the effects of AXs on the gut microbiota, especially rice based AXs. The only long term study on the effects of a rice bran AX by Zambrana et al. (2019) was performed on 96 infants over six months. Inclusion criteria were weaning infants aged between 6 and 12 months. This study reported a significant decrease in less-beneficial bacteria including *Camphylobactor* and *Clostridium* and increases in *Lactobacillus* and *Bacteroides* at a phylum level. This age range is a crucial time for the development of gut microbiota. At the same time, instability of the gut microbiome at this age makes changes throughout the study period hard to identify as a direct link to AX intake.

A smaller longitudinal study by Sheflin et al. (2017) showed significant increases in gut microbiota from AX consumption at the final time point (28 days) and no changes at the mid-way point (14 days). This study was conducted on 29 obese and overweight participants. Due to the short AX consumption timeframe, the findings suggest a time-dependent relationship between AX consumption and increase in beneficial gut microbiota.

Previous studies have also indicated a delicate dose-dependent relationship. Salden et al. (2018) tracked gut microbiota changes over six weeks in overweight and obese participants. This study compared 7.5 g/d AX intake to 15 g/d AX intake during a randomised double-blind placebo-controlled trial. There were no significant changes with the low dose, however, intake of the higher dose resulted in a decrease of total microbial diversity. The dosage of 15 g/d was one of the highest AX intakes observed in human and animal *in vivo* studies. Other studies of 25 days or shorter showed no changes in total diversity or at a species level, indicating that supplementation needs to be over an extended

period to see beneficial effects (Van Hees et al., 2019; Wu et al., 2018).

Previous research has shown the benefits of adding AX in the human diet. However, due to the varying structures and sources of AX, comparing their effects on gut microbes can be challenging.

5.2. Current gaps and emerging research

Wheat based AX is largely researched with studies on the relationship between AX intake and gut microbiota composition (Chung et al., 2019; Francois et al., 2012; Kjolbaek et al., 2020). There is minimal research on branched AXs, specifically rice based AX and AX oligosaccharides and their effects on gut microbiota composition. The field of rice bran could benefit from future research examining long term intake of AX and enzymatically modified AX on gut microbiota. The authors of this review are currently conducting a human study with an enzymatically modified rice based AX compound to determine its effects on the gut microbiota of healthy adults. Microbiota composition from different AX doses will be measured over a 24-week period to further profile the delicate dose dependent relationship AX appears to have on gut microbiota.

6. Conclusion

AX is a noteworthy functional food and important class of non-digestible fibre. Acting as a prebiotic, AX enables the stimulation of keystone gut microbial species, specifically *Bifidobacterium* spp. and *Lactobacillus* spp. The consequent beneficial effects include preventing dysbiosis of gut microbiota, arresting pathogen proliferation and ameliorating gastrointestinal disorders.

AX has a complex structure which differs between cereal types and different parts of the cereal grain. These structural differences impact how AXs are degraded and fermented by gut microbiota. Pre-treatment of cereal grains can enhance AX capabilities to be used by the gut microbiota. This process, however, leads to more structural diversity of the AXs in food products and chemical species of such products, that are often not disclosed by the manufacturers. These factors render comparing and contrasting the effects of AX on gut microbiota challenging.

Human *in vivo* studies have predominantly focused on wheat AX. Wheat based AXs have been shown to promote higher microbial diversity and proliferation of keystone species. Considering rice is an important staple food, additional research is needed to determine whether AX derived from rice can have similar results as those demonstrated by AX derived from wheat.

As there has only been one long-term study on the effects of a rice AX, further long-term research with different populations, study designs, and dosages of AX are needed to determine the effects of rice based AX on gut microbiota. This review highlights the need for further research into rice based AX and its effect on human health.

Declaration of competing interest

Declarations of interest: none.

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