Advances in Research on the Prebiotic Functions of Arabinoxylan and Arabinoxylooligosaccharides: Postprint

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Abstract

Regulation of gut health in livestock has become a key focus in modern animal husbandry. Arabinoxylan (AX) and arabinoxylo-oligosaccharides (AXOS), as novel prebiotics, demonstrate superior proliferative effects on probiotics such as bifidobacteria compared to fructooligosaccharides and other prebiotics. Furthermore, compared with fructooligosaccharides and other prebiotics, AX and AXOS can reach the hindgut for fermentation, producing non-branched short-chain fatty acids, inhibiting protein fermentation, and reducing the production of toxic substances (phenol, ammonia, etc.), thereby effectively regulating the health of the hindgut (colon and cecum). AX and AXOS of different structures possess distinct prebiotic functions, and there exists a synergistic prebiotic effect between AX and AXOS. This review summarizes recent research advances on the prebiotic functions of AX and AXOS, providing theoretical basis and guidance for their application in animal husbandry.

Full Text

Research Progress on Prebiotic Effects of Arabinoxylan and Arabinoxylan Oligosaccharides

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Abstract

Regulation of gut health in livestock has become a critical focus in modern animal production. As novel prebiotics, arabinoxylan (AX) and arabinoxylan oligosaccharides (AXOS) demonstrate superior proliferation effects on probiotics such as *Bifidobacterium* compared to fructooligosaccharides and other prebiotic

compounds. Moreover, AX and AXOS can reach the distal gut for fermentation, producing non-branched short-chain fatty acids while inhibiting protein fermentation and reducing the generation of toxic substances (phenol, ammonia, etc.), thereby effectively modulating hindgut health in the colon and cecum. The prebiotic functions vary with the structure of AX and AXOS, and synergistic effects exist between these compounds. This review summarizes recent research progress on the prebiotic functions of AX and AXOS, providing theoretical guidance for their application in the livestock industry.

Keywords: arabinoxylan; arabinoxylan oligosaccharides; prebiotic effects; gut health

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With growing concerns regarding the safety of livestock products and increasing restrictions on antibiotic usage, developing alternative strategies to modulate gut health has become increasingly important. Arabinoxylan (AX) and arabinoxylan oligosaccharides (AXOS) represent novel prebiotics that specifically promote the proliferation of beneficial bacteria, particularly *Bifidobacterium*, with effects significantly superior to those of fructooligosaccharides [1]. Recent studies have also demonstrated that AXOS and AX more effectively promote the growth of *Lactobacillus* [2] and *Bacillus* [3] compared to fructooligosaccharides and glucose. Furthermore, AX and AXOS are more likely to reach the distal gut for fermentation than fructooligosaccharides and other oligosaccharides, enabling more effective regulation of hindgut health [4]. Compared to fructooligosaccharides, xylooligosaccharides (XOS) can reduce colon DNA damage caused by toxic substances generated from protein fermentation [5]. Consequently, research on the prebiotic functions of AX and AXOS has become a focal point in recent years.

AXOS are enzymatic hydrolysis products of AX, with composition varying according to the xylan source and the enzymatic properties of xylanases. These products may include AXOS, XOS, feruloylated arabinoxylan oligosaccharides (FXOS), and other oligosaccharides, as well as branched hydrolysis products such as xylose and ferulic acid, which exert distinct prebiotic and physiological effects. Current research on AX and AXOS has primarily concentrated on their applications, while the relationship between their structure and function remains unclear, and reports on metabolic mechanisms within bacteria are lacking. This review addresses the prebiotic functions of AX and AXOS by examining three key aspects: the enzymatic properties of xylanases, the structure-function relationships of AX and its enzymatic products, and microbial metabolism of these compounds, thereby providing theoretical foundations for their development and application in production systems.

1.1 Structure of AX

Xylan constitutes a major component of plant cell walls, linking lignin and cellulose, and represents the primary hemicellulose and the second most abundant

renewable resource in nature [6]. It is widely distributed in hardwood (15–30%), softwood (7–10%), and herbaceous plants (<30%). The xylan backbone consists of xylose residues connected via β-1,4-glycosidic bonds, while its branching structure varies by source. In cereal grains (wheat, corn, and oats), xylan exists primarily as AX, with arabinose substituents as the main side chains. In contrast, xylan from hardwood (birch, beech, etc.) features acetyl and glucuronic acid groups as primary substituents. Arabinose typically undergoes di- or mono-substitution at the C2 or C3 positions of the backbone, whereas acetyl groups mainly mono-substitute at the C3 position [7]. In addition to these two side-chain substituents, xylan branching structures include various other groups such as ferulic acid, glucuronic acid, and *p*-coumaric acid [8].

