Arabinoxylans in piglet nutrition: A review of impacts and mechanisms on gut health and microbiota regulation

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Abstract

Arabinoxylans (AXs), the primary hemicellulose found in cereals and grasses, play a crucial role in regulating immunity, metabolism, and various physiological processes underscoring their value as essential components in dietary nutrition. Considering the extensive research on AXs in piglet nutrition, this paper systematically reviews their impacts on gut health and microbiota in piglets, as well as the underlying mechanisms of action. AXs have been shown to mediate gut barrier fortification through tight junction protein upregulation and orchestrate mucosal immunity homeostasis, consequently ameliorating early-weaning-associated diarrheal pathogenesis in piglets. Additionally, AXs function as microbial ecological modulators through selective enrichment of beneficial commensal microbiota (e.g., Bifidobacterium spp. and Lactobacillus spp.), while simultaneously stimulating microbial biosynthesis of short-chain fatty acids and ferulic acid exhibiting potent antioxidant and anti-inflammatory activity, thereby maintaining the intestinal health of piglets. This review offers valuable insights into their potential as a dietary intervention to support gut health and immune function in early-weaned piglets. However, most studies focus on single-source AXs such as wheat or corn, with limited exploration of novel sources or comparative effects of source combinations. Future research should systematically investigate the molecular mechanisms of AXs action, provide data-driven guidance for selecting AXs sources in feed formulations, and establish optimal inclusion levels in practical feeding regimens. Such efforts will further solidify the precision nutrition potential of AXs in promoting sustainable and healthy growth in piglets.

Keywords: arabinoxylans, gut health, gut microbiota, intestinal barrier, piglet

Introduction

An early weaning strategy has been commonly adopted by pig farmers to improve the productivity of sows in the modern pig industry ⁽¹⁾. However, this practice imposes significant physiological stress on piglets, marked by abrupt dietary transitions and maternal separation. Such stressors frequently trigger intestinal dysfunction, manifesting as diarrhea (30-50% incidence), growth retardation, and elevated morbidity (15-20% mortality), resulting in substantial economic losses ⁽²⁻⁴⁾.

Post-weaning diarrhea is a multifactorial gastrointestinal disease that is mainly attributed to intestinal barrier dysfunction (5,6). The intestinal barrier generally consists of the mechanical, mucosal, immune, and microbial barriers, which effectively maintain intestinal homeostasis by cooperating with each other (7). Notably, the microbial barrier (intestinal microbiota) exerts protective effects through nutrient competition, pathogen exclusion, and antimicrobial metabolite production, while simultaneously modulating immune responses (8). Weaning-induced gut microbiota dysbiosis in piglets disrupts this protective mechanism, predisposing to intestinal infections and diarrheal pathogenesis, a phenomenon paralleled in human inflammatory bowel disorders (5, 6, 9). This mechanistic understanding has driven intensive investigation into nutritional interventions targeting microbial improvement in weaned piglets, with dietary fiber emerging as a research priority for diarrhea mitigation. Dietary fiber has been recognized as the main energy source for intestinal microbial fermentation (10), thus affecting the intestinal bacterial composition and microbial metabolic activity. Adding dietary fiber to the diet has been shown to benefit the intestinal morphology and intestinal barrier integrity, leading to reduced incidence of diarrhea in weaning piglets (11, 12). Short-chain fatty acids (SCFAs) are the main metabolites produced by microbial fermentation of dietary fiber, which is the main way for dietary fiber to offer benefit to the host intestinal health (13). Accumulating evidence supports the contention that dietary fiber alleviates intestinal disorders by producing SCFAs, which are involved in the activation of epithelial cell proliferation and differentiation, the maintenance of mucosal integrity, and the attenuation of inflammation (14).

Notably, different dietary fibers showed different effects on microbial composition and diversity, and thus the therapeutic effect on intestinal diseases depends on the specific type of dietary fibers (10). Arabinoxylans (AXs) are one of the most abundant hemicelluloses found in the cell walls of cereal plants. Due to their diverse biological activities, such as prebiotic and immunomodulatory properties, antioxidant functions, and potential therapeutic applications in intestinal diseases, AXs have become a focal point in scientific research (15). The colonic metabolism of AXs is mediated through microbiota-derived enzymatic activity, primarily involving xylanase and α-L-arabinofuranosidase, which catalyze AXs hydrolysis to generate xylooligosaccharides (XOS). These intermediates are subsequently metabolized by gut microbiota into bioactive compounds, including SCFAs and ferulic acid (16, 17). Accumulating evidence substantiates that dietary AXs enhance intestinal barrier integrity through modulation of gut microbial composition and upregulating the mRNA expression of tight junction-related proteins, such as claudin-1 and occludin (18). The experimental study further demonstrated that AXs can reduce inflammatory mediators (TNF-α, IL-1β, and IL-6) and oxidative stress levels (MDA), and regulate the intestinal microbiota in the mouse colitis model, thereby alleviating the occurrence of colonic inflammation and diarrhea (19, 20). Given these mechanistic insights, recent investigations have systematically characterized AXs' therapeutic potential against post-weaning diarrhea in piglets, revealing significant improvements in intestinal morphology, digestive and absorptive functions, barrier function, and the composition of the microbiota (21-23).

