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Review

Grain-associated xylanases: occurrence, variability, and implications for cereal processing

Emmie Dornez, Kurt Gebruers, Jan A. Delcour and Christophe M. Courtin*

Laboratory of Food Chemistry and Biochemistry, Leuven Food Science and Nutrition Research Centre (LFoRCe), Katholieke Universiteit Leuven, Kasteelpark Arenberg 20 – bus 2463, B-3001 Leuven, Belgium (Tel.: +32 16 32 19 17; fax: +32 16 32 19 97; e-mail: christophe.courtin@biw.kuleuven.be)

Xylanases (EC 3.2.1.8) hydrolyse the backbone of cereal cell wall arabinoxylans and often have a significant impact on cereal-based processes and end-products. The use of microbial xylanases as processing aids in this respect is well established and has been extensively studied. Much less research has focused on inherently present cereal-associated xylanases and their possible impact. Cereals produce xylanases for remodeling and expansion of cereal cell walls during normal cell growth and for more drastic cell wall degradation during seed germination. Besides these endogenous xylanases, cereals also contain microbial xylanases from micro-organisms populating the outer grain kernels layers. Unfortunately, these microbial xylanases are often inhibited by wheat proteinaceous xylanase inhibitors and they hence escape standard xylanase activity measurements. It is more correct to refer to these activity levels as 'apparent' xylanase activity levels. As a result, the occurrence of cereal-associated xylanases might have been largely underestimated in the past and hence unjustly been disregarded. The levels and the types of cereal-associated xylanases differ strongly between grain species, varieties, and tissues, and are largely affected by grain growing conditions. These variations in the levels of grain-associated xylanase activity affect several cereal-based food and feed applications. This paper provides an overview of the occurrence and variability of cereal-associated xylanases and of their potential impact on bread making, shelf life of refrigerated doughs, brewing, animal feed efficiency, pasta production, and wheat gluten–starch separation.

Xylanases and xylanase inhibitors

From a functional point of view, endo-β-(1,4)-D-xylanases (EC 3.2.1.8, xylanases), are the most important arabinoxylan (AX) degrading enzymes. They hydrolyse internal β-(1,4)-linkages between xylose residues in the xylan backbone (Fig. 1) and, while doing so, drastically affect molecular mass (MM) and solubility of AX, and hence also their functionality. Although AX are only relatively minor constituents of grain, the unique physico-chemical properties of both water extractable (WE-AX) and water unextractable (WU-AX) AX affect grain functionality in biotechnological processes such as the production of bread (Courtin & Delcour, 2002), pasta (Ingelbrecht, Moers, Abecassis, Rouau, & Delcour, 2001; Ingelbrecht, Verwimp, Grobet, & Delcour, 2001), and beer (Debyser, Derdelinckx, & Delcour, 1997b), and the gluten–starch separation (Frederix, Van Hoeymissen, Courtin, & Delcour, 2004; Wang *et al.*, 2003; Wang, Hamer, van Vliet, & Oudgenoeg, 2002), and during storage of refrigerated doughs (Courtin, Gys, & Delcour, 2006; Courtin, Gys, Gebruers, & Delcour, 2005; Gys, Courtin, & Delcour, 2003). Hydrolysis of AX by selected xylanases is, therefore, a frequently used strategy in the cereal-based industry to adjust processing, yield, and/or end-product quality.

Most xylanases are produced by bacteria and fungi, but they can also be found in plants, insects, snails, crustaceans, marine algae, and protozoa (Dekker & Richards, 1976). Around 300 xylanases have been identified to date (Brenda, 2008; CAZy, 2008). Based on amino acid sequence and structural similarities, they have been classified into glycoside hydrolase (GH) families 5, 7, 8, 10, 11, 16, 26, 43, 52, and 62 (CAZy, 2008; Collins, Gerday, & Feller, 2005;

* Corresponding author.

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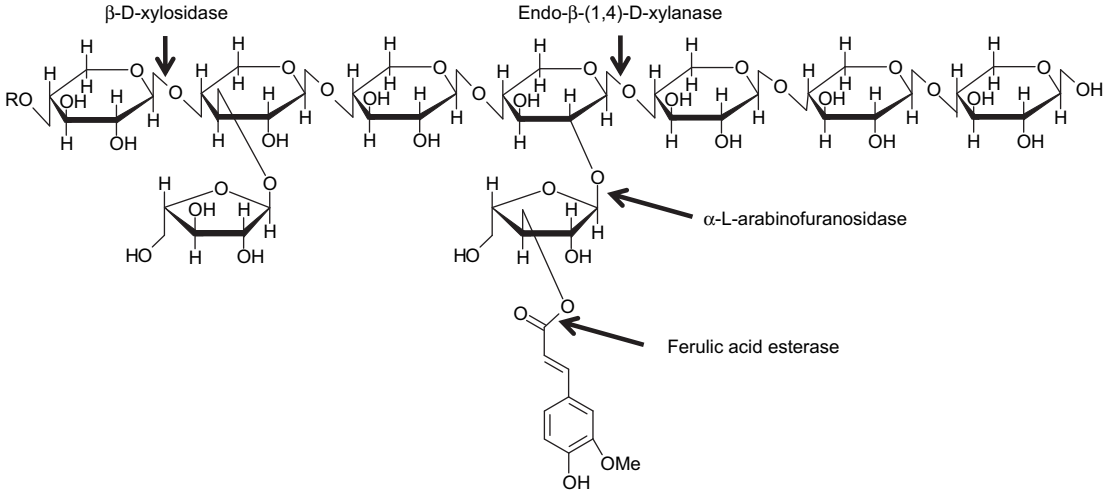