AX structure varies not only among different sources [9] but also among different tissues from the same plant species [10], manifesting as differences in average degree of polymerization (avDP), average degree of arabinose substitution (avDAS), and substituent types. The avDP and avDAS values are commonly used to characterize the structural features of AX and AXOS. Consequently, different xylanases with distinct enzymatic properties yield different hydrolysis products, all of which can influence gut microbial fermentation to varying degrees [11–13]. Based on solubility, AX can be classified as water-extractable (WE-AX) or water-unextractable (WU-AX). While both types share similar side-chain compositions, WU-AX exhibits higher avDP and arabinose substitution degrees than WE-AX [14]. Ferulic acid plays a crucial role in WU-AX structure formation [15], and WU-AX represents the predominant form of AX in most plants [15].

1.2 Prebiotic Functions of AX

In human nutrition research, AX is recognized as a prebiotic that promotes the proliferation of beneficial gut bacteria [11] and reduces blood triglyceride levels [17]. However, in livestock nutrition, AX is generally considered an anti-nutritional factor, particularly for monogastric animals. Under weakly alkaline conditions, AX increases viscosity, forming viscous chyme in the animal gut that reduces nutrient digestibility [18]. Undigested nutrients provide abundant substrates for pathogen proliferation, potentially triggering outbreaks of *Clostridium perfringens* and causing necrotic enteritis [19–20]. Therefore, xylanase supplementation in wheat-based diets has become a common practice. Xylanases improve nutrient utilization, animal growth performance, and gut microbiota composition by increasing beneficial bacteria [21–22] while reducing pathogen populations [23–24]. Nevertheless, the anti-nutritional effects of AX vary among monogastric species. For instance, Damen et al. [11] reported that AX could increase *Roseburia* populations in rat colons, an effect likely related to AX dosage and structure.

The majority of WU-AX from cereal feed passes through the entire intestinal tract without degradation, thereby increasing digesta transit rate in rats [25] and humans [26] similar to other insoluble fibers. Although WU-AX is difficult

to degrade, *in vitro* studies have confirmed its fermentability to produce volatile fatty acids and promote probiotic growth [27]. However, Hopkins et al. [28] found in an *in vivo* study that AX did not promote *Bifidobacterium* but instead increased *Bacteroides* populations. Conversely, Hughes et al. [29] observed in *in vitro* fermentation that high-molecular-weight AX significantly promoted *Bifidobacterium* growth, though this effect diminished with increasing molecular weight. Damen et al. [11] demonstrated that WE-AX, WU-AX, and AXOS all significantly reduced cecal pH and promoted fermentation in the colon and cecum. Discrepancies among these studies may stem from methodological differences, including *in vitro* versus *in vivo* approaches, single versus continuous fermentation, and pure culture versus mixed bacterial fermentation. Additionally, variations in AX source, dosage, and structure can lead to divergent results (Table 1). Therefore, research on AX prebiotic functions must emphasize structural characterization under consistent methodological frameworks.

The utilization of AX by gut microbes primarily depends on the presence of polysaccharide utilization loci (PULs) that encode enzymes for AX degradation. Bacterial capacity to degrade AX is closely related to its structure, as both avDP and avDAS values influence utilization efficiency [12]. To date, only the xylan-degrading PULs of *Bacteroides ovatus* have been characterized, containing two gene loci that express 21 distinct enzymes (Figure 1 [Figure 1: see original paper]) [30].

Complete AX degradation requires synergistic action of multiple enzymes [31], including endo-1,4-β-D-xylanase (EC 3.3.1.8), β-D-xylosidases (EC 3.2.1.37), and debranching enzymes such as α-L-arabinofuranosidase (EC 3.2.1.55), acetylxylan esterase (EC 3.1.1.72), and ferulic acid esterase (EC 3.1.1.73) (Figure 2 [Figure 2: see original paper]). Endo-xylanases randomly cleave the xylan backbone to produce short-chain xylooligosaccharides, while xylosidases act exolytically to further degrade xylooligosaccharides to xylose and can also weakly hydrolyze xylan from the non-reducing end. Debranching enzymes cleave various side-chain substituents. Differences in amino acid sequences and spatial structures determine distinct cleavage sites, leading to classification into different glycoside hydrolase (GH) families such as GH5, GH7, and GH8 [32]. Complete xylan degradation requires coordinated action of these enzymes [33]. Xylanases and debranching enzymes from different microbial sources exhibit varying enzymatic properties, including optimal pH, isoelectric point, Michaelis constant [34], and differences in backbone and side-chain cleavage sites [35]. Xylanase supplementation reduces WU-AX molecular weight, facilitating its conversion to WE-AX and further degradation to AXOS [36].