Therefore, this review summarizes the effects of AXs on piglets' gut health and microbiome and elucidates the mechanisms by which AXs regulate gut health in piglets, which aims to offer insights into the potential application of AXs as a dietary intervention measure for improving gut health in piglets.

Literature Search Strategy

The search was mainly conducted through Google Scholar and secondarily through searches in databases such as PubMed, Web of Science, and Scopus for publications from 2015 to 2025. The search terms included combinations of "arabinoxylan" or "AX" or

"arabinoxylan-oligosaccharide" or "AXOS" and "gut health" or "intestinal barrier function" or "Intestinal immune" or "gut microbiota" or "fermentation" or "short-chain fatty acids" or "SCFA" and "pig" or "piglets" or "young pigs", as well as related terms regarding the sources and structure of arabinoxylan (such as "sources", "Structure", "barley", "sorghum", "bagasse", "fermented mash", "Degree of branching", "viscosity"). Additional articles were retrieved from the reference lists of selected papers and relevant reviews. Only peer-reviewed articles published in English were included. The selection basis of the research was its correlation with AXs and the intestinal health of piglets.

Chemical Composition and Structural Diversity of AXs

The main cereals, including wheat, rye, oats, corn, barley, and sorghum, are the traditional raw ingredient sources for the extraction of AXs ⁽²⁴⁾. Among all the grain-derived AXs, the wheat AXs and corn AXs are the most predominant types used in the food and feed industry ^(25, 26). In recent years, novel raw ingredients such as hull-less barley bran, sugarcane straw, citron, and distillers' grains have become sustainable and promising sources for extracting AXs ^(15, 27-29) (Table 1).

The AXs present in most plants-derived ingredients consist of arabinose, xylose, glucose, and galactose, among which xylose accounts for the largest proportion of AXs, followed by arabinose, with galactose and glucose accounting for a relatively small proportion. AXs' main structure contains a chain of linear (1,4)- β -D-xylopyranoside units, which can be substituted with α -L-arabinofuranosyl units through α -(1,2) and/or α -(1,3) glycosidic linkages $^{(30)}$ (Figure 1). Consequently, four different substitution patterns of xylopyranosyl, including unsubstituted, monosubstituted at O-2, monosubstituted at O-3, or disubstituted at O-2 and O-3, exist in the natural AXs sources $^{(31)}$. It is reported that AXs extracted from different raw ingredients sources exhibit distinct substitution patterns of the xylopyranosyl backbone which decide the ratio of arabinose to xylose (Ara/Xyl) in individual AXs molecule $^{(32)}$. The pattern and extent of substitution patterns on the xylopyranosyl backbone of AXs varied by plant origin and plant tissue location with Ara/Xyl ranging from 0.11 to 2.41 (Table 1). As shown in table 1, the Ara/Xyl of shell-less barley (Ara/Xyl: 0.11) is the lowest, that of sorghum is the highest (Ara/Xyl: 2.41), and the

next is wheat bran (Ara/Xyl: 0.94). Similarly, bagasse has been reported to contain an AX content comparable to that of wheat bran, but with markedly lower arabinose substitution on the xylan backbone (the Ara/Xyl is around 0.2, compared to 0.6 for wheat bran) (33). A lower Ara/Xyl ratio indicates reduced AX branching, which, according to Kale et al., also influences AX viscosity (34). Higher viscosity can negatively affect nutrient digestibility in piglets (35), whereas a lower Ara/Xyl ratio facilitates microbial degradation (36, 37). To date, no studies have investigated the application of AXs from these alternative sources in piglets, with existing experimental work focusing predominantly on wheat bran-derived AXs (table 2). Given these structural and functional differences, exploring AXs from underutilized sources such as hull-less barley or bagasse may offer novel opportunities to enhance fermentability, modulate gut microbiota, and improve gut health in piglets.

