Fiber and nonstarch polysaccharide content and variation in common crops used in broiler diets[1]

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ABSTRACT The current paper reviews content and variation in fiber and nonstarch polysaccharides (NSP) of common crops used in broiler diets. The cereal grain is a complex structure, and its cell walls (CW) differ in their composition and hence properties. Arabinoxylan (AX), mixed linkage (1→3; 1→4)-β-glucan (β-glucan), cellulose, and the noncarbohydrate component lignin are the predominant polymers in cereals. They occur in different proportions depending on the species and tissue type. Rye, triticale, wheat, corn, and sorghum are all rich in AX, whereas barley and oats contain a high level of β-glucan. The AX from rye, wheat, and triticale and β-glucan from barley and oats are to a large extent soluble, whereas the solubility of AX found in corn and sorghum is lower than the other cereals. The ratio of arabinose to xylose gives a crude indication of the AX structure, which varies between the endosperm, the aleurone and the outer grain layers as well as between the same tissues from different grains. Varietal differences in AX structure of the endosperm are also identified. From the analysis of the released oligomers after hydrolysis with a specific (1→3,1→4)-β-D-glucan hydrolase, it is found that the ratio of trisaccharides (degree of polymerization 3) and tetrasaccharides (degree of polymerization 4) varies depending on the source, being higher in barley than in oats but lower than in wheat. The molecular weight of β-glucan is higher than that of AX, and both polymers contribute to the viscosity of the extract. However, because AX molecules are more resistant to degradation than β-glucan, the use of AX rich grains in broiler diets is usually more problematic than those containing high concentrations of β-glucan. The cereal coproducts (brans and hulls) are concentrated sources of cellulose, lignin, and insoluble AX, but β-glucan can also be present mainly in rye and wheat brans. The CW composition of seeds and grains of protein crops and feedstuffs are different from that of cereals. The main CW polymers are pectic substances (homogalacturonan, rhamnogalacturonan type I and II, xylogalacturonan, and arabinogalactans type I and II), xyloglucans, and cellulose, but there are significant differences in the composition of the parenchymatous (cotyledon) tissues and that of the hulls. In the hulls, cellulose is the predominant polysaccharide, followed by acidic xylans and pectic substances. The implications of the heterogeneous CW for the action of exogenous enzymes are discussed.

Key words: fiber, nonstarch polysaccharide, arabinoxylan, β-glucan, broiler

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INTRODUCTION

Broiler diets have traditionally been based on relatively few feedstuffs, in some countries such as the United States and Brazil, the diets are based primarily on corn and soybean meal, which supply the majority of energy and protein in the diet. With this diet regimen, nutrient utilization in corn and soybean meal is usually considered to be high. Worldwide, however, several other cereals such as wheat, barley, triticale, oats, and rye along with their various coproducts have been used as energy contributors (Pettersson and Åman, 1989; McNab and Smithard, 1992; Choct et al., 1999; Steenfeldt, 2001; Svihus and Gullord, 2002). Although soybean meal still is by far the largest protein provider in livestock production (Krautgartner et al., 2012), other protein crops such as peas, lupins, fava beans, rapeseed meal or cake, sunflower, and so on have a protein composition (Jezierny et al., 2010) that can replace soybean meal.

A common feature of cereal grains, cereal coproducts and protein crops other than corn and soybean are their generally higher nonstarch polysaccharides (**NSP**) content and fiber (NSP plus lignin) composition, particularly in soluble form (Theander et al., 1989; Bach Knudsen, 1997). For instance, fiber, soluble

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fiber in particular, have been found to have a detrimental influence on the utilization of nutrients in broilers (Pettersson and Åman, 1989; Choct and Annison, 1990; Mcnab and Smithard, 1992). This is due to the physical presence of fiber in the gastrointestinal tract where the physical barrier of the cell walls (**CW**) can encapsulate potentially available nutrients (i.e., protein in the aleurone cells). In addition, the viscous properties of soluble NSP may interfere with the digestion process and thereby reduce the digestibility of other nutrients (i.e., fat and protein) (Choct and Annison, 1992; Steenfeldt, 2001). Consequently, the fiber components have by far the largest negative impact on the digestibility of nutrients in the broilers and lead to lower AME content as found for some wheat varieties (Annison, 1991; Choct et al., 1999; Steenfeldt, 2001).

The main purpose of the present paper is to review content and variation in fiber and NSP of common crops used in broiler diets. Because cereal grains constitute the largest part of NSP and fiber in the diet for broilers, most emphasis will be devoted to cereal CW polysaccharides. The paper will be based on a literature review and use data that have been generated in-house in the authors' laboratory when analyzing a variety of feedstuffs for the carbohydrate composition.

CHEMISTRY OF NSP AND FIBER

NSP

Nonstarch polysaccharides consist of a series of soluble and insoluble polysaccharides primarily present in primary or secondary plant CW (Selvendran, 1984; Carpita and Gibeaut, 1993; McDougall et al., 1996; Vincken et al., 2003; Figure 1). The building blocks of the CW polysaccharides are the pentoses arabinose and xylose; the hexoses glucose, galactose, and mannose; the 6-deoxyhexoses rhamnose and fucose; and the uronic acids glucuronic and galacturonic (or their 4-O-methyl ethers). Although the CW polysaccharides are built from only 10 common monosaccharides, each monosaccharide can exist in 2-ring (pyranose and furanose) forms, and these residues can be linked through glycosidic bonds at any one of their 3, 4, or 5 available hydroxyl groups and in 2 (α or β) orientations. As a result, CW polysaccharides can adopt a huge number of 3-dimensional shapes and, thereby, offer a vast range of functional surfaces. The NSP can also be linked to lignin and suberin, which provide hydrophobic surfaces. In addition, charged groups on polysaccharides (i.e., the acid group on uronic acids) can affect the ionic properties and be esterified at different degrees.

The most important CW polysaccharide is cellulose that forms a network of cellulose microfibers (Figure 1). Cellulose is present in all CW of both mono- and dicotyledonous plants. For the other CW there is a distinct difference between mono- and dicotyledonous plants, as mixed linkage β-glucan and arabinoxylan (**AX**) are the main CW polysaccharides of cereals, whereas xyloglucans, gluco- and galactomannans, and pectic polysaccharides (arabinogalactans, pectins, and so on) are the main CW polysaccharides of protein-rich seeds and grains. These polysaccharides together with cellulose are present in various proportions in the different types of CW, depending on the function of the CW within the tissues.

Cellulose is composed of linear homopolymers of D-glucopyranosyl residues linked via consecutive β-(1→4) linkages. Because the hydrogen of the –OH group at C-3 is in close proximity to the ring oxygen of the adjacent residue, it hydrogen-bonds between O-3 and O-5, thus helping to stabilize the glucan chains, intermolecularly (Selvendran, 1984). Interchain associations are stabilized by hydrogen bonds between O-6 of a glucose residue in one chain and the oxygen of the glycosidic bond (O-1), between glucose residues, in an adjacent chain. All the cellulose molecules are arranged in an ordered manner within the microfibrils. These microfibrils are a remarkably distinctive feature of the CW of all higher plants in which cellulose is organized in crystalline regions interspersed by noncrystalline amorphous regions. Cellulose is present in all plant tissues; in endosperm, cotyledons, and germ CW, however, it is present at a much lower level than in the outer cell tissues.

