Biochemical Aspects of Non-Starch Polysaccharides

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Abstract

Polysaccharides are macromolecules of monosaccharides linked by glycosidic bonds. Non-starch polysaccharides (NSP) are principally non-α-glucan polysaccharides of the plant cell wall. They are a heterogeneous group of polysaccharides with varying degrees of water solubility, size, and structure. The water insoluble fiber fraction include cellulose, galactomannans, xylans, xyloglucans, and lignin, while the water-soluble fibers are the pectins, arabinogalactans, arabinoxylans, and β-(1,3)(1,4)-D-glucans (β-glucans). Knowledge of the chemical structure of NSP has permitted the development of enzyme technology to overcome their antinutritional effects. The physiological effects of NSP on the digestion and absorption of nutrients in human and monogastric animals have been attributed to their physicochemical properties: hydration properties, viscosity, cation exchange capacity and organic compound absorptive properties. This paper reviews and presents information on NSPs chemistry, physicochemical properties and physiological effects on the nutrient entrapment.

Keywords: non-starch polysaccharides, glucans, arabinoxylans, viscosity

1. Definition and classification of non-starch polysaccharides

Polysaccharides are widespread biopolymers, which quantitatively represent the most important group of nutrients in botanical feed. Carbohydrates constitute a diverse nutrient category ranging from sugars easily digested by the monogastric animals in the small intestine to dietary fibre fermented by microbes in the large intestine [1].

Dietary fibre (DF) is now defined as food material, particularly plant material, that is not hydrolysed by enzymes secreted by the human digestive tract but that may be digested by microflora in the gut.

The types of plant material that are included within the definitions of DF may be divided into two forms, based on their water solubility

- Insoluble dietary fibre (IDF) which includes celluloses, some hemicelluloses and lignin;
- Soluble dietary fibre (SDF) which includes β-glucans, pectins, gums, mucilages and some hemicelluloses.

The IDF and SDF compounds, apart from lignin, are known collectively as non-starch polysaccharides (NSP), which was one of the earlier definitions of DF.

In animal nutrition as "non-starch-polysaccharides (NSP)" are summerized polysaccharides, which cannot be degraded by endogeneous enzymes and therefore reach the colon almost indigested. Individual NSP groups have different chemical and physical characteristics that result in various effects on physiology of intestine and on organism in general.

Many of these physiological definitions have their basis on observations and work by Trowell [2,3], Burkitt and others [4] and Painter [5]. Dietary fibre has been described as the skeletal remains of plant cells in diets which are not digested by human digestive enzymes [6]. These definitions typically include the fiber components: nonstarch polysaccharides (NSP) and resistant oligosaccharides (RO), lignin, substances

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associated with the NSP and lignin complex in plants, and other analogous carbohydrates, such as resistant starch (RS) and dextrins, and synthesized carbohydrate compounds, like polydextrose.

This definition was then expanded to include all polysaccharides and lignin which are not digested by the endogenous enzymes of man [6]. Because of the possibility that under some conditions starch is not completely digested, some scientists redefined dietary fibre as being comprised of non-starch polysaccharides plus resistant starch and lignin [7]. The similarity of the definitions is that the polysaccharides that are not digested by human endogenous enzymes, also known as non-starch polysaccharides or non α-□glucan [8], are the major components of dietary fibre [9]. Schneeman [10] and Graham and Åman [11] on the other hand, based on solubility, separated dietary fibre into two physicochemical groups. First, insoluble dietary fibre, which is mainly composed of cellulose, lignin and some hemicelluloses and second, soluble dietary fibre such as pectins, gums, mucilages and other hemicelluloses. The chemical classification of dietary fibre can be seen in Table 1.

Table 1. Chemical classification of dietary fibre [12]