Regulation of AXs on intestinal health of piglets

AXs are dietary bioactive polysaccharides with immunomodulatory, anti-inflammatory, prebiotics, and metabolic regulatory functions, particularly in glucose homeostasis, lipid metabolism, and microbial metabolism⁽³⁸⁻⁴²⁾. Their dual role in energy metabolism positions them as promising functional food components for livestock nutrition, with potential applications. As piglets undergo the stress of weaning, their gastrointestinal systems are highly susceptible to disturbances, leading to issues such as diarrhea, reduced appetite, and impaired nutrient absorption ⁽⁴³⁾. As shown in table 2, AXs improve intestinal morphology, enhance barrier integrity, and modulate immune responses, thereby supporting gut health and promoting overall performance ⁽²¹⁻²³⁾. This section summarized recent studies on how AXs influence intestinal morphology, barrier function, and immunity in weaned piglets, ultimately promoting better overall health and performance.

Effect of AXs on intestinal morphology and digestion of piglets

The integrity of the intestinal structure is essential for effective nutrient digestion and absorption in piglets, primarily reflected in the morphology of the intestinal epithelium, including villus height, crypt depth, and their ratio ⁽⁴⁴⁾. A reduced villus height-to-crypt depth ratio typically indicates impaired mucosal function, which can hinder nutrient digestion and absorption. In contrast, an increased ratio is associated with improved

mucosal function and enhanced nutrient absorption (45, 46). Recent studies have shown that adding 1% AXs to the diet of weaned piglets increases ileal villus height and improves the digestibility of NDF ⁽⁴⁷⁾. Additionally, wheat bran rich in AXs (64%-69%) significantly enhanced villus height and villus-to-crypt depth ratio in piglets compared to corn and pea fibers, boosting the activity of digestive enzymes like trypsin and lipase (48). However, a study confirmed that the presence of AXs reduced the digestibility of nutrients in pig diets and that the addition of xylanase and arabinofuranosidase improved the degradation of AX and the overall digestibility of nutrients (49). Similarly, the viscosity of wheat arabinoxylan exerted an anti-nutritional effect by reducing protein digestibility in pigs, increasing the quality of chyme and enhancing water-holding capacity (50). Reduced digestibility can occur from impeded digestion or absorption or from increased endogenous losses. Through its viscous nature, AXs may decrease nutrient digestibility by reducing diffusion of digestive enzymes and nutrients and reducing the rate of diffusion of nutrients from the digesta to the absorptive membrane (35). The evidence has indicated that while viscosity is certainly a factor in arabinoxylans' anti-nutritional effects (like reduced nutrient absorption), it's not the only mechanism^(51, 52). By adding enzymes (such as xylanase), the digestibility of nutrients in the digestive tract can be improved. When xylanase was added to hydrolyze AXs in the piglet diet, the villus height and nutrient digestibility in the jejunum were both improved compared to the control group (basic diet without xylanase), and daily gain increased by 12% (53). Previous studies have shown that the partial hydrolysis of AXs by xylanase could produce oligosaccharides (e.g., arabinoxylan-oligosaccharides and XOS) that are more readily fermented by beneficial bacteria, suggesting that the enzymatically degradation of AXs would enhance their prebiotic effect in the hindgut (54-56). Low A/X ratios facilitate bacterial enzymatic access, accelerating fermentation and SCFAs production (36, 37). Enzymes can enhance fermentation and increase the production of short-chain fatty acids by reducing molecular weight (55, 57). There are even studies reporting that the combination of Xyn, Afd, and FE had a superior efficacy relative to Xyn alone in improving the application of cereal bran in piglet diets ⁽⁵⁸⁾. Enzymatic modification of AXs has been shown to promote the growth and bioavailability of beneficial gut

microbiota ^(19, 59). Therefore, xylanase does not eliminate its prebiotic effect. But over-hydrolysis degrades arabinoxylan-oligosaccharides into non-prebiotic xylose; optimal enzyme dosage is critical.

Overall, AXs could improve intestinal morphology by increasing the villus-to-crypt depth ratio, which expands the intestinal absorption surface area. AXs have a potential positive effect on the intestinal structure and nutrient absorption in piglets, but the complex impact on digestibility should also be considered. The use of xylanase and arabinofuranosidase can improve the degradation of AXs and enhance nutrient digestibility, without affecting their prebiotic effect.