Arabinoxylan is formed from a linear backbone of (1→4)-β-D-xylopyranosyl residues (X) mainly substituted with α-L-arabinofuranosyl residues (A) to varying degrees at the O-2 position, the O-3 position or both resulting in 4 structural elements in the molecular structure of AX: monosubstituted X at O-2 or O-3, disubstituted X at O-2,3 and unsubstituted X (Figure 2; Voragen et al., 1992; Izydorczyk and Biliaderis, 1995). The arabinose to xylose ratio is often used to characterize the structure of AX. The relative amount and the sequence of distribution of the structural elements in AX from the different cereals vary depending on the source (Izydorczyk and Biliaderis, 1995). It is agreed, however, that the distribution of arabinose along the xylose backbone is nonrandom; for some cereal AX, i.e., barley endosperm, the structure is more regular than that of wheat and probably other cereals (rye, corn, sorghum, rice; Voragen et al., 1992; Izydorczyk and Biliaderis, 1995). The structure of AX is also different in the endosperm compared with the outer layers; in the outer layers glucuronic acid (or its 4-O methyl ester) and galactose are also present. These AX are described as glucuronoarabinoxylan or heteroxylan (Figure 2; Saulnier et al., 2007b).

β-Glucan is composed of linear homopolymers of D-glucopyranosyl residues linked mostly via 2 to 3 consecutive β-(1→4) linkages that are separated by a single β-(1→3) linkage. Longer segments of consecutively β-(1→4)-linked glucose residues with a degree of polymerization (**DP**) 5 to 28 are less frequent (Figure 3; Izydorczyk and Dexter, 2008; Wood, 2010). From the analysis of the released oligomers after hydrolysis with a specific (1→3, 1→4)-β-D-glucan hydrolase, it

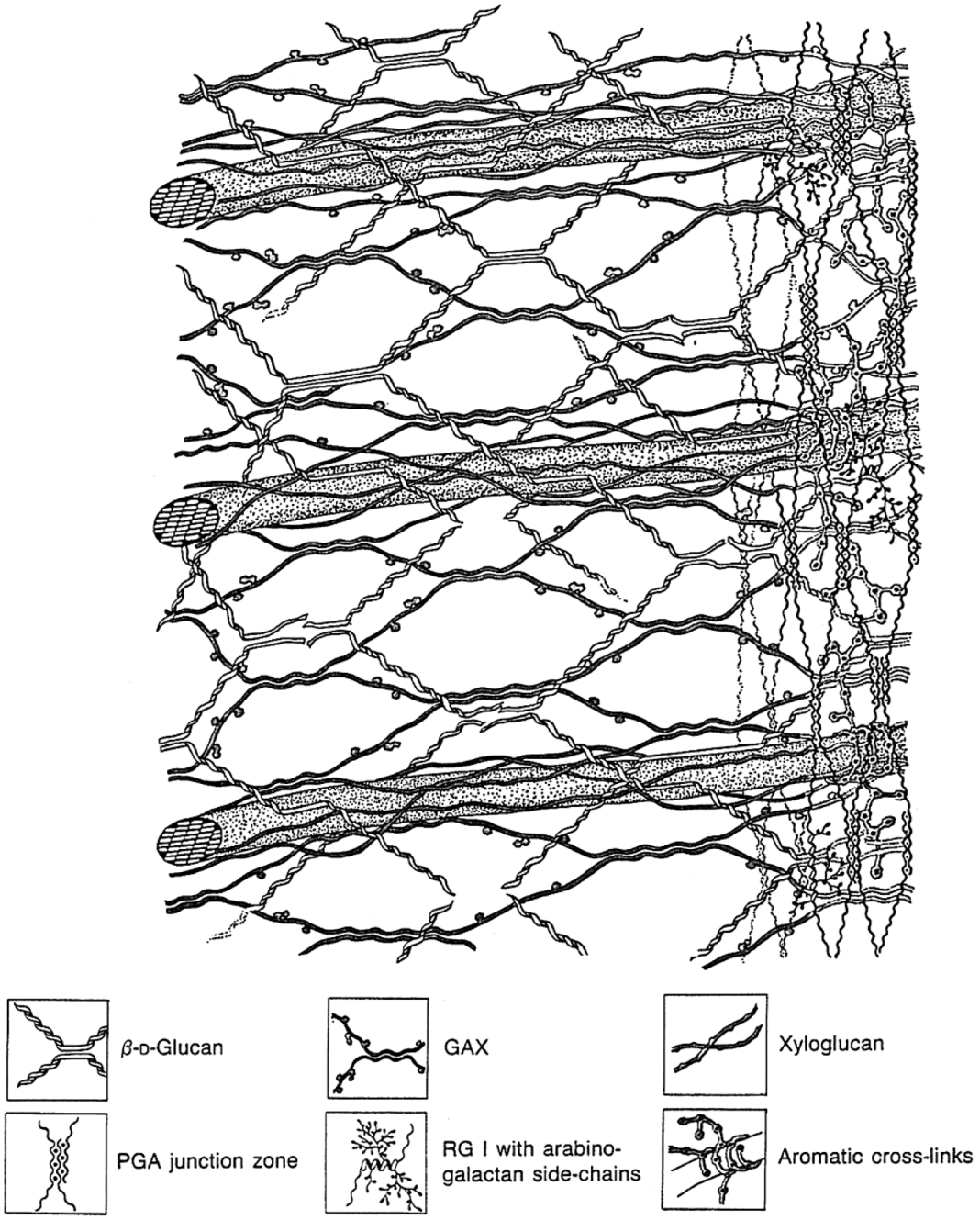

Figure 1. Cell wall model showing cellulose fibrils interlocked by glucurono-arabinoxylans (GAX). Some of the GAX are wired onto the cellulose fibrils by phenolic linkages, whereas the substituted parts of GAX block hydrogen bonding. A small amount of pectic substances (PGA, RG1) are also present. Reprinted from Carpita and Gibeaut (1993; Structural models of primary cell walls in flowering plants: Consistency of molecular structure with the physical properties of the walls during growth. Plant Journal. Volume 3, pages 1–30. Copyright 1993. http://onlinelibrary.wiley.com/doi/10.1111/j.1365-313X.1993.tb00007.x/abstract;jsessionid=0AFAA4F878BC80757CB6AE5A0369DA43.f01t01).

was found that the released trisaccharide units (DP 3) and tetrasaccharide units (DP 4) accounted for 90 to 95% of total oligosaccharides and the longer oligomers (DP $\geq$ 5) accounted for 5 to 10% of the oligosaccharides (Figure 3).

Xyloglucans are the main noncellulosic polysaccharide (**NCP**) structures present in dicotyledons (Caffall and Mohnen, 2009). Xyloglucans consist of a backbone of β-(1→4)-linked D-glucose units, which is heavily branched with xylose and β-galactose residues, attached to some of the xylose units. The xylose units can be further substituted with fucose or arabinose. Xyloglucans can be associated to the cellulose microfibrils.

Pectins represent a heterogeneous group of CW polysaccharides with the main structural elements: homogalacturonan, rhamnogalacturonan type I and II, xylogalacturonan, and arabinogalactans type I and II (Vincken et al., 2003; Caffall and Mohnen, 2009; Figure 4). The main structure of pectin is a polymer of α-(1→4)-linked D-galacturonic acid residues (homogalacturonan) with varying degree of methyl-esterification of the C-6 carboxyl group, acetyl-esterification at the O-2, or