Fibre	Main chain	Side chain	Description
Polysaccharides			
Cellulose	Glucose	None	Main structural component of plant cell wall. Insoluble in concentrated alkali; soluble in concentrated acid.
Noncellulose			
Hemicellulose	Xylose Mannose Galactose Glucose	Arabinose Galactose Glucuronic acid Glucuronic acid	Cell wall polysaccharides containing backbone of 1-4 linked pyranoside sugars. Vary in degree of branching and uronic acid content. Soluble in dilute alkali.
Pectic substances	Galacturonic acid	Rhamnose Arabinose Xylose Fucose	Components of primary cell wall and middle lamella. Vary in methyl ester content. Generally, water-soluble and gel-forming.
Mucilages	Galactose-mannose Galactose-mannose Arabinose-xylose Galacturonic acid-rhamnose	Galactose	Synthesized by plant secretory cells; prevent desiccation of seed endosperm. Food industry use, hydrophilic, stabilizer (e.g. guar).
Gums	Galactose Glucuronic acid-mannose Galacturonic acid-rhamnose	Xylose Fucose Galactose	Secreted at site of plant injury by specialized secretory cells. Food and pharmaceutical use (e.g. karaya gum).
Algal polysaccharides	Mannose Xylose Glucuronic acid Glucose	Galactose	Derived from algae and seaweed. Vary in uronic acid content and presence of sulfate groups. Food and pharmaceutical use (e.g. carrageenan, agar).
Lignin	Sinapyl alcohol Coniferyl alcohol p-Coumaryl alcohol	3-D structure	Non-carbohydrate cell wall component. Complex cross-linked phenyl propane polymer. Insoluble in 72% sulfuric acid. Resists microbial degradation.

Non-starch polysaccharides are principally non-α-glucan polysaccharides of the plant cell wall. They are a heterogeneous group of polysaccharides with varying degrees of water solubility, size, and structure.

Non-starch polysaccharides, according to Ebihara and Kiriyama [13], and Englyst and Hudson [14], refer to all carbohydrate fractions and types of dietary fibre, with the exception of lignin, either soluble or insoluble. Included are pectic

substances, hemicelluloses, celluloses and gums (guar) and mucilages [15,16].

Cellulose, hemicellulose and pectic substances are known as plant cell wall NSP since they comprised 80-90% of the plant cell wall [16]. Resistant starch, theoretically, falls outside the NSP concept, but practically it depends on the method used to eliminate starch. Southgate divided NSP in plant foods into structural and non-structural polysaccharides. Table 2 illustrates major types of NSP in plant foods.

Table 2. Major types of NSP in plant foods [15]

Primary source	Major groups	Components present	Summary of structures	Distribution in foods
Structural materials of the plant cell wall	Cellulose		Long chain β-glucans	All cell walls
	Non-cellulosic polysaccharides	Pectic substances	Galacturonans	Mainly in fruits and vegetables
		Hemicelluloses	Arabinogalactans Arabinoxylans Glucurono-arabinoxylans Glucuronoxylans Xylo-glucans β-Glucans	 Cereals Cereals Fruits/vegetables Fruits/vegetables Cereals
Non-structural polysaccharides	Gums, mucilages		Wide range of heteropoly-saccharides	Seeds and fruits

The classification of NSP was based originally on the methodology used for extraction and isolation of polysaccharides. Classification by differences in solubility lacks precision with respect to both chemical structures and biological functions. The term crude fibre (CF) refers to the remnants of plant material after extraction with acid and alkali and includes variable portions of the insoluble NSP. Neutral detergent fibre (NDF) refers to the insoluble portion of the NSP plus lignin, and acid detergent fibre (ADF) refers to a portion of insoluble NSP comprised largely, but not exclusively, of cellulose and lignin. The complexity in the structure has made it almost impossible to draw a clear-cut classification of NSP. Bailey [17] classified NSP into three main groups, namely cellulose, non-cellulosic polymers and pectic polysaccharides.

Sasaki et al. [18,19] classified NSPs into water-soluble and water-insoluble fractions which delineate their functions and chemical structure [20,21,22]. The solubility of NSP is determined not only by their primary structure, but also by how they are bound to other cell wall components (protein and lignin). Water-soluble NSP have opposite effects on water binding capacity and viscosity than the insoluble fiber fraction [19].

The water insoluble fraction include cellulose, galactomannans, xylans, xyloglucans, and lignin, while the water-soluble fibers are the pectins, arabinogalactans, arabinoxylans, and β-(1,3)(1,4)-D-glucan (β-glucan) [23].

Water-soluble β-glucans and arabinoxylans are the NSP of major concern when feeding poultry diets with high cereal grain content. β-Glucans are linear polymers of glucose with β-(1,3)(1,4) glycosidic links. Arabinoxylans consist of long backbone chains of β-(1,4) anhydro-D-xylopyranosyl to which are attached single α-L-arabinofuranosyl residues at the 2- or 3-position [24].