Fig. 1. Structure of arabinoxylan (AX) and the sites of attack by xylanolytic enzymes involved in its degradation. The backbone of AX is composed of β-(1,4)-linked xylose residues, which can be substituted with arabinose residues on the C(O)-2 and/or C(O)-3 position. Ferulic acid can be esterified on the C(O)-5 position of arabinose. Endo-β-(1,4)-D-xylanases (EC 3.2.1.8) cleave the xylan backbone internally, β-D-xylosidases (EC 3.2.1.37) remove xylose monomers from the non-reducing end of xylo-oligosaccharides, α-L-arabinofuranosidases (EC 3.2.1.55) remove arabinose substituents from the xylan backbone, and ferulic acid esterases (EC 3.1.1.73) remove ferulic acid groups from arabinose substituents.

Henrissat, 1991). However, according to Collins *et al.* (2005), only the sequences classified in GH families 5, 7, 8, 10, 11, and 43 contain truly distinct catalytic domains with a demonstrated xylanase activity. All plant xylanases identified so far belong to GH family 10 (Simpson, Fincher, Huang, & Cameron-Mills, 2003), while the large majority of microbial xylanases belong to either GH family 10 or 11.

In general, GH family 10 xylanases have MMs exceeding 30 kDa and a rather complex structure as they are made up of catalytic as well as non-catalytic modules held together by flexible linker regions (Kulkarni, Shendye, & Rao, 1999). The overall structure of the catalytic domain of GH family 10 xylanases is a cylindrical eightfold α/β-barrel resembling a salad bowl (Subramaniyan & Prema, 2002). The catalytic site, which contains a pair of glutamates, is located in an open cleft at the narrower end of the salad bowl, near the carboxyl terminus of the barrel (Jeffries, 1996). GH family 10 xylanases hydrolyse the glycosidic bond through a double displacement mechanism, and retain the anomeric configuration of the glycosidic oxygen (Collins *et al.*, 2005). The non-catalytic modules can be involved in carbohydrate binding or thermostabilisation (Kulkarni *et al.*, 1999).

GH family 11 xylanases generally have low MMs (typically around 20 kDa) and high pI values, although some exhibit low pI values (Torronen & Rouvinen, 1997). They are made up of a single catalytic domain, containing two mostly antiparallel β-sheets and one α-helix, and their structure resembles that of a partially closed right hand (Torronen, Harkki, & Rouvinen, 1994). Similar to what is the case for GH family 10 xylanases, the active site contains a pair of glutamates as catalytic residues, located in an open cleft. Hydrolysis also occurs through a double displacement mechanism with retention of the anomeric configuration (Collins *et al.*, 2005).

Microbial xylanases are routinely used in diverse applications, such as bread making, gluten–starch separation, animal feeds, clarification of juices, liquefaction of fruits and vegetables, *etc.*, to improve processing, yields, and/or end-product quality. Cereal-associated xylanases have been largely disregarded in the past, although it is likely that varying levels of grain-associated xylanase activity contribute to the frequently observed seasonal wheat quality variability.

To date, three different types of proteinaceous xylanase inhibitors have been identified in common wheat, *i.e.* TAXI (*Triticum aestivum* xylanase inhibitor) (Debyser & Delcour, 1998), XIP (xylanase inhibiting protein) (McLauchlan *et al.*, 1999), and TLXI (thaumatin-like xylanase inhibitor) (Fierens *et al.*, 2007). TAXI, XIP, and TLXI contents in wheat are rather high, and differ strongly between wheat varieties. TAXI contents range from 70 to 200 ppm (Bonnin *et al.*, 2005), from 17 to 137 ppm (Dornez, Joye, Gebruers, Lenartz *et al.*, 2006), and from 81 to 190 ppm (Croes, Gebruers, Luyten, Delcour, & Courtin, 2009), while XIP contents range from 210 to 560 ppm (Bonnin *et al.*, 2005), from 234 to 355 ppm (Dornez, Joye, Gebruers, Lenartz *et al.*, 2006), and from 156 to 371 ppm (Croes *et al.*, 2009). TLXI contents range from 51 to 150 ppm (Croes *et al.*, 2009). TAXI-type inhibitors have also been purified from other cereals such as durum wheat (TDXI), rye (SCXI), and barley (HVXI) (Goesaert, Gebruers, Brijs, Courtin, & Delcour, 2003a). XIP-type inhibitors have also been identified in durum wheat (Goesaert, Gebruers, Brijs, Courtin, & Delcour, 2003b), rye (Elliott, McLauchlan, Williamson, & Kroon, 2003; Goesaert *et al.*, 2003b), barley

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