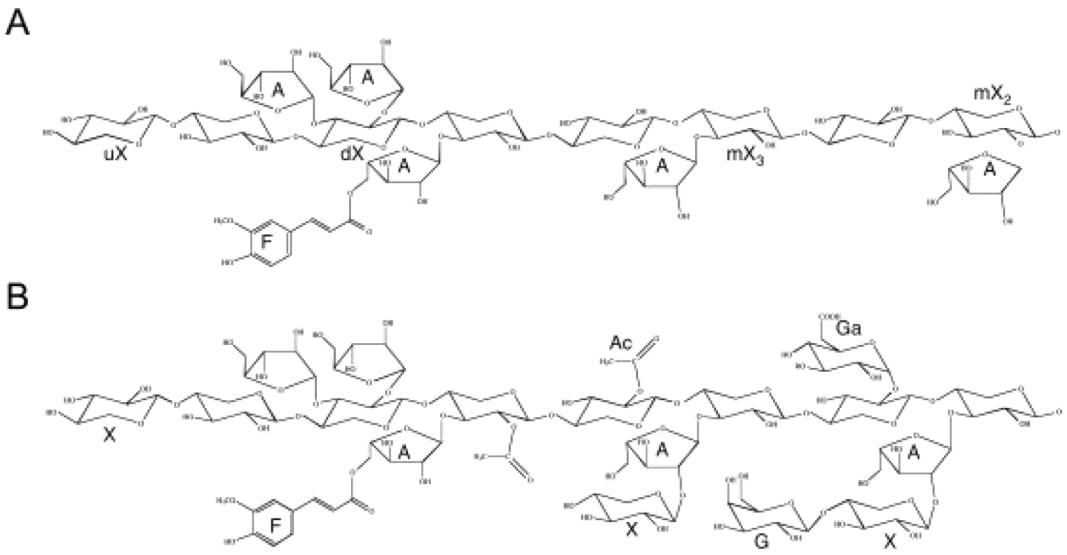

Figure 2. Main structural features of arabinoxylan (AX) from endosperm (A) and outer tissues of cereal grains: A, arabinose; X, xylose; G, galactose; Ga, glucuronic acid; F, ferulic acid; uX, unsubstituted xylose; dX, di-substituted xylose; mX_3, mono-substituted xylose; mX_2, O-2 monosubstituted xylose. Reprinted from Saulnier et al. (2007a with permission from Elsevier).

at O-2 and O-3. The degree of methyl-esterification, the degree of ethyl-esterification and the distribution of the esters over the backbone vary significantly depending on the source. Rhamnogalacturonan I has a backbone of alternating α-(1→2)-linked L-rhamnose and α-(1→4)-linked D-galacturonic residues, with side chains of arabinan, galactan, and arabinogalactans attached to the O-4 position of some of the rhamnose residues. The proportion of branched rhamnose residues varies from 20 to 80% depending of the source, development stage, and plant tissue. Rhamnogalacturonan II is a complex polysaccharide composed of a backbone of α-(1→4)-linked D-galacturonic residues substituted at C-2 or C-3 with aldehydro- and keto-sugar oligosaccharides. Xylogalacturonan consist of a homogalacturonan backbone, which is substituted by one or more β-(1→3)-linked D-xylose residues. Xylogalacturonan is mostly found in reproductive tissue including soybean and with a variable substitution. Arabinans are branched molecules consisting of α-(1→5)-linked L-arabinoxyl residues substituted with one or more α-arabinofuranosyl residues at the O-2 or O-3 position, or at both positions. These arabinosyl side chains may be branched by arabinoxyl residues at the O-2 or O-3 position, or at both positions. Arabinogalactan type I (**AG-I**) and II (**AG-II**) have both a linear backbone of β-(1→4)-linked D-galactosyl residues, which may be lowly branched or branched with short chains of α-(1→5)-linked L-arabinoxyl residues at the O-3 position (AG-I) or highly branched with side chains of β-(1→6)-linked D-galactosyl resi-

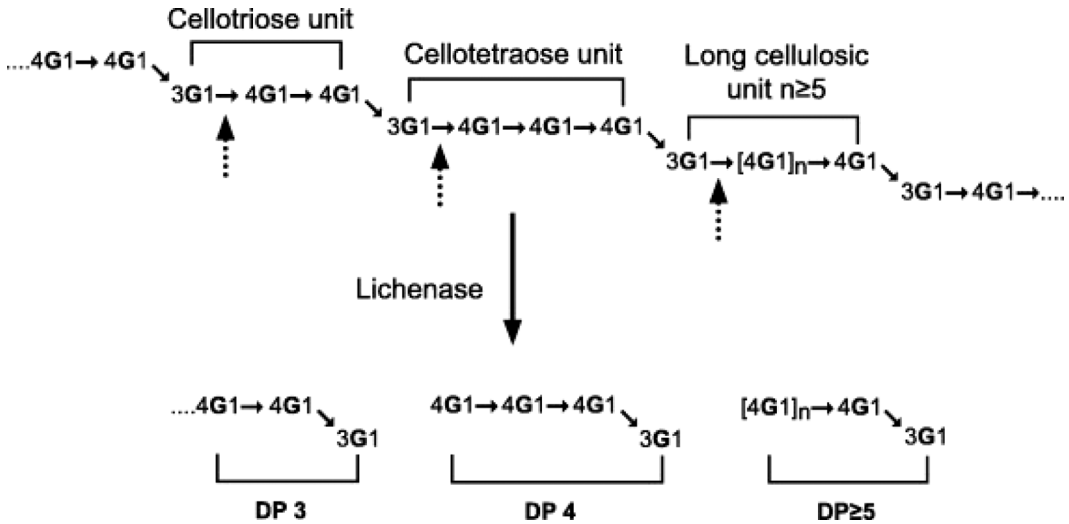

Figure 3. General molecular structure of β-glucan and hydrolysis products obtained upon digestion of β-glucan with lichenase. DP, degree of polymerization. Reprinted from Izydorczyk and Dexter (2008 with permission from Elsevier).

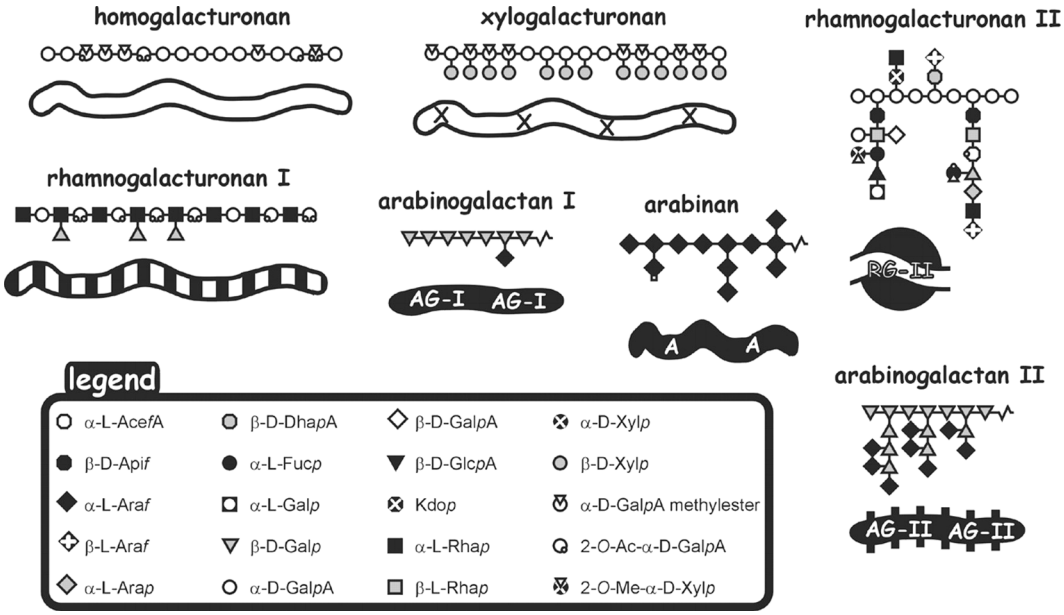

Figure 4. Schematic representative structure of the constituent polysaccharides from pectin. Reprinted from Vincken et al. (2003, http://www.plantphysiol.org/ Copyright American Society of Plant Biologists).

dues with 1 to 3 residues in length. Some β-(1→3)-D-galactan backbone are substituted with single arabinopyranosyl residue, whereas rhamnose and glucuronic acid may also be present in side chains.