NSP in plants

The concentrations and types of these fibrous polysaccharides vary between different parts of the plant. The cell wall polysaccharides of cereals are comprised mainly of arabinoxylans and β-glucan, with smaller quantities of cellulose [24]. The main polysaccharides constituents of wheat endosperm cell walls are arabinoxylans [25,26], whereas arabinoxylans and β-glucans predominate in wheat aleurone layers, and arabinoxylans and cellulose predominate in cell walls of pericarp/testa [27,28,29].

Lineback and Rasper [24] stated that arabinoxylan accounts for approximately 88% of wheat endosperm cell wall polysaccharides, of which one third to one half is soluble in water. Although arabinoxylan remains the principal constituent in

aleurone, testa, and pericarp layers, the arabinoxylans in the testa and pericarp are quite different from endosperm cell walls. In the testa and pericarp they exist as glucoronoarabinoxylans that are linked to other macromolecules, such as lignin or protein or both, and this form of arabinoxylan is water-insoluble. This agrees with the findings of Delcour et al. [30] who showed that the degree of water-soluble NSP decreases from the inner to the outer layer of the wheat kernel.

The NSP content and type can also differ among grains. The NSP content relative to dry matter is lower in wheat kernel (11.4%) than in rye (13.2%) and barley (16.7%). Arabinoxylan is the predominant NSP in wheat (6-8%) and rye (8.9%), while β-glucan is the predominant NSP in barley (7.6%) [31].

Choct and Annison [32] classified different plants based on their total NSP content from low to high as follows: rice, sorghum, maize, wheat, triticale, rye and barley. Although such a classification goes some way in defining the effect of NSP on diet digestibility, it is necessary to further differentiate the types of NSP. The ratio arabinoxylan : ß-glucan is higher in rye and wheat than in barley or oats. Furthermore, while the proportion of soluble arabinoxylans in the total arabinoxylan content may be very low (less than 10%), the soluble ß-glucan to total ß-glucan ratio is high in barley and oats (54 and 80% respectively) [33].

The NSP content of plants varies not only in accordance to the plant species but also varies between genotype or cultivar of the same species. Furthermore the agronomic cultivation conditions, such as environmental factors prior to harvest and storage conditions after harvest, can influence NSP content.

NSP chemistry

These polysaccharides are typically long polymeric carbohydrate chains containing up to several hundred thousand monomeric units. The polysaccharides differ by the number and type of monomeric units linked together, the order in the chain, the types of linkages between the various monomers, the presence of branch points in the backbone of the molecule, and those having acidic groups present (for example, uronic acids in pectins).

According to Choct [34], polysaccharides are polymers of monosaccharides joined through glycosidic linkages and are defined and classified in terms of the following structural considerations: (a) identity of the monosaccharides present; (b) monosaccharide ring forms (6-membered pyranose or 5-membered furanose); (c) positions of the glycosidic linkages; (d) configurations (α or β) of the glycosidic linkages; (e) sequence of monosaccharide residues in the chain, and (f) presence or absence of non-carbohydrate substituents. Monosaccharides commonly present in cereal cell walls are: (a) *hexoses*: D-glucose, Dgalactose, D-mannose; (b) *pentoses*: L-arabinose, D-xylose, and (c) *acidic sugars*: D-galacturonic acid, D-glucuronic acid and its 4-O-methyl ether.

The NSP may be relatively simple, such as the cereal ß-D-glucans which are linear polymers of glucose with ß-(1-3),(1-4) glycosidic links (Figure 1). The other major cereal polysaccharides, the arabinoxylans, are more complex being composed of two sugars, arabinose and xylose, in a branched structure. Even more complex polysaccharides may be present if legumes are used in the ration. The main NSP of lupins is a highly complex branched-chain structure containing long ß-(l-4)-D-galactose sidechains attached to a pectin-like mainchain of rhamnose and galacturonic acid linked by ß-(1-4) and α-(l-2) bonds respectively. There are also side chains α-(l-5)-L-arabinose.

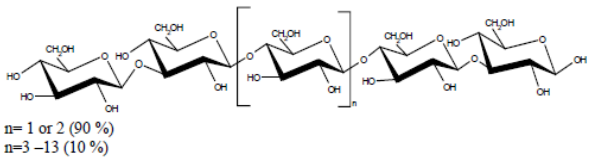

Figure 1. Structure of β-.glucan

Physicochemical properties of water-soluble NSP

The structure of plant cell wall influences the physical and chemical properties of the individual NSP and these vary considerably between different polymers and different molecular weights of the same polymer [34].