Effect of AXs on intestinal barrier of piglets

Intestine is not only an important organ responsible for digestion, absorption, and metabolism of dietary nutrients, but also acts as a defense barrier against pathogens from the external environment ⁽⁶⁰⁾. The gastrointestinal barrier is a complex system that encompasses the mucosal layer, the epithelial cells interconnected by tight junction proteins, and the non-epithelial mucosal cells (21). Tight junction proteins, such as zonula occludens-1 (ZO-1), claudin, and occludin, are the components that maintained the integrity of mechanical barrier, playing a critical role in regulating intestinal permeability (46, 61, 62). Disruption of this barrier can lead to increased intestinal permeability, which allows harmful substances to enter the bloodstream (46). Studies have shown that 2.55% AXs consumption could reduce intestinal permeability of weaned piglets, indicated by reduced serum diamine oxidase (DAO) level and lower horseradish peroxidase flux in both small intestine and colon, which might be attributed to enhanced mRNA expression of ZO-1 and chloride channel-related proteins in the small intestine (63, 64). Moreover, the physical barrier is further protected by the mucus layer, which is secreted by goblet cells ⁽⁶⁵⁾. Researches have reported that 2.55% AXs supplementation increases the number of goblet cells per crypt in the mid-colon of weaned piglets compared to the control group, highlighting its role in enhancing mucosal barrier protection (64, 66). As an oligosaccharide after AXs hydrolysis, 0.05% XOS have been found to increase goblet cell number and density in weaned piglets, which also increases mucin secretion and protein barrier factors (67, 68). Similarly, AXs hydrolysates alleviated Caco-2 cell barrier damage by upregulating the transepithelial electrical resistance and increasing the protein expression of claudin-1. (69). Accordingly, AXs increase the number of goblet cells and enhance the function of the mucus secretion, thereby avoiding the exposure of epithelial cells to various hazards. In summary, AXs enhance the expression of tight junction proteins such as ZO-1 and Claudin, as well as mucus secretion, which helps prevent the penetration of harmful substances

(such as pathogens, toxins, and xenobiotics) and promotes the overall intestinal health of piglets.

Effect of AXs on intestinal immunity of piglets

This section reviews the impact of AXs on the immune system, inflammatory markers, and gut health, highlighting their potential to reduce diarrhea and support recovery during the critical post-weaning period. AXs exhibit broad immunomodulatory activity across different species. In tumor-bearing mice, AXs significantly inhibited transplanted tumor growth by enhancing the phagocytic activity of natural killer cells and macrophages and increasing interleukin-2 (IL-2) production (70). Transcriptomic analysis by Zhang et al (42) revealed that AXs upregulated immune-related genes such as IL-1β and IL-6. And studies in immunosuppressed mice demonstrated improvements in thymus and spleen indices, alleviation of spleen damage, and overall enhancement of immune function (71). These findings consistently highlight that AXs promote the activation and proliferation of immune cells and regulate cytokine secretion, thereby strengthening host defenses and maintaining immune balance. Building on these results in mice, studies in piglets have shown that AXs exert similar but more context-specific effects during the critical post-weaning period, when stress commonly induces immune dysregulation, intestinal inflammation, and diarrhea.

Previous studies have indicated that the incorporation of 1% AXs into the diet significantly decreased ileal and colonic IL-6 levels while markedly increasing colonic secretory immunoglobulin A (sIgA) and IL-10 concentrations in weaned piglets $^{(47)}$. Similarly, dietary supplementation of 1% AXs has been shown to decrease concentrations of pro-inflammatory cytokines IL-6 and IL-12, while increasing contents of sIgA and anti-inflammatory cytokine IL-10 in the ileal mucosa of piglets $^{(72)}$. Furthermore, 1% AXs also independently enhance immune responses, particularly by upregulating pancreatic-associated protein (PAP) in weaned piglets, a marker for inflammation and antibacterial activity $^{(73)}$. Dietary supplementation with 2.55% AXs significantly downregulated the expression of pro-inflammatory factors (tumor necrosis factor- α (TNF- α), IL-1 β , IL-6) and genes associated with the TLRs/MyD88/NF- κ B signaling pathway (the myeloid differentiation factor 88 (MyD88) and the toll-like receptor (TLR)-2)

(63). The nuclear factor-kappa B (NF-κB) signaling pathway is generally considered a key target for coordinating the expression of pro-inflammatory cytokines and is involved in regulating both innate and adaptive immune responses (74). These findings suggest that AXs can effectively enhance immune function and reduce inflammation in piglets, potentially improving their overall health during the post-weaning period. The most recent studies have shown that dietary supplementation with 1% AXs effectively increased weight gain and reduced diarrhea rates in piglets (47, 72), as demonstrated by improved intestinal morphology and immune barrier function. Therefore, AXs can effectively reduce diarrhea rates of piglets during the post-weaning period by improving intestinal morphology, enhancing barrier function, and regulating immune responses.