Lignin

Lignin is not a carbohydrate, but will be treated as one anyway because it is tightly associated to CW polysaccharides and many of the older and still commonly used analytical methods for fiber determination include lignin. It is, therefore, difficult to discuss the physiochemical properties and degradation of carbohydrates in the gastrointestinal tract without including lignin in the description. Lignin is formed by the polymerization of coniferyl, *p*-coumaryl, and sinapyl alcohols (Davin et al., 2008). These phenylpropane units are linked by an irregular 3-dimensional pattern of ether and carbon-carbon bonds in which one of the carbons may be part of the aromatic ring. Lignin may be covalently linked to polysaccharides both directly through sugar residues and indirectly via ferulic acid esterified to polysaccharides (Iiyama et al., 1994; Davin et al., 2008). Lignin tends to hold the polymers in place and will consequently cement and anchor the cellulose microfibrils and other matrix polysaccharides, and in this way stiffen the walls, making it very rigid and difficult to degrade by the microorganisms in the large intestine.

MEASUREMENTS OF NSP AND FIBER

A broad variety of analytical methods have been used for the analysis of fiber in feeds. The crude fiber method (Henneberg and Stohmann, 1859) is the oldest method and is still used in the proximate analysis of feeds. The detergent methods were developed by Van Soest and coworkers (Van Soest, 1963, 1984; Van Soest and Wine, 1967) and were originally developed for the analysis of fiber rich feedstuffs (roughages) but has later also been applied to concentrated feeds. More recently, the enzymatic-gravimetric AOAC (Association of Official Analytical Chemists) procedures (Prosky et al., 1985) and the enzymatic-chemical Englyst (Englyst et al., 1994) and Uppsala procedures (Theander et al., 1994) for the analysis of fiber (dietary fiber) have been developed. These latter methods were originally developed for foods, but have also been used when analyzing feedstuffs (Theander et al., 1989; Bach Knudsen, 1997).

The principles in the analysis of fiber and NSP using the enzymatic-chemical method described by Bach Knudsen (1997) are illustrated in Figure 5. This methodology uses celluloses resistance to hydrolysis with 2 *M* sulfuric acid, thereby enabling separation of cellulose from NCP. Information concerning polymers making up the NCP fraction can be gained from the monomeric sugar residues (i.e., NCP arabinose and xylose are markers for AX and NCP glucose for mixed linkage β-glucan in cereals, uronic acids for the backbone in pectin, and arabinose, galactose, and other markers of the side groups in pectic polysaccharides).

A comparison of results obtained when analyzing the same feedstuffs by different analytical methods show distinct differences; crude fiber values are much lower than values obtained by the neutral detergent fiber method, and these are somewhat lower than those obtained by the enzymatic-chemical method (Brøkner et al., 2012; Bach Knudsen et al., 2013). The differences in analytical values between the neutral detergent method and the enzymatic-chemical method were dependent on

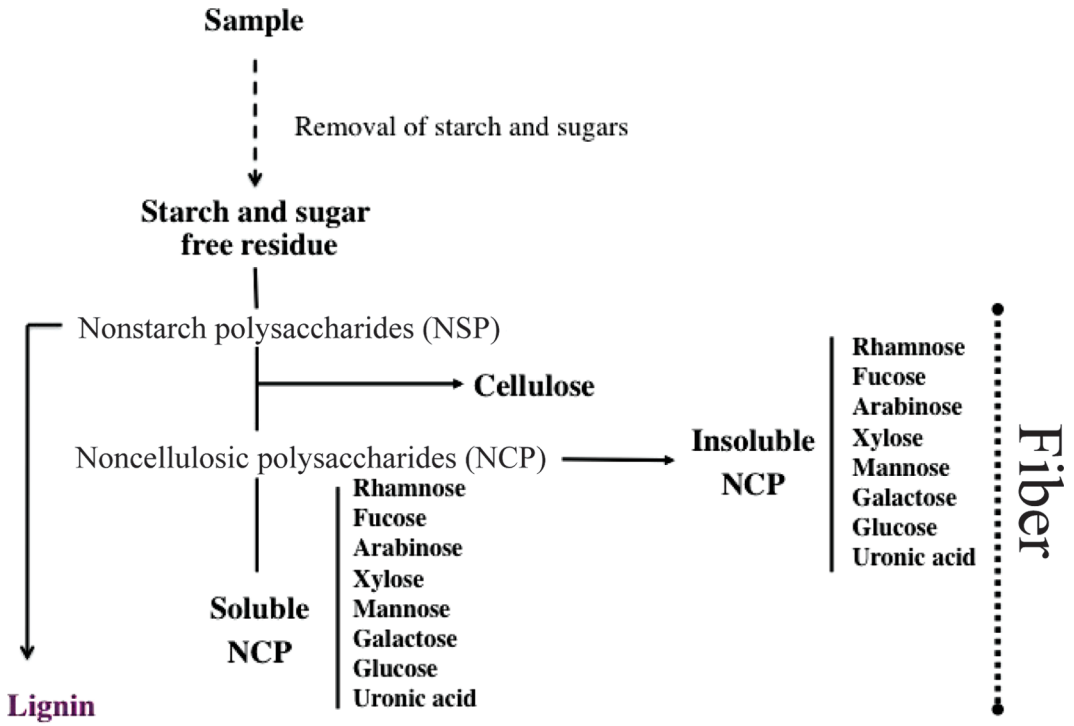

Figure 5. Determination of nonstarch polysaccharides, lignin, and fiber by enzymatic-chemical procedure. Color version available in the online PDF.

the feed matrix; for feedstuffs with low levels of soluble fiber the difference is limited, whereas it may be substantial for pectin-rich feedstuffs as for instance sugar beet pulp.

NSP, LIGNIN, AND FIBER IN CEREALS

General Structure of Cereal Grains

The cereal grain is a complex structure, composed of tissues containing CW with different properties and composition as illustrated for wheat in Figure 6 and the sectional layers of corn, wheat, and barley in Figure 7 (Saulnier et al., 2007b). The CW from the outer part of the kernel primarily play a role in protection, and the CW in these tissues are consequently thick, hydrophobic, and consist of cellulose, xylans, and significant amounts of lignin. In endosperm tissues that include the aleurone layer, the CW are thin and hydrophilic, and primarily made up of 2 polymers: AX and β-glucan. The CW polysaccharides of the aleurone, although part of the endosperm, are largely insoluble

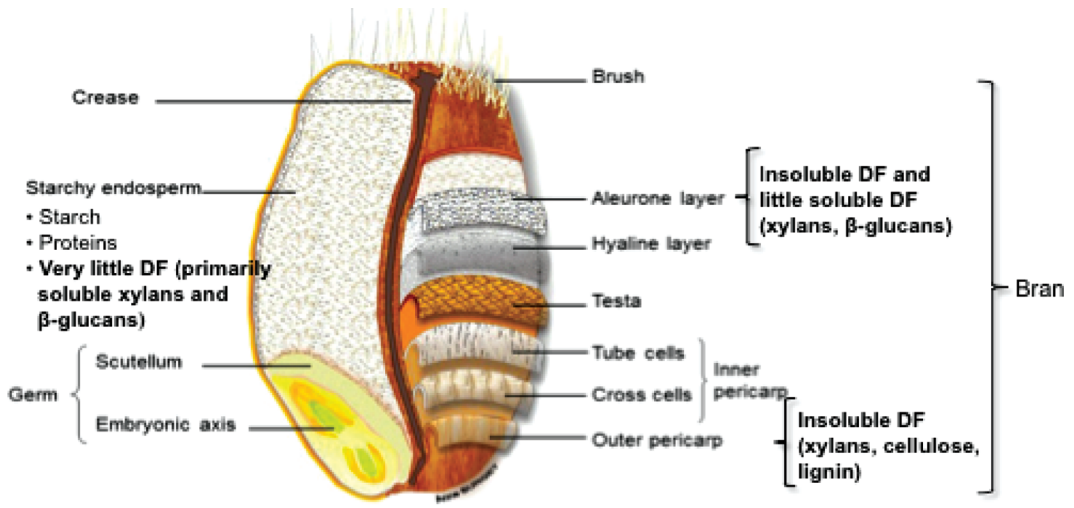

Figure 6. Cross-section of a whole wheat kernel grain with location of specific compounds. DF, dietary fiber. Adapted from Surget and Barron (2005). Color version available in the online PDF.

