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Review

Arabinoxylans, gut microbiota and immunity

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ABSTRACT

Arabinoxylan (AX) is a non-starch polysaccharide found in many cereal grains and is considered as a dietary fiber. Despite their general structure, there is structural heterogeneity among AX originating from different botanical sources. Furthermore, the extraction procedure and hydrolysis by xylolytic enzymes can further render differences to theses AX. The aim of this review was to address the effects of AX on the gut bacteria and their immunomodulatory properties. Given the complex structure of AX, we also aimed to discuss how the structural heterogeneity of AX affects its role in bacterial growth and immunomodulation. The existing literature indicates the role of fine structural details of AX on its potential as polysaccharides that can impact the gut associated microbial growth and immune system.

Contents

1. Introduction

In the recent years there has been an increased interest in the area of dietary fibers in food. This interest has been triggered by many health related properties associated with dietary fibers such as decreasing the risk for type 2 diabetes mellitus (T2D), cardiovascular disease, and colon cancer (Kaczmarczyk, Miller, & Freund, 2012; Mudgil & Barak, 2013; Sorensen et al., 2014). An important dietary fiber is arabinoxylan (AX) which is the main non-starch polysaccharide in cereals (Stone, 2009). In most cereals the cell wall of endosperm cells and aleurone layer consists of about 60–70% arabinoxylans (Izydorczyk & Biliaderis, 1995). In wheat bran, arabinoxylan accounts for about 11–26% of wheat bran (Apprich et al., 2014). In this review we aimed to address the effects of AX on the gut bacteria and their immunomodulatory properties. Given the complex structure of AX, we also aim to discuss how the structural heterogeneity of AX affects its role in bacterial growth and immunomodulation.

2. Arabinoxylan

In wheat grain, the major polymer of the cell wall is arabinoxylan (AX) (Saulnier, Sado, Branlard, Charmet, & Guillon, 2007). Even though they occur as a minor constituent of the grain, due to the unique physico-chemical properties of AXs they play an important role in cereal food industry, including bread making (Courtin & Delcour, 2002), gluten-starch separation (Frederix, Van hoeymissen, Courtin, & Delcour, 2004), refrigerated dough syruping (Courtin, Gys, Gebruers, & Delcour, 2005; Simsek & Ohm, 2009) and in animal feeds (Bedford & Schulze, 1998). However, despite

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their ability to exert physical changes to a system, they also possess the ability to exert biological changes to a system: AXs have been associated with beneficial health effect in patients with impaired glucose tolerance (Garcia et al., 2007). They observed that AX consumption improved postprandial metabolic responses in subjects with impaired glucose tolerance. AX extracted from wheat bran has been shown to have potent effects on innate and acquired immune response in mice (Cao et al., 2011). Many researches indicated the immunomodulatory properties of AX using a modified AX from rice bran (Gollapudi & Ghoneum, 2008; Pérez-Martínez et al., 2015; Zheng, Sugita, Hirai, & Egashira, 2012).

Although AX from different sources differ in their substitution along the xylan backbone, a general structure can be assigned for AX (Izydorczyk & Biliaderis, 1995). AX consists of a backbone of β-(1,4)-linked xylose residues, which are substituted with arabinose residues on the C(O)-2 and/or C(O)-3 position (Dornez, Gebruers, Delcour, & Courtin, 2009). Phenolic acids such as ferulic acid, can be ester linked on the C(O)-5 position of arabinose. Under oxidative conditions, these ferulic acid residues undergo oxidative cross-linking forming inter/intra chain diferulic acid bridges (Geissman & Neukom, 1973). The structure of AX and enzymes involved in its degradation are shown in Fig. 1 (adapted from Grootaert et al., 2007).

Two different classes of AX exist in wheat. The first class includes water-extractable AXs (WE-AXs), which account for about 25–30% of AXs in wheat flour and the second class consists of water-unextractable AXs (WU-AXs), which account for the remainder of AXs in wheat flour (Meuser & Suckow, 1986). WE-AXs are loosely bound to the cell wall surface (Mares & Stone, 1973). In contrast, WU-AXs are retained in the cell wall by covalent and non-covalent interactions with AXs and proteins, lignin and cellulose (Iiyama, Lam, & Stone, 1994). AXs can be hydrolyzed by enzymatic and/or chemical means to produce AX hydrolyzates with varying length of the backbone (degree of polymerization, DP) and degree of substitution (DS). Thus, the structural details of an AX are dependent on its source, method of extraction, enzymes used for its hydrolysis, etc.