Effect of AXs on gut microbiota and metabolites of piglets

As fermentable substrates in the colonic ecosystem, dietary fibers selectively promote the proliferation of beneficial microbiota while inducing structural remodeling of microbial communities and stimulating SCFA production (75, 76). As shown in figure 2, there are a large number of microorganisms between the ileum and cecum, but only specific bacterial strains possess the enzymatic machinery required for AXs degradation, including endo-1,4- β -xylanase, which cleaves β -1,4 glycosidic bonds in the xylan backbone to produce XOS, followed by α -L-arabinofuranosidases and β -xylosidase, which further break down the structure (77-81). These enzymes hydrolyze α -1,2 and α -1,3 bonds to release arabinose residues, while esterases such as feruloyl esterases release ferulic acid, enhancing the degradation process (Figure 2) (82). For example, Bifidobacterium adolescentis expresses arabinofuranosidases (AbfA and AbfB) that specifically remove arabinose from mono- and disubstituted xylose residues (83). Similarly, Bacteroides species utilize extracellular endoxylanases to degrade xylan, supported by a diverse glycoside hydrolase repertoire (84, 85). These coordinated enzymatic activities enable AXs to shape microbial communities and generate metabolites like SCFAs and ferulic acid, collectively supporting gut health. Extensive preclinical studies utilizing rodent models have consistently demonstrated that AXs supplementation significantly enhances the proliferation of beneficial microbial taxa, including Bifidobacterium spp. and Lactobacillus spp.,

concomitant with elevated SCFAs concentrations in the gastrointestinal tract ^(19, 86, 87). The underlying mechanisms of AXs-mediated SCFAs production have been elucidated through studies of microbial cross-feeding dynamics, which involve complex metabolic interactions and nutrient exchange between diverse microbial species or strains ⁽⁸⁸⁾.

As shown in table 3, emerging evidence suggests that dietary supplementation with AXs can modulate gut microbial ecology and enhance the production of microbial metabolites such as short-chain fatty acids in piglets. During the weaning stage of piglets, the stage induces pathophysiological alterations in intestinal structure and barrier function, coupled with significant dysbiosis of the gut microbiota, ultimately precipitating post-weaning diarrhea (43, 89). Gorham et al. reported that adding 5% AXs to piglet diets resulted in an increase in the abundances of certain genera such as *Prevotella*, *Mitsuokella*, and Lactobacillus, while decreasing the abundances of genera such as Clostridium, Mogibacterium, and Streptococcus (90). 1% and 2.55% AXs consumption has been shown to enrich the colonization of probiotics (Lactobacillus and Bifidobacterium) in the cecum of piglets (47, 63), which could inhibit the growth of pathogenic bacteria and improve gut health in weaning piglets ^(91, 92). Early studies have demonstrated that 8% AXs were highly fermentable in the pig cecum, as indicated by increased concentrations of SCFAs (particularly propionate) and decreased abundances of protein fermentation end products (93). The most recent *in vitro* study showed that the fermentation of 1% AXs by pig manure microbiota exhibited higher production of butyric acid and ferulic acid (72). These findings are corroborated by multiple studies indicating that AXs supplementation promotes beneficial bacterial growth while modulating SCFA profiles and reducing intestinal pH in piglets ^(58, 72, 94). As products of bacterial fermentation, SCFAs could decrease intestinal pH (conducive to the growth of many beneficial microorganisms), increase the bioavailability of calcium and magnesium, inhibit the growth of potentially harmful bacteria ⁽⁹⁵⁾, and play a crucial role in maintaining intestinal barrier integrity. Moreover, the biological activity, fermentation behavior, and gut microbiota modulation of AXs have been influenced by their structural characteristics, with lower molecular weight AXs reported to exert greater prebiotic effects (95). Low-branched AXs have fewer arabinose substitutions on the xylan

backbone, making them more accessible to microbial enzymes like *Bifidobacterium*'s arabinofuranosidases and xylanases ⁽⁹⁶⁾. Highly branched AXs resist degradation due to steric hindrance from dense arabinose side chains ⁽⁹⁶⁾. Most Bifidobacterium species preferentially grow on AXs-derived oligosaccharides ⁽⁹⁷⁾, and cross-feeding interactions have been proposed whereby Bacteroides and Bacilli depolymerize long-chain AXs into smaller oligomers subsequently fermented by *Bifidobacterium* ⁽⁹⁸⁾. Consequently, low-branched AXs function as more effective prebiotics for *Bifidobacterium* owing to their structural simplicity and compatibility with bacterial enzymatic systems, whereas highly branched forms require cooperative microbial degradation and display slower fermentation kinetics.

In summary, AXs act as fermentable substrates that selectively promote beneficial microbiota and SCFA production, with fermentability largely determined by molecular weight and branching degree. Low-branched AXs are readily degraded by Bifidobacterium, whereas highly branched forms require cooperative microbial breakdown. Evidence from both in vitro and in vivo studies, including rodent and piglet models, consistently demonstrates that AXs supplementation modulates gut microbial composition, enhances SCFA yield (notably butyrate, propionate, and ferulic acid), reduces intestinal pH, and supports intestinal barrier integrity, thereby contributing to overall gut health. These collective effects underscore the potential of AXs as a dietary intervention strategy for improving gut health in young animals.