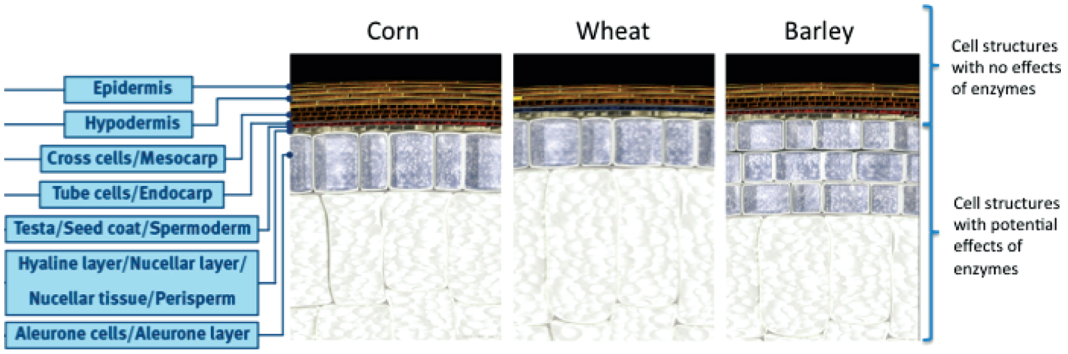

Figure 7. Cross-section of the outer layers and the starchy endosperm of corn, wheat, and barley. Adapted from Kampffmeyer (2009), Food Innovation GmbH, Hamburg, Germany. Color version available in the online PDF.

in contrast to the CW polysaccharides of the remaining endosperm.

The proportion of the main polysaccharides present in the NSP fraction of cereals, AX, cellulose, and β-D-glucan, vary significantly depending on the species, but also on the different tissues of the grains (Saulnier et al., 2007b; Izydorczyk and Dexter, 2008). For example, rye, triticale, wheat, and corn are rich in AX, whereas barley and oats exhibit a high level of β-glucan (Theander et al., 1989; Bach Knudsen, 1997). In addition, low amounts of other polymers such as glucomannan and arabinogalactan peptides are also reported in these walls. Additionally, noncarbohydrate constituents such as phenolic acids (ferulic acid, cumaric acid, caffeic acid, and so on; Sosulski et al., 1982; Bunzel et al., 2001), lignins and proteins are also important constituents of the CW of cereals (Iiyama et al., 1994).

AX and β-Glucan of Cereal Grains

Arabinoxylan is the major polymer in the CW of most cereals (Voragen et al., 1992; Izydorczyk and Biliaderis, 1995; Tables 1 and 2) and with different structural features as indicated by the arabinose/xylose (**A/X**) ratio that can vary in the whole grain from 0.48 in barley to 0.74 in corn and in flour from 0.53 in wheat to 1.06 in corn (Table 1). Even in cereals where the substitution patterns are almost the same (e.g., wheat and rye; Tables 1 and 2), the fine structure can be rather different (Izydorczyk and Biliaderis, 1995). Differences in structural features are the main reason why a much larger proportion of the AX in wheat and rye is soluble compared with AX in barley and oats (Tables 1 and 2). It can be noted that whereas the substitution pattern is higher in the flour of barley and corn than in the whole grain, the opposite is the case for wheat. In wheat the arabinose residues are mainly present as single side-chain units as mono-substitutions on position O-3 (**mXyl$_3$**; 21%) or di-substitutions on positions O-2 and O-3 (**dXyl**; 13%) of the xylosyl residues of the backbone. Mono-substitution on O-2 (**mXyl$_2$**) is rare in wheat. On average 66% of xylosyl residues of the backbone in wheat are unsubstituted (**uXyl**; Saulnier et al., 2007b). Although the structural features of water extractable AX (soluble AX) in wheat are well documented, less information is available for water non-extractable AX (insoluble AX), which represents the major part of the AX in the CW of wheat endosperm (Saulnier et al., 2007b). The structural features of insoluble AX have been studied after alkaline extraction and showed that it was very close to that of soluble AX, but the average molecular weight and A/X ratio were slightly higher for insoluble AX than for soluble AX (Izydorczyk and Biliaderis, 1995). The higher A/X ratio corresponds to a higher proportion of uXYL in insoluble AX compared with soluble AX, whereas the proportion of dXyl was similar in soluble and insoluble AX of wheat.

The aleurone layer is a specific tissue of cereal endosperm, and although structurally closely related to the starchy endosperm (Figures 6 and 7), the AX exhibits specific features (Bacic and Stone, 1981b) that encapsulate potentially available nutrients as seen in studies with pigs (Bach Knudsen and Hansen, 1991; Glitsø et al., 1998; Le Gall et al., 2009). In contrast to endosperm AX, the aleurone AX is not soluble and has a lower A/X ratio in both wheat and barley (wheat, 0.3–0.4; barley, 0.5) compared with the starchy endosperm AX (Bacic and Stone, 1981a; Table 3). The AX in the aleurone layer is also more heavily esterified than the AX of the starchy endosperm, and ferulic acid and dehydrodiferulic acid are present (Rhodes et al., 2002; Antoine et al., 2003). Some *p*-coumaric acid is also present in the aleurone CW (Rhodes et al., 2002).

The molecular weight ($\boldsymbol{M_w}$) of water-soluble AX in wheat is in the range of 200 to 300 kD but with a high polydispersity index ($I = M_w/M_n$) of 1.7 to 2, reflecting a range of polymers exhibiting different masses and structures. For instance, Dervilly et al. (2000) isolated a range of polymers with M_w varying from 70 kD up to 655 kD and A/X ratios from 0.4 to 1.2 (Dervilly et al., 2000; Dervilly-Pinel et al., 2001). However, no simple relationship was observed between M_w and the structure of the polymers. Studies of the molecular weight of insoluble AX from wheat endosperm solubilized by

Table 1. Nonstarch polysaccharides (NSP), lignin, and fiber composition (% of DM) of cereal grains and flour[1]

	Corn				Wheat				Barley			
Item[2]	Grain		Flour		Grain		Flour		Grain		Flour	
NSP												
β-glucan[3]	0.1		0.1		1.0		0.4		4.1		3.2	
Cellulose	2.0		0		1.8		0.3		4.0		1.2	
NCP	7.0	(1.2)[4]	2.1	(0.8)	9.5	(2.8)	3.2	(1.6)	14.6	(5.7)	9.0	(4.1)
Glucose	0.8	(0.2)	0.5	(<0.1)	1.2	(0.4)	0.5	(0.2)	5.0	(3.9)	3.9	(2.9)
AX	4.7	(0.5)	1.0	(0.5)	7.3	(1.8)	2.3	(1.0)	8.4	(1.2)	4.2	(0.7)
Arabinose	2.0	(0.3)	0.5	(0.3)	2.8	(0.8)	0.8	(0.3)	2.7	(0.5)	1.8	(0.3)
Xylose	2.7	(0.2)	0.5	(0.2)	4.5	(1.1)	1.5	(0.7)	5.6	(0.7)	2.4	(0.4)
A/X	0.74	1.30	1.06	1.18	0.62	0.74	0.53	0.42	0.48	0.90	0.75	0.75
Total NSP	9.0		2.1		11.3		3.5		18.6		10.2	
Klason lignin	1.1		0.4		1.8		—		3.2		1.4	
Fiber	10.1		2.6		13.1		3.5		21.8		11.6	
Soluble NSP, %	11.8		31.2		21.7		44.3		26.1		40.2	

[1]Data from Bach Knudsen (1997) and K. E. Bach Knudsen (unpublished data).