2.1. *Endo-β-(1,4)-D-xylanases (xylanases)*

Xylanases are the major enzymes involved in AX degradation. They cleave AXs by internally hydrolyzing the 1,4-β-D-xylosidic linkage between xylose residues in the xylan backbone in a random manner (Collins, Gerday, & Feller, 2005; Dornez et al., 2009). Over 290 xylanases have been identified (Fierens, 2007) and have been grouped into six different glycoside hydrolase (GH) families (5, 7, 8, 10, 11 and 43) (Collins et al., 2005; Dornez et al., 2009). The degradation pattern of each of these enzymes can be different, giving rise to different enzymatic products. For example, most of the glycoside hydrolases that are classified in the GH 10 family are endo-β-1,4-xylanases which degrade AX with high degree of substitution (DS) into smaller fragments (Pollet, Delcour, & Courtin, 2010). GH 11 xylanases preferably cleave unsubstituted regions of the backbone and require three unsubstituted consecutive xylose residues for hydrolysis. Hence, GH 11 xylanases have a low activity on heteroxylans with a high degree of substitution (Pollet et al., 2010).

2.2. *Arabinofuranosidases*

α-L-Arabinofuranosidase (α-L-arabinofuranosidase arabinofuranohydrolase, EC 3.2.1.55, arabinofuranosidase) is an exo-enzymes that hydrolyze terminal nonreducing α-arabinofuranoses from arabinoxylans (Saha, 2000). Arabinofuranosidases have been classified into seven glycoside hydrolase families (GH 2, 3, 10, 43, 51, 54 and 62) (Lombard, Golaconda, Drula, Coutinho, & Henrissat, 2014). Arabinofuranosidase from different families can have different substrate specificities. For example, arabinoxylan arabinofuranohydrolase-D3 (AXHd3) from *Bifidobacterium adolescentis* (GH43) releases only C3-linked arabinose residues from double-substituted xylose residues (Van den Broek et al., 2005) while α-L-arabinofuranosidases from *Clostridium thermocellum* (GH51) catalyze the hydrolysis of α-1,3-arabinosyl substitutions of AX (Taylor et al., 2006).

The structure of native AX itself is complex. Yet the degradation of this complex structure by a repertoire of xylanase and arabinofuranosidases with different substrate specificities, gives rise to an even complex cocktail of products. This is one of the reasons that make the identification of structure-biological response relationships difficult for AX. AXs are complex heteroxylans with different DP, DS and type of substitution molecule (Joseleau, Cartier, Chambat, Faik, & Ruel, 1992; Pollet et al., 2010). The hydrolysis products of AX degradation (AX hydrolyzates) depend on the substrate specificity of the hydrolysis enzyme, giving rise to AX hydrolyzates with varying DP and DS. Thus, the intestinal microflora and the epithelial cells are exposed to an array of AX hydrolyzates with different fine structural details. Given the diversity of the native AX and the AX hydrolyzates, it is important to elucidate if there is a relationship between these structural details and their biological implications.

3. Human gut microbiota and AX

The intestine is an important organ that consists of a huge surface area and permits vital interactions with micro-organisms living within the intestine, referred to as gut microbiota (Cani, Everard, & Duparc, 2013; Walter & Ley, 2011). The gut microbiota exerts significant impacts on the host physiology, such as the control of energy homeostasis, the immune system, digestion and vitamin synthesis (Cani et al., 2013) and inhibition of pathogen colonization (Wardwell, Huttenhower, & Garrett, 2011).

The human diet is rich in plant and animal derived glycans such as AX. A large array of these glycans is resistant to digestion by human enzymes and relies on microbial enzymes for their digestion. The fermentation of these glycans by microbes yield energy for the microbial growth, and the end products such as short chain fatty acids (SCFA), mainly acetate, propionate and butyrate have profound effects on the health of the host (Tremaroli & Backhed, 2012). Butyrate acts mainly as the energy substrate for the colonic epithelium because it is the preferred energy source of colonocytes (Hamer et al., 2008; Koropatkin, Cameron, & Martens, 2012). Acetate and propionate are absorbed into the blood stream and travel to the liver where they get incorporated into lipid and glucose metabolism, respectively (Rombeau & Kripke, 1990). Thus, acetate and propionate act as energy source to peripheral tissue cells. In addition to that, SCFA have an important effect on the host immune system as well. Low levels of butyrate modify the cytokine production profile of T_H cells (Kau, Ahern, Griffin, Goodman, & Gordon, 2011), promote intestinal epithelial barrier integrity and have also been associated with colonic tumor suppression (Hamer et al., 2008). In addition to being absorbed by the host, acetate is linked to maintaining the intestinal barrier function (Kau et al., 2011), and preventing colonization of some enteric pathogens (Fukuda et al., 2011).

The functional association among the intestinal microbiota, intestinal epithelial cells and the host immune system helps maintain the balance between tolerance and immunity to pathogenic or nonpathogenic microbes, or food ingredient. The fermentation of arabinoxylanoligosaccharides (AXOS) in vitro resulted in predominant production of acetate followed by propionate and butyrate