The mechanisms underlying the regulation of intestinal health of piglets by AXs

The interaction among the intestinal microbiota, intestinal epithelial cells, and the host immune system maintained the balance between tolerance and immunity to pathogenic or nonpathogenic microbes ⁽⁹⁹⁾. AXs have been shown to modulate the TLRs/MyD88/NF-κB signaling pathway, resulting in reduced expression of pro-inflammatory genes and chloride channel-related proteins, thus alleviating intestinal inflammation ⁽⁶³⁾. *In vitro* studies using Caco-2 cell models have revealed that AXs treated with endo-1,4-β-xylanase could attenuate intestinal barrier damage by inhibiting the TLRs/MyD88/NF-κB pathway and activating the TLRs/PKC pathway. Therefore, MyD88 appears to be a key point in the

signaling pathways regulated by AXs ⁽⁶⁹⁾. Similarly, Huang et al. reported that AXs, fermented by gut microbiota, produce ferulic acid and butyric acid, which improve host immunity by promoting relative abundance of *Bifidobacterium pseudocatenulatum* and suppressing activation of TLR4/NF-κB signaling ⁽⁷²⁾. AXs also significantly increased the abundance of *Lactobacillus* and *Bifidobacterium* in the colon of piglets ^(47,63). Researches have shown that *Bifidobacterium* suppressed NF-κB activation and pro-inflammatory cytokines and thus inhibited Cl excessive secretion ^(100,101). The genus *Lactobacillus* has been reported to inhibit proinflammatory cytokine expression and TLR-4 linked NF-κB activation in experimental colitis ⁽¹⁰²⁾. *Lactobacillus* and *Bifidobacterium* produce acetate and lactate through fermentation, and these acetates can then be utilized by butyrate-producing bacteria in the gut to generate butyrate ⁽¹⁰³⁾.

As the main metabolites produced by AXs fermentation, SCFAs interact with specific receptors on the surface of intestinal cells, activating diverse signaling pathways that modulate host intestinal homeostasis, cell proliferation, and metabolic functions (104, 105). Propionate and butyrate have been found to be potent activators of the activator protein-1 (AP-1) pathway, with butyrate being the more potent of the two, regulating the release of inflammatory cytokines, thereby enhancing the host's intestinal immune function (106-108). The AP-1 pathway is one of the most important for cell proliferation as well as for intestinal epithelial differentiation (109). Additionally, during T-cell activation, the AP-1 plays a crucial role in mediating chromatin remodeling (110). However, it remains unproven whether AXs exert anti-inflammatory effects via AP-1 activation. In summary, AXs in particular altered the microbial composition (Bifidobacterium and Lactobacillus) of the distal small intestine and colon, increasing the concentration of ferulic acid and SCFAs, thereby reducing the production of proinflammatory cytokines by inhibiting the TLRs/MyD88/NF-κB signaling pathway activation (Figure 3). While AXs-mediated anti-inflammatory effects in piglets are primarily attributed to TLRs/MyD88/NF-кВ suppression and microbial modulation, the potential involvement of AP-1 signaling remains speculative. Moreover, further validation is needed for the specific metabolic pathways of AXs from various sources within the piglet intestine, given that diet formulations must

account for the selection of AXs raw material sources.

Conclusion and Future Directions

AXs consumption enhances SCFAs and ferulic acid production by promoting the colonization of beneficial bacteria such as Bifidobacterium and Lactobacillus in the piglet, thereby fostering a healthier intestinal microenvironment and reducing dysbiosis-associated disease risks. AXs also strengthen intestinal barrier function, modulate immune responses, and mitigate inflammation, collectively supporting their role as a microbiota-targeted nutritional intervention to alleviate post-weaning syndrome in commercial piglet production. However, most studies focus on single-source AXs such as wheat or corn, with limited exploration of novel sources (novel raw ingredients such as hull-less barley bran, sugarcane straw, citron, and distiller's grains) or comparative effects of source combinations. Future research should systematically investigate the molecular mechanisms of AXs action, provide data-driven guidance for selecting AXs sources in feed formulations, and establish optimal inclusion levels in practical feeding regimens. Much less is known about the effects of AXs molecular weight on regulating mucus layer thickness or tight junction protein expression compared to other bioactive properties. The relationship between the structure of AXs and intestinal health still requires further investigation. Such efforts will further solidify the precision nutrition potential of AXs in promoting sustainable and healthy growth in piglets.

While the present review focused on piglets, the underlying mechanisms by which AXs modulate gut microbiota composition, stimulate SCFA production, and reinforce intestinal barrier function are of direct relevance to human nutrition. Owing to the close physiological and microbial parallels between pigs and humans, evidence derived from porcine models offers meaningful translational insights. Furthermore, AXs from different sources have considerable potential as functional food ingredients to support the health benefits mediated by microorganisms in humans.