[2]NCP, noncellulosic polysaccharides; AX, arabinoxylan; A/X, arabinose/xylose ratio.

[3]Measured by specific method of McCleary and Glennie-Holmes (1985).

[4]Values in parentheses are soluble components.

$BaOH_2$ have shown higher M_w than in soluble AX without any major effect on the polydispersity index (Gruppen et al., 1991).

The highest concentration of β-glucan is found in barley and oats (Tables 1 and 2). The β-glucan from different genera of cereals share the same general molecular structure, but exhibit variation in features such as the ratios of β-(1→4)/ β-(1→3) linkages, presence and amount of long cellulose-like fragments, ratios of cellotriosyl/cellotretrasyl units, and molecular size (Lazaridou et al., 2007). For instance, the molecular ratio of DP3/DP4 varies from 2.3 to 3.4 in barley, which is higher than in oats (1.5–2.3), but lower than in wheat (3–4.5; Lazaridou et al., 2007). Differences in the ratio of DP3/DP4 isolated from different varieties within the different cereals can be attributed to genotypic (normal, waxy, high amylose starches) and environmental factors. The analysis of β-glucan extracted from whole grains gives an average molecular structure of these polymers, but the structure also varies between tissues. Thus, a study with barley (Izydorczyk and Dexter 2008) reported that the β-glucan DP3/DP4 ratio present in the aleurone (3.8–4.1) and pericarp (3.7–4.2) tissues exhibited much higher variation range compared with their counterparts in the endosperm CW (2.7–3.2).

The reported M_w of β-glucan from barley and oats are variable and influenced by the methods and solvents used for the extraction, interactions to hydrolytic enzymes present in the grains before extraction as well as the methods used for the determination (Izydorczyk and Dexter, 2008). In a study with Canadian hull-less barley extracted with water at 45 and 95°C, the M_W ranged from 0.2×10^6 to 2.4×10^6 and from 0.8×10^6 to 5.9×10^6, respectively (Storsley et al., 2003). Other studies have reported M_w at 1.6×10^6 and 1.3×10^6 extracted by hot water (90°C) from several US waxy and nonwaxy barley varieties and 0.6×10^6 to 2.7×10^6 for water-soluble β-glucan from barley (Beer et al., 1997).

Variation in NSP and Fiber Composition of Cereal Grains and Coproducts

The concentration of total NSP in cereal grains varies from 9.0% in corn and up 23.3% in oats and of lignin from 1.1% in corn and up to 6.6% in oats, giving rise to a variation in fiber from 10.1% in corn and up to 29.8% in oats (Tables 1 and 2; Bach Knudsen, 1997). The values reported in Tables 1 and 2 are generally comparable with values reported in other parts of Scandinavia and Australia. Across the cereals, AX is the main NSP component followed by cellulose and β-glucan; the concentration of β-glucan in particular varies from hardly anything in corn (0.1%), to intermediate in wheat, rye, and triticale (0.7–1.7%), to high in barley and oats (2.8–4.1%). From the A/X ratios, it is also apparent that there are big variations in the structural features of AX molecules caused by the type of grains and the relative proportions of the different tissues; i.e., in barley and oats the contribution of the AX from the hulls (mostly nonsubstituted AX) to total AX in the grain is relatively much larger than is the case for bran from wheat and rye. It can also be noted in Tables 1 and 2 that the solubility of NSP in corn is much lower than is the case from the other cereals. The reason for that is most likely the higher cross-linkages of the AX for corn compared with the other cereals as indicated by the much higher total and bound phenolic acid concentration in corn than in wheat, rice, and oats (Sosulski et al., 1982).

In a recently published work based on results from the EU FP6 HEALTHGRAIN program, which included detailed analyses of 150 bread wheat lines and 50 lines of other cereals (durum wheat, spelt, *Triticum monococcum*, *Triticum dicoccum*, rye, oats, and barley) grown on a single site (the HEALTHGRAIN diversity screen) and of a smaller set of 26 wheat and 5 rye lines grown in 6 environments, it was found that the different

Table 2. Nonstarch polysaccharide (NSP), lignin, and fiber composition (% of DM) of cereal grains, brans, and hulls[1]

	Whole grain				Bran			Hull	
Item[2]	Sorghum	Triticale	Rye	Oats	Corn	Wheat	Rye	Barley	Oats
NSP									
β-Glucan[3]	0.1	0.7	1.7	2.8	0.2	2.4	4.5	1.6	1.4
Cellulose	1.4	2.1	1.4	8.2	8.9	7.0	3.9	19.2	19.6
NCP	4.0	(0.5)[4] 10.9	(3.5) 13.3	(4.3) 15.0	(4.0) 28.6	(3.8) 29.2	(3.0) 38.4	(6.2) 28.6	(2.0) 30.8	(1.3)
Glucose	0.8	(0) 1.2	(0.5) 2.5	(0.6) 3.3	(2.8) 1.5	(0.9) 3.4	(0.7) 6.6	(1.3) 2.5	(1.3) 2.0	(0.8)
AX	2.4	(0.2) 8.5	(2.4) 9.5	(3.2) 9.7	(0.5) 20.7	(1.6) 23.2	(1.8) 29.2	(4.5) 23.5	(0.3) 24.0	(0.2)
Arabinose	1.3	(0.1) 3.5	(1.0) 3.6	(1.2) 1.8	(0.3) 7.8	(0.8) 8.5	(0.7) 7.8	(1.2) 5.1	(0.3) 2.8	(0.2)
Xylose	1.1	(<0.1) 5.0	(1.4) 5.9	(2.0) 8.0	(0.2) 12.9	(0.8) 14.7	(1.1) 21.4	(3.3) 18.4	(—) 21.2	(—)
A/X	1.23	2.00 0.71	0.77 0.61	0.63 0.22	0.65 0.61	0.74 0.58	0.78 0.36	0.33 0.28	— 0.13	—
Total NSP	5.4	13.1	14.7	23.2	37.6	36.4	42.2	47.8	50.4	
Klason lignin	2.4	2.0	2.1	6.6	3.0	7.0	6.8	11.5	14.8	
Fiber	7.8	15.1	16.7	29.8	40.5	43.4	49.0	59.4	65.2	
Soluble NSP, %	11.4	22.7	25.6	13.3	9.1	7.3	12.8	3.3		2.0

[1]Data from Bach Knudsen (1997) and K. E. Bach Knudsen (unpublished data).
[2]NCP, noncellulosic polysaccharides; AX, arabinoxylan; A/X, arabinose/xylose ratio.
[3]Measured by the specific method of McCleary and Glennie-Holmes (1985).
[4]Values in parentheses are soluble components.

grains were separated according to their fiber components (Figure 8; Shewry et al., 2013) by using principal component analysis. Principal component analysis is a common statistical tool used for visualizing groupings of samples and for identifying variables. The method involves a mathematical procedure that transforms a number of correlated variables into a small number of uncorrelated variables called principal components. The plots showed that although there was little separation between bread wheat lines, spelt, and durum wheat, the other cereal species, barley, rye, and oats, form separate distinct clusters that do not overlap with each other or with the wheat cluster. From the loading plots it can also be seen that rye lines are directed in the corners with the high level of total AX and soluble AX and barley and oats in the corner with a high level of β-glucan (Shewry et al., 2013).