Another factor that differentiates the physical properties among polysaccharides is the way the monomer units of polysaccharides are linked together [35]. Different sugars often give polysaccharides with very similar physical properties if they are linked together in the same way.

On the other hand, despite being built up from the same monomer units, polysaccharides can have different physical properties when the monomer units are linked together in different way.
The physiological effects of NSP on the digestion and absorption of nutrients in human and monogastric animals have been attributed to its physicochemical properties. The main physicochemical properties of NSP that are of nutritional significance include: (a) hydration properties; (b) viscosity; (c) cation exchange capacity; (d) organic compound absorptive properties [36].
The hydration properties of NSP influence its water holding capacity and water binding capacity [36]. These depend on the physicochemical structure of the molecule and its ability to incorporate water within the molecular matrix.
The viscosity properties of the NSP depend on its molecular weight or molecule size (linear or branched), its ionically charged groups, the surrounding structures and the concentration of NSP [31].
The cation exchange capacity is formed because the three-dimensional structure of the NSP molecule allows a chelation of ions to occur.
The organic compound absorptive properties of NSP are due to the capacity of the NSP to bind small molecules by both hydrophobic and hydrophilic bond interactions.

Antinutritive effects of the NSP

Two models have been proposed for the anti-nutritive role of soluble NSP in broiler diets, either that of encapsulation in which the NSP coat inhibits the access of digestive enzymes to the starch, fat and protein and/or the fact that the presence of NSP in the intestinal lumen increases the viscosity of the intestinal contents. As yet the exact anti-nutritive role of NSPs has not been fully identified but it is probable that it involves both these mechanisms.
Early work identified the soluble β-glucans and arabinoxylans as being the fractions most responsible for impeding digestion by causing a viscous intestinal environment [37,38,39,40,41]. This high gut viscosity is associated with the incapability of the animals to digest cellulose, arabinoxylans, or β-glucans [42,43]. The rate of digestion of a feed and the absorption of the products of digestion relies on the formation of a complex between the digestive enzyme and its substrate and subsequent release of its product, and the diffusion of the product to the enterocytes for absorption to occur [42]. Unimpeded movement of enzymes, substrates and products by diffusion through the gut is essential for digestion. As the viscosity of the digesta increases by the NSP, the diffusion decreases. Moreover, the NSP gel may act as a physical barrier between substrates, enzymes and digestion end-products [44], thus limiting the mix of nutrients with pancreatic enzymes and bile acids [45]. NSP complex may reduce the brush border diffusion of nutrients, limiting their exposure to the brush border enzymes and absorption by the enterocytes [45]. Dietary NSP may also increase the thickness of the unstirred water layer of the mucosa *via* their interaction with the mucopolysaccharides [46,47], and NSP may bind the brush border digestive enzymes [48], that limit fats, proteins and carbohydrates digestion and absorption. Therefore, NSP may reduce the digestion and absorption of nutrients by its physicochemical effect in the intestinal tract.

NSP determination

The oldest and most commonly used method for analysis of fiber in feedstuff is the crude fiber method [49]. This method measures only a fraction of the fiber components because it can solubilize some of the structural polysaccharides and lignin. The detergent method [50,51] provides a more descriptive measurement of the fiber that is insoluble in neutral detergent (NDF: neutral detergent fiber), and in acid detergent (ADF: acid detergent fiber). The NDF measures hemicellulose, cellulose and lignin, while ADF measures cellulose and lignin allowing calculation of hemicellulose by difference. This calculation does not give the exact measurement of NSP because water-soluble and water-insoluble NSP may be lost in the NDF procedure, starch and protein may contaminate the NDF residue, and hemicellulose may be left in the ADF fraction [36]. More precise procedures of NSP analysis including enzymatic-chemical method, or Englyst method, [52,14] and the non-enzymatic gravimetric method of Prosky [53], have shown to be the main approaches for the NSP measurement [54,55,36]. The enzymatic-chemical method has been shown to be easier and quicker to perform than the non-enzymatic gravimetric method of Prosky [55]. Knudsen [36] described that the

enzymatic-chemical method yields information on the monomeric composition of the NSP divided into soluble and insoluble fractions. This method gives a general view of the functional properties of the fiber, in particular when working with identifiable cell wall material.

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