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Table 1: Chemical Composition of Arabinoxylans from Various Sources

AXs Source	Extraction Method	Monosaccharide Composition (mol%)	Ara/Xyl [†]	Reference
Sorghum flour	Po (OH) and 100/ NoOH	Ara: Xyl: Glc	2.41	(22)
	Ba (OH) ₂ and 10% NaOH	=63.4: 26.3: 10.3	2.41	(32)
Wheat bran	0.44 mol/L NoOH	Ara: Xyl: Gal: Glcd: Man [‡]	0.04	(111)
	0.44 mol/L NaOH	=27.8: 29.7: 2.0: 2.9: 0.1	0.94	. ,
Wheat bran	An alkaline extraction and		0.57	
	enzyme-assisted extraction			
Dyra bran	1%(w/v) NaBH ₄ in	Ara: Xyl: Glc: =	0.6	(112)
Rye bran	saturated Ba(OH) ₂	36.53:61.31:2.16	0.0	
Corn Bran	Alkali extraction	Ara: Xyl: Gal: Glc: Rha: GalA: GlcA§	0.56	(113)
	Alkan extraction	=27.46:48.52:12.08:4.28:0.43:1.02:6.21	0.30	
Oat grain	0.26 mol/L NaBH ₄	Ara: Xyl: Gal: Glc: UA [¶]	0.11	(114)
	of 6 mol/L NaOH	= 9: 78: 1: 10: 2	0.11	
	0.26 mol/L NaBH4	Ara: Xyl: Gal: Glc: UA	0.42	(114)
	of 6 mol/L Ba(OH) ₂	= 27: 43: 3:2: 4	0.43	

Hull-less barley bran	An alkaline (0.375M NaOH) extraction	Ara: Xyl: Gal: Glc: Man =51.55: 30.13: 10.33: 5.09: 2.9	0.58	(27)
Hull-less barley bran				
Citron	DEAE-Sepharose Fast Flow and Sephadex G-100 column chromatography	Ara: Xyl: Man: Glc	0.93	(28)
Sugarcane Straw	A two-step alkaline extraction	Ara: Xyl: Man: Glc: Gal = 1.15: 10: 0: 0.97: 0	0.11	(29)
Sugarcane bagasse	An alkaline extraction and enzyme-assisted extraction		0.2	
Chinese liquor distillers grain	Alkali extraction	Ara: Xyl: Glc: Gal: Rha = 36.5: 55.5: 3.7: 3: 1.2	0.66	(15)

[†] Ara/Xyl, the molar ratio of arabinose to xylose

[‡] Ara is arabinose; Xyl is xylose; Gal is galactose; Glc is glucose; Man is mannose.

[§] Rha is rhamnose; GalA is galacturonic acid; GlcA is glucuronide.

[¶] UA is glyoxylate.

Table 2: Regulation of AXs^{\dagger} on intestinal health of piglets

AXs source		Supplement level	Age of piglets	Significant results	References	
XX/1 1	Xylanase was added to	Weaning piglets	The inflammatory and antibacterial PAP [‡] ↑	(73)		
Wheat bran			hydrolyze AXs in wheat bran	Enterotoxigenic <i>Escherichia coli</i> induced responses ↓	()	
	(vv.la a a4		26 – 28 d	Intestinal secretory immunoglobulin A concentrations, goblet	(64)	
	(wheat	4.96%		cell number ↑		
endosperm)				Intestinal transcellular permeability ↓		
NAVous	(xx/boot	eat 4.96%	26 – 28 d	The mRNA level of ZO-1 and TLR-2 § \uparrow	(63)	
NAXsus (wheat endosperm)	(wneat			TNF- α and IL-10 in the serum $^{\P}\downarrow$		
				The mRNA levels of MyD88 and IL-1 β^{\perp} \downarrow		
Wheat endosperr	m	2%	Suckling piglets	Large intestinal fill and relative weight of large intestinal \\$\\$	(115)	
	Xylanase was added to	Weaning piglets (7.48 ± 0.24 kg BW)	Average daily gain, nutrient digestibility and villus height in the	(53)		
/			Xylanase was added to hydrolyze AXs in diet			jejunum ↑
	Diarrhea ↓					
Corn stalks	10/	$28 \pm 3 d$	Diarrhea incidence ↓	(47)		
	1%		Intestinal villus height, antioxidase activity, and $sIgA^{\#}$ contents \uparrow			
Wheat bran		1%	Weaning piglets	Diarrhea incidence ↓	(72)	

 $(6.87 \pm 0.14 \text{ kg BW})$

The sIgA concentration ↑

Protein expression of TLR4 and NF- κB^{∇} \uparrow

The mRNA level of pro-inflammatory cytokines in the ileum \$\rightarrow\$

[†]AXs, arabinoxylans

[‡]PAP, protein pancreatitis associated protein;

[§]ZO-1, zonula occludens-1; TLR-2, toll-like receptor 2;

[¶]TNF-α, tumor necrosis factor-α; IL-10, interleukin 10;

¹MyD88, myeloid differentiation factor 88; IL-1β, interleukin 1β;

^{*}sIgA, secretory immunoglobulin A;

 $^{{}^{\}nabla}\!TLR4,$ toll-like receptor 4; NF- $\!\kappa B,$ nuclear factor kappa B.