A French study investigated the variation in the amount of soluble AX and in their fine structure among wheat cultivars (90 lines; Saulnier et al., 2007b). Soluble AX represented from 0.3 to 0.8% of flour (DM basis), and the A/X ratio varied from 0.39 to 0.57 for the population. The average proportions of un-, mono-, and disubstituted xylose was 66.2, 20.8, and 13%, respectively, and with a strong correlation between the A/X ratio and the proportion of dXyl ($r = 0.90$, $P < 0.001$) and uXyl ($r = -0.83$, $P < 0.001$), whereas the correlation was very small with mXyl ($r = -0.34$, $P = 0.001$). Another study with 20 cultivars further showed that although the A/X ratios of soluble AX and xylanase extractable AX were different, there was a strong correlation between the A/X ratios of soluble AX and xylanase extractable AX ($r = 0.78$; Ordaz-Ortiz and Saulnier, 2005). Thus, the variation in the structure of AX observed among wheat varieties for soluble AX was also observed for insoluble AX. From the EU FP6 HEALTHGRAIN germplasm collection, 50 bread wheat varieties were selected based on the content of total and soluble AX (Toole et al., 2011). By the use of FT-IR spectroscopic mapping of thin transverse sections of grain variation in the CW, the AX composition between cultivars was identified. In some varieties, the AX consisted almost entirely of low-substituted AX and in others almost entirely of highly substituted AX, whereas a third group represented a mixture of the 2 forms. In a follow-up study with 6 cultivars, the proportion of mono-, di-, and unsubstituted xylose was investigated in 2 replicates. The results showed that variation in the composition and structure of the endosperm cell wall AX is present between wheat cultivars (Toole et al., 2011). Although environmental conditions will also influence the amount and structure of AX in the cereal endosperm, the variations within cereals and between cereals are mainly genetically determined. This was demonstrated in a study where parental lines exhibiting extreme values (high and low) for viscosity of wheat flour and water extract were crossed and the crosses were grown at 2 locations. In this study a very

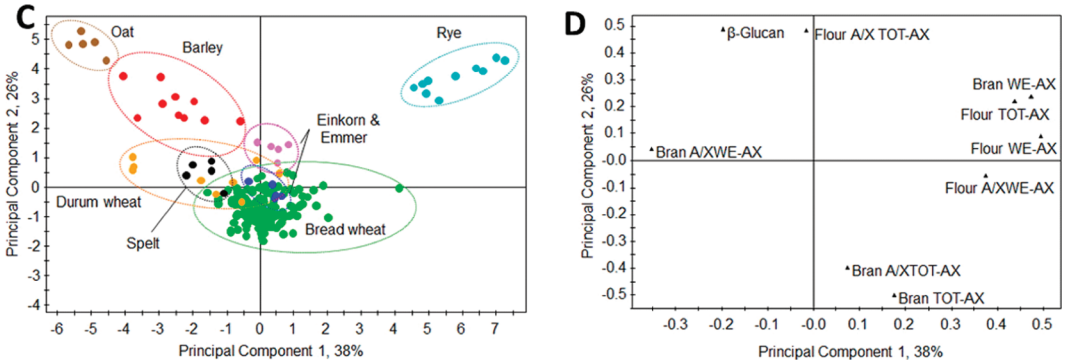

Figure 8. Principal component analysis (PCA) of 200 cereal genotypes colored by cereal class: (C,D) scores and loading plot of PCA model constructed from fiber constituents as model variables. Reprinted from Shewry et al. (2013). Color version available in the online PDF.

strong correlation between the 2 growth locations was found (Saulnier et al., 2007b).

Both AX and β-glucan in solution (soluble NSP) give rise to viscosity. The viscosity of both polymers in solution is directly related to the fundamental molecular structure (molecular conformation, molecular weight, and molecular weight distribution) and the concentration of the polymer. Both polymers exhibit the same behavior that depend on the reduced concentration $c[\eta]$, where c is the concentration and $[\eta]$ is the intrinsic viscosity. The intrinsic viscosity varies between polymers and is influenced by the M_w. Because M_w is higher of β-glucan than of AX, the influence of β-glucan on viscosity will be higher than of AX. However, β-glucan is more sensitive to M_w reduction than is the case for AX as seen when β-glucan is exposed to baking or during passage through the small intestine of pigs (Kasprzak et al., 2012). Therefore, although β-glucan may give rise to a higher viscosity in vitro than AX, the negative impact of AX on the digestibility may be higher than of β-glucan, primarily due to the fact that AX is more resistant to degradation under gut conditions.

Cereal coproducts derived from the cereal processing industry consist of flours that for various reasons cannot be used for human consumption and, most often, brans and hulls that are coproducts from the flour milling industries. Distillers dried grains with soluble (**DDGS**), which is a coproduct from the bioethanol industry, can also find its way into poultry diets. Because these processes typically concentrate either the starchy endosperm or the outer layers of the grain the concentration of NSP, lignin and fiber can be either lower or higher than those of the parent grains. Thus, the concentration of NSP in the flours of corn and wheat is only 2.1 to 3.5% and with no or low levels of lignin, whereas the concentration of NSP in the brans from corn, wheat, and rye is in the range of 36 to 42% and of lignin 3 to 7%, and in hulls from barley and oats in the range of 48 to 50% and 12 to 15%, respectively (Tables 1 and 2). Because the dry milling processes concentrate tissues with specific properties, the proportion of soluble NSP (as % of total NSP) in the flour will be higher and in the bran and hull fractions lower than in whole grains (Tables 1 and 2). For the brans and hulls, the variation in NSP, lignin, and fiber may also be higher than those of the whole grain due to variation in the processing conditions.

NSP, LIGNIN, AND FIBER IN PROTEIN CROPS AND FEEDSTUFFS

General Structure of Seeds and Grains

Seeds and grains of protein crops and feedstuffs have in general a similar structure as in cereals; the outer part of the kernel primarily plays a role in protection and the CW of these tissues are consequently thick, hydrophobic, and contain a high level of cellulose, xylo-

Table 3. Nonstarch polysaccharide residues (% of total neutral sugars) of endosperm and aleurone tissues of wheat and barley[1]

	Wheat		Barley	
Item	Endosperm	Aleurone	Endosperm	Aleurone
Arabinose	34	17	9	23
Xylose	53.5	48	10	44
A/X[2]	0.63	0.35	0.90	0.52
Mannose	7	1	2	2
Galactose	2.5	3	—	2
Glucose	3	31[3]	79[3]	29[3]

[1]Data from Mares and Stone (1973), Fincher (1975), and Bacic and Stone (1981a).

[2]A/X, arabinose/xylose ratio.

[3]The bulk (97–98%) of glucose arises from β-glucan.

Table 4. Nonstarch polysaccharide (NSP), lignin, and fiber composition (% of DM) of legumes[1]

	Soybean			Pea			Lupine (*Lupinus angustifolius*)				Fava bean
				Whole	Cotyledon	Hull	Whole	Cotyledon	Hull		
Item[2]	Meal		Hull								
NSP	5.9		32.2	5.3	1.2	54.0	14.2	0.9	48.1	8.1	
Cellulose	15.1	(6.3)[3]	32.2	12.1 (5.2)	8.3 (4.3)	31.9 (13.7)	31.9 (20.4)	30.0 (20.7)	32.7 (11.5)	10.8	(5.0)
NCP	0.2	(0.1)	0.6 (0.3)	0.1 (<0.1)	0.2 (0.2)	0.6 (0.3)	0.3 (0.1)	0.4 (0.3)	0.3 (0.2)	0.1	(0.1)
Rhamnose	2.6	(0.9)	4.4 (1.3)	3.6 (2.0)	4.0 (2.2)	3.9 (2.2)	4.7 (2.7)	3.8 (2.4)	6.9 (2.9)	2.4	(1.5)
Arabinose	1.7	(0.2)	8.0 (0.3)	1.3 (0.2)	0.4 (0.2)	11.7 (0.9)	3.3 (0.1)	0.7 (0.3)	11.1 (0.8)	1.2	(0.2)
Xylose	1.3	(0.4)	5.0 (2.1)	0.2 (<0.1)	0.3 (0.3)	0.4 (0.1)	1.0 (0.4)	0.5 (0.3)	2.9 (0.8)	0.2	(<0.1)
Mannose	4.2	(1.7)	2.5 (1.3)	0.6 (0.4)	0.8 (0.5)	1.4 (0.9)	17.4 (13.5)	21.4 (15.2)	1.7 (0.7)	0.6	(0.4)
Galactose	0.6	(0.5)	1.0 (0.7)	3.1 (0.5)	0.8 (0.2)	1.9 (1.9)	0.9 (0.3)	1.0 (0.8)	1.0 (0.1)	3.2	(0.4)
Glucose	4.5	(2.4)	10.7 (6.6)	3.0 (1.9)	1.7 (0.7)	11.6 (7.3)	4.2 (3.1)	2.0 (1.2)	8.6 (5.9)	3.2	(2.4)
Uronic acids	21.0		64.5	17.4	9.5	85.9	46.1	30.8	80.9	19.0	
Total NSP	1.8		2.1	1.0	n.m.[4]	n.m.	0.3	0.7	1.7	2.0	
Klason lignin	22.8		66.6	18.4	n.m.	n.m.	46.4	31.6	82.5	21.0	
Fiber		27.6		28.9	51.8	25.6	44.3	67.2	14.0		24.9
Soluble NSP, %			18.9								