3.1 AXOS Structure and Function

In the absence of exogenous xylan-degrading enzymes, AX entering the gut can be degraded by bacterial xylanases (primarily from *Bacteroides* spp.) into oligosaccharides, which are transported into bacterial cells and further hydrolyzed to monosaccharides (xylose and arabinose) for utilization (Figure 3

[Figure 3: see original paper]) [13]. The avDP and avDAS values of AX and AXOS significantly influence fermentation patterns and prebiotic functions [12]. However, structure-function research on these compounds has yielded inconsistent findings. Generally, higher avDP values correlate with weaker prebiotic effects for AXOS and XOS [37]. Recent studies have challenged this notion, demonstrating that *Paenibacillus* JDR-2 can efficiently utilize high-avDP AX, even more effectively than glucose [3]. The impact of avDAS values remains controversial: Damen et al. [11] reported no effect on prebiotic function, whereas Sharma et al. [38] and Rumpagaporn et al. [39] demonstrated that higher avDAS values impede AX degradation in both *in vitro* and *in vivo* fermentation systems. This hindrance can be alleviated by supplementing debranching enzymes, supporting the latter view [6]. Rumpagaporn et al. [39] also showed that AX from rice and sorghum, which possess simpler branching structures, ferment more rapidly than those from corn and wheat. Beyond arabinose substitution, ferulic acid side chains also affect fermentation, with higher ferulic acid content rendering AX and AXOS more resistant to degradation [40]. Therefore, prebiotic function research must extend beyond avDP and avDAS to examine fine structural details.

3.2 AXOS Metabolism and Utilization

Microbial fermentation of AXOS and XOS produces unbranched short-chain fatty acids (USCFAs), which lower intestinal pH and inhibit pathogen growth. Butyrate serves as an energy source for colonocytes, stimulates colonic epithelial growth [41], and exhibits anti-tumor properties [42], while acetate and propionate participate in lipid and glucose metabolism upon absorption [43]. Studies by Duncan et al. [44] and Geboes et al. [45] demonstrated that colonic acetate can enhance butyrate production by *Roseburia* spp. and *Faecalibacterium prausnitzii*. Additionally, hindgut fermentation of oligosaccharides inhibits protein fermentation [46], reducing toxic metabolite formation and disease risk [47]. Isobutyrate and isovalerate are commonly used as markers for intestinal protein fermentation [48–49]. Due to their structural properties, AX and AXOS are less completely degraded in the foregut compared to fructooligosaccharides, enabling them to reach the hindgut more effectively. Consequently, AX and AXOS with high avDP and avDAS values can more effectively regulate hindgut health [4].

Many chronic colonic diseases, such as colorectal cancer, originate in the distal colon [36]. Fructooligosaccharides are typically degraded in the proximal gut and rarely reach the distal colon to exert regulatory effects [4]. Similarly, low-avDP AXOS and XOS are broken down in the proximal colon with minimal distal fermentation [5], whereas high-avDP AXOS, XOS, and AX can reach the hindgut, where they inhibit microbial protein degradation and reduce toxic metabolite production, thereby promoting distal gut health [51].

AX and AXOS also exhibit synergistic effects. Partial replacement of WU-AX with AXOS increases colonic butyrate content by enhancing *Roseburia* activity

in rats [43]. Substituting AXOS for a portion of WE-AX extends the prebiotic effects of WE-AX to the distal colon [12], significantly reducing branched-chain fatty acid production while increasing *Bifidobacterium* populations [11]. Furthermore, simultaneous supplementation with WU-AX, WE-AX, and AXOS increases *Bifidobacterium* and *Roseburia* numbers, elevates butyrate and total SCFA concentrations, and reduces branched-chain fatty acids in the cecum and colon without increasing total bacterial counts [11]. These combination effects can guide the formulation of AX/AXOS with other oligosaccharides, as demonstrated by the synergistic prebiotic benefits of inulin and XOS combinations [54].

As antibiotic use becomes increasingly restricted, gut health regulation will be a priority for future livestock production. Gut microorganisms play a crucial role in maintaining intestinal health, and AX and AXOS represent novel prebiotics that offer non-invasive, safe modulation of gut microbiota by increasing beneficial bacteria and reducing pathogens. However, the complex structure-function relationships of AX and AXOS remain uncertain. Future research must prioritize detailed structural analysis, particularly at the fine structural level. Currently, most studies have focused on humans and rodents, with limited reports on livestock species. Compared to model animals such as humans, rodents, and fish, poultry lack a well-developed colon structure, and interspecies physiological differences may influence the efficacy of AX and AXOS applications. Therefore, additional research is needed to evaluate AX and AXOS in livestock species. Moreover, the metabolic pathways and mechanisms underlying microbial utilization of AX and AXOS require further investigation. Employing novel analytical approaches such as microbial transcriptomics and metabolomics will provide deeper insights into these metabolic processes, offering stronger theoretical foundations for functional studies and practical applications.

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