Table 3 Effects of AXs[†] on large intestinal microbiota and metabolites of piglets

Source	Stage	In vivo/in vitro	Supplement level	Effects on gut microbiota	Effects on metabolites	Reference
\	9-week-old male pigs	In vivo	8%	Prevotella intermedia, Ruminococcus obeum, and Faecalibacterium prausnitzii ↑	Acetate, propionate and total SCFA† in the caecum ↑	(94)
Wheat	piglets (BW: 19±1.9kg)	In vivo	8%	Microbial biomass, Faecalibacterium prausnitzii ↑	Propionate ↑	(93)
Wheat	39-week-old male pigs	In vivo	5%	$Prevotella, Mitsuokella, and Lactobacillus \uparrow$ $Clostridium, Mogibacterium, and$ $Streptococcus \downarrow$	Total SCFAs ↑ NH3 concentrations ↓	(90)
Wheat	Weaned piglets at 26-28 days of age	In vivo	2.55%	$Lactobacillus$ and $Bifidobacterium \uparrow$		(63)
wheat endosperm	Suckling piglets	In vivo	2%		Propionic acid ↑	(115)
Corn	Pig feces	In vitro	/	Prevotella_9↑	Acetate and lactate ↑	(77)
Wheat bran	35-d-old weaned piglets	In vivo	/		Acetic acid and butyric acid ↑	(58)

Corn	28±3 day-old weaned				Lactic acid, acetic acid, and		
	•	In vivo	1%	Lactobacillus and Bifidobacterium \uparrow	total organic acids in the ileum	(47)	
stalks	stalks piglets			\uparrow			
Wheat	The feces of	T • • •	/		Ferulic acid ↑	(72)	
bran	45±3-day-old piglets	In vitro			Total SCFA and butyric acid ↑		
				Microbial α diversity ↑	Acetic acid, butyric acid and		
Wheat	weaned piglets (BW:	: In vivo	1%	Streptococcus, Bacilli and Bifidobacterium	•	(72)	
bran	6.87±0.14 kg)			(Bifidobacterium pseudocatenulatum) ↑			
- C	510 / _511 · 11 g/			Lactobacillus amylovorus ↓			

[†]AXs, arabinoxylans;

[‡]SCFA, Short-chain fatty acid.

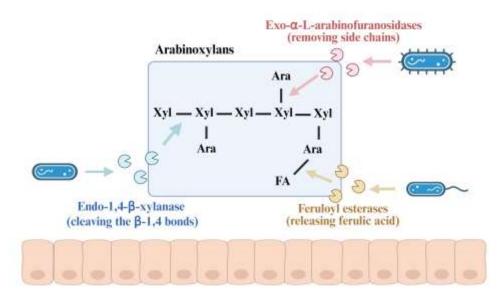


Figure 1 The main structure of arabinoxylans.

Figure 2 Degradation of arabinoxylans by bacteria. Ara, arabinose; Xyl, xylose; FA, ferulic acid.

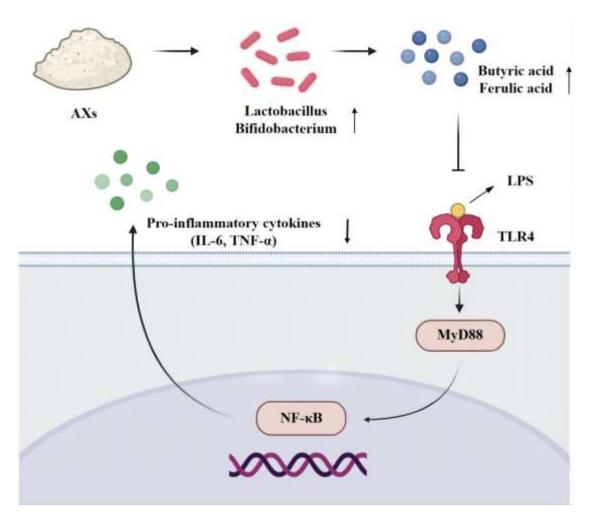


Figure 3 The mechanisms underlying the regulation of intestinal health of piglets by AXs. AXs, arabinoxylans; TLR4, toll-like receptor 4; MyD88, myeloid differentiation factor 88; IL-6, interleukin-6; TNF- α , tumor necrosis factor- α ; NF- κ B, nuclear factor kappa B