[1]Data from Bach Knudsen (1997), Canibe et al. (1997), and K. E. Bach Knudsen (unpublished data).
[2]NCP, noncellulosic polysaccharides.
[3]Values in parentheses are soluble components.
[4]Not measured.

glucans, and acidic pectic substances. Some of the seeds or grains may also contain significant amounts of lignin in their cells. In cotyledon or germ tissues, the CW are thin and hydrophilic and primarily composed of pectic polysaccharides, xyloglucans, and cellulose (Tables 4 and 5). Of the protein sources listed in Tables 4 and 5, soybean meal, rapeseed meal, and sunflower meal are by-products from the production of soybean oil, rapeseed oil, and sunflower oil, whereas peas, lupines, and fava beans are ground seeds and grains. The concentration of fiber (and protein) in the meals of soybean, rapeseed, and sunflower will consequently be higher than in the grains and seeds.

Variation in NSP and Fiber Composition of Seeds and Grains

The concentration of total NSP in protein crops and feedstuffs varies from 17.4% in peas and up to 46.1% in lupines, lignin from 0.3% in lupines, and up to 13.3% in rapeseed meal, giving rise to a variation in fiber from 18.4% in peas and up to 46.4% in lupines (Tables 4 and 5; Bach Knudsen, 1997; Canibe et al., 1997).

The proportions of the main polysaccharides present in the CW of protein-rich crops and feedstuffs varies widely as indicated by the NCP residue composition in Tables 4 and 5. This is partly due to the fact that protein crops and feedstuffs derive from different botanical families: Leguminosae (soybean meal, peas, fava beans, lupines), Cruciferae (rapeseed), Compositiae (sunflower), and so on, but also due to a diverse composition of the individual tissues making up the seed (Siddiqui and Wood, 1977; Cheetham et al., 1993; Huisman et al., 1998; Caffall and Mohnen, 2009; Pustjens et al., 2013). Like in cereals, cellulose is found in all CW materials but with the highest concentration in the hulls (Tables 4 and 5). In the hulls of soybeans, peas, lupines, and sunflowers, there is also a high level of acetic xylans and acetic pectic substances, whereas the same does not seems to be the case with the hulls from rapeseed, where polysaccharides of arabinan and arabinogalactans are more important. Arabinan (in the case of peas and rapeseed; Siddiqui and Wood, 1977; Ralet et al., 1993b; Pustjens et al., 2013), arabinogalactans (in the case of soybeans and rapeseed; Huisman et al., 1998; Pustjens et al., 2013), and galactans (in the case of lupines; Cheetham et al., 1993) are present either free or linked to rhamnogalacturonans. A feature that also seems consistent across the protein-rich feedstuffs are the low solubility of the acetic pectic substances in the hulls. In a study with pea hulls, it was found that the pectic substances present in the highly cellulosic pea-hull were much less solubilized after extrusion-cooking than was the case with pectic substances present in a primary CW (i.e., sugar beet pulp; Ralet et al., 1993a).

Lignin is present in relatively low levels in the CW of the cotyledon and hulls of soybeans, peas, and lupines, whereas the level of lignin is substantially much higher

Table 5. Nonstarch polysaccharide (NSP), lignin, and fiber composition (% of DM) of protein crops and feedstuffs[1]

	Rapeseed								Sunflower					
Item[2]	Meal		Cake		Germ		Hull		Whole		Cotyledon		Hull	
NSP														
Cellulose	5.2		5.9		4.5		10.8		12.4		1.4		24.5	
NCP	16.8	(5.5)[3]	14.6	(4.3)	12.0	(4.3)	24.5	(7.3)	18.9	(5.1)	4.6	(1.6)	31.7	(8.1)
Rhamnose	0.3	(0.1)	0.2	(0.1)	0.3		0.8		0.4	(0.2)	0.1		0.6	
Arabinose	4.3	(1.2)	4.4	(1.3)	4.0		7.1		3.0	(0.8)	1.5		3.4	
Xylose	1.7	(0.4)	1.7	(0.2)	1.9		1.8		6.1	(0.3)	0.5		14.5	
Mannose	0.5	(0.1)	0.5	(0.1)	0.5		0.7		1.3	(0.1)	0.6		1.2	
Galactose	1.8	(0.6)	2.0	(0.5)	1.8		2.7		1.3	(0.5)	0.5		1.1	
Glucose	2.1	(0.9)	0.8	(0.3)	0.8		1.5		0.7	(0.3)	0.3		2.9	
Uronic acids	6.1	(2.2)	5.0	(1.8)	2.2		9.5		6.0	(2.9)	1.1		7.9	
Total NSP	22.0		20.5		16.5		35.3		31.2		6.0		56.2	
Klason lignin	13.3		9.0		1.0		26.2		13.0		0.6		23.9	
Fiber	35.4		29.5		17.4		61.5		44.2		6.6		80.1	
Soluble NSP, %	15.5		14.4		24.7		11.9		11.3		24.2		10.1	

[1]Data from Bach Knudsen (1997), Canibe et al. (1997), and K. E. Bach Knudsen (unpublished data).

[2]NSP, nonstarch polysaccharides; NCP, noncellulosic polysaccharides.

[3]Values in parentheses are soluble components.

in the meal and cake from rapeseed and sunflowers, primarily due to the high lignification of the hulls of these 2 crops. This has a strong impact on the solubility of the NSP, which is generally lower particularly in the hulls of rapeseed and sunflowers compared with the hulls of peas, soybeans, and lupines.

POTENTIAL EFFECTS OF EXOGENOUS ENZYMES ON NSP AND FIBER

As discussed above, the CW materials present in mono- and dicotyledonous plants have a very diverse chemical and structural composition and organization. Although exogenous enzymes are available that potentially can degrade all types of NSP, several factors such as degree of lignification, cross linkages, structural organization, and the time the digesta remains in the foregut limits the effects in practice. For instance, in cereals it is primarily the NSP that are present in the CW of the starchy endosperm and the aleurone layers that can be degraded by exogenous enzymes. Studies with pigs have shown that the outer layers of wheat and rye are almost completely resistant to degradation, even after passing through the large intestine (Bach Knudsen and Hansen, 1991; Glitsø et al., 1999). For protein-rich feedstuffs, the greatest effects of exogenous enzymes are to be expected on the NSP present in the cotyledon and germ, whereas the NSP present in the hull layer represent rigid structures that are difficult to degrade. In addition to these restrictions caused primarily by the physical properties of the CW, the fine structure of the polysaccharides making up the CW will probably also play a role in the efficiency of the exogenous enzymes.

CONCLUSION

The organization of the different CW polysaccharides varies substantially between tissues within and between species. Arabinoxylan and β-glucan of the endosperm and aleurone tissues of cereals and pectic polysaccharides of cotyledon and germ of protein crops and feedstuffs are the NSP with the greatest potential to be degraded by exogenous enzymes.

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